



Review

# The Sugar-Signaling Hub: Overview of Regulators and Interaction with the Hormonal and Metabolic Network

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**Abstract:** Plant growth and development has to be continuously adjusted to the available resources. Their optimization requires the integration of signals conveying the plant metabolic status, its hormonal balance, and its developmental stage. Many investigations have recently been conducted to provide insights into sugar signaling and its interplay with hormones and nitrogen in the fine-tuning of plant growth, development, and survival. The present review emphasizes the diversity of sugar signaling integrators, the main molecular and biochemical mechanisms related to the sugar-signaling dependent regulations, and to the regulatory hubs acting in the interplay of the sugar-hormone and sugar-nitrogen networks. It also contributes to compiling evidence likely to fill a few knowledge gaps, and raises new questions for the future.

**Keywords:** sugar; pathway; sensing; crosstalk; regulation; hormone; nitrogen

## 1. Introduction

Plant growth and development are regulated by many factors including light, temperature, water, sugars, and plant hormones. As plants are autotrophic organisms, they produce their carbon skeletons through photosynthesis in the form of sugars that serve as structural components and energy sources throughout their life [1]. Sugars are also signaling entities; therefore, perception and management of sugar levels by plants are critical for their survival. Plants have evolved a complex mechanistic system to sense different sugars, including sucrose, hexoses, and trehalose. These sugars elicit adequate responses, some of which are specific to the type of sugar [2–6]. Sugar signaling is also a mechanism that plants use to integrate various internal and external cues to achieve nutrient homeostasis, mediate developmental programs, and orchestrate stress responses [6]. In addition, the carbon and nitrogen metabolisms are closely connected with each other at almost all stages of plant growth and development. The coordination and the integration of the C and N metabolic and signaling pathways appear crucial for the improvement of plant performances [7,8]. Besides nutrients, plant hormones play a determining role in plant development and are key transmitters of developmental programs [9]. In addition, the interaction between sugars and plant hormones

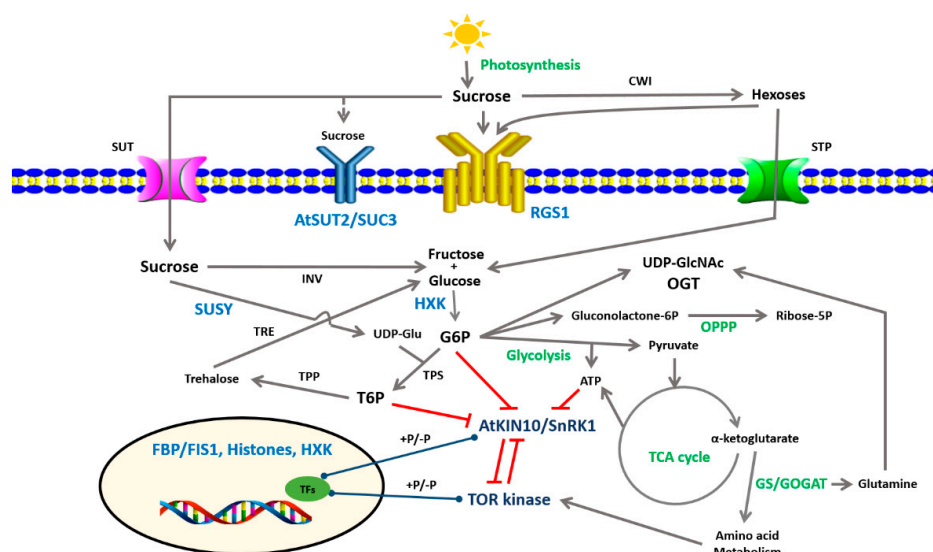
is orchestrated to finely regulate the main biological processes throughout the plant life cycle. In this context, and with a view to understanding the mechanisms involved in the sugar and plant hormone networks, it is important to decipher their crosstalk with sugars during plant development. The present review emphasizes the emerging understanding of the main sugar signaling pathways in plants and the array of molecular and biochemical mechanisms that mediate the effects of the sugar signal. To provide a comprehensive idea about the relevance of the sugar-signaling-dependent regulation of plant functioning, this review also addresses the interplay between sugar, nitrogen, and the main plant hormones, while focusing on certain biological contexts. This work also underlines a few emerging linker molecular actors that deserve to be further investigated.

## 2. Sugar Signaling Pathways

### 2.1. Disaccharide Signaling Pathways

Sucrose is the main sugar for systemic source-to-sink transport in plants. The dual role of sucrose, i.e., as an energy source and a signaling entity, was evidenced by many experiments showing that non-metabolizable sucrose analogs could mimic the effect of sucrose while its derivative hexoses (glucose and fructose) have very low efficiency [10–13]. The best-known example is the sucrose-specific down-regulation of *BvSUT1* (*Beta vulgaris* Sucrose Transporter 1), encoding the phloem-located proton-sucrose symporter, which is neither elicited by hexoses nor affected by mannoheptulose, a hexokinase inhibitor [10]. By doing so, sucrose signaling regulates the expression of its own transporter at the site of phloem loading and thereby may control photo-assimilated partitioning between source and sink. Sucrose signaling controls not only plant metabolism but also plant development [6,14–18]. However, the mechanism of sucrose perception remains unknown. Barker et al. (2000) proposed the plasma membrane sucrose transporter AtSUT2/SUC3 as a putative sucrose sensor (Figure 1) [19]. AtSUT2/SUC3 shares structural features with the yeast glucose sensors Snf3 and Rgt2. The tonoplast low-affinity sucrose transporter SUT4 that interacts with five cytochrome b5 family members may also mediate sugar signaling [20]. Downstream of sucrose sensing, calcium, calcium dependent-protein kinases (CDPKs), and protein phosphatases could transmit sucrose signals [21,22]. All these findings show clearly that the questions of sucrose sensors and the sucrose signaling pathway are still open, and future research could investigate whether other actors such as sucrose synthase (a sucrose-degrading enzyme) [23] or BZR1-BAM (a transcription factor containing a non-catalytic-amylase (BAM)-like domain [24]) might be part of this mechanism.

Like sucrose, trehalose 6P (T6P) is a non-reducing disaccharide, synthesized from UDP-glucose (UDPG) and glucose 6-phosphate (Glc6P) by trehalose 6P synthase (TPS), and then dephosphorylated into trehalose by trehalose 6P phosphatase (TPP, Figure 1) [25]. *Arabidopsis thaliana* has 11 TPS and 10 TPP genes [26], and large TPS and TPP gene families are present in other flowering plants [27–29]. The T6P pathway has emerged as an important regulatory mechanism in plants that affects cell metabolism, plant growth, and abiotic stress responses [30–33]. More interestingly, T6P levels appear to follow sucrose levels, which makes it an essential signal metabolite in plants, linking growth and development to carbon availability [34]. These findings led to the proposal of the Suc-T6P nexus model, assuming that T6P is both a signal and a negative feedback regulator of sucrose levels [31,32,35]. This tight relationship between T6P and sucrose contributes to maintaining sucrose levels within an optimal range depending on cell type, developmental stages, and environmental cues [31,32,35].



**Figure 1.** Schematic representation of the sugar metabolism (green) and signaling (blue) pathways. Sugar sensing involves for example glucose sensors (HXK: Hexokinase, OGT: O-Glucose *N*-acetyl transferase); fructose sensors (i.e., FBP/FIS1, fructose-1,6-bisphosphatase), sucrose and hexose sensors (RGS1, regulator of G-protein signaling), and putative sucrose sensors (SUSY, SUcrose SYnthase, putative sucrose transporter AtSUT2/SUC3). Downstream of sugar perception are two energy sensors: AtKIN10/SnRK1 (sucrose-non-fermentation-related protein kinase1) and TOR-kinase (target of rapamycin kinase). CWI: cell wall invertase; G6P: glucose 6-phosphate; GS/GOGAT: glutamine synthetase/glutamate oxoglutarate aminotransferase; INV, invertase; OPPP: oxidative pentose phosphate pathway; STP: Sugar transport protein; SUT: sucrose transporter; TCA cycle: Tricarboxylic acid cycle; TFs: transcription factors; TPS: T6P synthase; TPP: trehalose 6P phosphatase; T6P, trehalose 6-phosphate; UDPGlc: Uridine diphosphate glucose; UDPGlc-NAC: UDP *N*-acetylglucosamine.

## 2.2. Hexose-Dependent Pathways

Plant cells possess intracellular and extracellular sugar sensors. In many plants, the regulator of G-protein signaling 1 (RGS1), a seven-transmembrane-domain protein located on the plasma membrane, plays a critical role as an external sugar sensor (Figure 1) [36]. It could function as a plasma membrane sensor or partner responding to changes in glucose, fructose, and sucrose levels [37]. RGS1 proteins deactivate G-protein and sugars accelerates GTP hydrolysis by  $G\alpha$  subunits, and leads to RGS1 phosphorylation by WINK [with no lysine8 (K)] kinase. As a result, RGS1 is internalized by endocytosis, associated with sustained activation of G-protein-mediated sugar signaling [38]. High concentrations of D-glucose rapidly induce RGS endocytosis through AtWNK8 and AtWNK10, whereas low sustained sugar concentrations slowly activate the AtWNK1 pathway [39], allowing the cells to respond adequately to high and low intensities of sugar signals.

The first intracellular glucose sensor demonstrated in plants was AtHXX1, an *Arabidopsis thaliana* mitochondrion-associated (type B) hexokinase [40–43]. AtHXX1 is involved in the regulation of many processes [6,44], and its function as a glucose sensor was confirmed by the characterization of the *Arabidopsis gin2* (glucose insensitive 2) mutant [42]. When the metabolic activity of AtHXX1 was uncoupled from its signaling activity, its glucose-sensing function was found to be independent of its catalytic activity [42]. Moreover, AtHXX1 has a nuclear signaling function [43], where it interacts with two unconventional partners, the vacuolar  $H^+$ -ATPase B1 (VHA-B1) and the 19S regulatory particle of the proteasome subunit (RPT5B) to form a hetero-multimeric complex for the recruitment of hypothetical transcription factors. Such a multimeric complex may bind to the promoters of glucose-inducible genes to modulate their expression. The sensing role of AtHXX1 appears to

have been evolutionarily conserved and to be shared by HXK in many other species including potato (StHXK1 and 2) and rice (OsHXK5 and 6) [45,46]. In addition, Hexokinase-Like1 (HKL1, a mitochondrion-associated non-catalytic homolog of *AtHXK1*) [47,48] and *AtHXK3* (a plastidial hexokinase) [49] may also be part of hexose signaling. Irrespective of its well-known sensor function, recent studies have revealed new physiological functions of glucose phosphorylation by *AtHXK* [50,51].

We currently have no evidence of the role of fructokinase (FRK), which catalyzes the irreversible phosphorylation of fructose, in the fructose-sensing process [44]. However, combining cell-based functional screen and genetic mutations, Cho and Yoo (2011) identified the nuclear-localized fructose 1-6-bisphosphatase (FBP/FIS1, Fructose-Insensitive 1) as a putative fructose sensor uncoupled from its catalytic activity [52]. Meanwhile, Li et al. (2011) characterized the ANAC089 transcription factor as a fructose-sensitivity repressor in *Arabidopsis* [53]. Other researchers isolated two FRK-like proteins (FLN1 and FLN2) that are components of the thylakoid-bound PEP (plastid-encoded polymerase) complex in *Arabidopsis thaliana*, regulate plastidial gene expression, and are essential for plant growth and development [54]. It will be interesting to determine whether there is a connection between these different fructose sensors and how these two hexose pathways could interact.

### 2.3. Energy and Metabolite Sensors

#### 2.3.1. SnRK 1: Sucrose Non-Fermenting Related Protein Kinase 1

*AtKIN10/AtKIN11/SnRK1* is a serine/threonine kinase that shares high sequence identity with yeast SnF1 and mammal AMPK (5' AMP-activated Protein Kinase), and is considered as the energy-signaling hub controlling many regulatory proteins [55,56]. The evolutionary conservation of this protein function is demonstrated by its heterotrimeric structure, with one catalytic  $\alpha$ -subunit and two regulatory  $\beta$  and  $\gamma$  subunits [57], as well as the functional complementation of the yeast *snf1* mutant with the rye orthologue [58]. In plants, SnRK1 plays a crucial role in the reprogramming of metabolism, the adjustment of growth and development, and plant responses to different biotic and abiotic stresses [55]. SnRK1 controls the expression of more than one thousand genes coding for transcription factors and proteins involved in chromatin remodeling, and also acts through post-translational regulation of several key metabolic enzymes and certain transcription factors [59–63]. There exists a positive correlation between the expression profile of genes regulated by *AtKIN10* and the profile of genes regulated by sugar starvation [61]. These authors reported that the regulation of SnRK1 activity and signaling required the phosphorylation of a highly conserved threonine residue close to the active site in the catalytic  $\alpha$ -subunit. The dephosphorylation of SnRK1 $\alpha$  by PP2C phosphatases may reverse the activation loop and provide mechanisms for the integration of environmental cues [64]. The complex interplay of SnRK1 and SnRK2/ABA with the clade of PP2C phosphatases has been demonstrated in the ABA signaling pathway, where both types of protein kinases encompass common downstream targets such as different bZIP transcription factors [63]. In addition, the involvement of micro RNAs in SnRK1-mediated signal transduction appears plausible [65]. It is noteworthy that at least part of the gene responses related to the SnRK1 pathway might be independent of HXK1 signaling.

#### 2.3.2. TOR Kinase: A Target of Rapamycin Kinase

TOR-kinase is evolutionarily conserved in all eukaryotic organisms, and plays a central role in the integration of endogenous (energy and nutrient status) and exogenous (environmental factors) signals to modulate growth and development. In plants, TOR-kinase has been identified only as the TORC1 complex, whose organization is similar in animals and yeast. The complex encompasses the TOR partners RAPTOR (kontroller of growth protein 1 (KOG1)/regulatory-associated protein of mTOR) and LST8 (small lethal with SEC13 protein 8) [66]. The crucial function of TOR-kinase lies in the positive regulation of metabolism and growth through the synthesis of proteins [16]. TOR-kinase activity seems to control nitrogen and carbon assimilation, and has a fundamental role in embryogenesis, meristem activity, leaf and root growth, senescence, and life span through the inhibition of autophagy [67–70].

As a result of TOR activation, growth is resumed, and reserve compounds, starch, lipids, and proteins are stored [71].

Sugars generally induce the activity of TOR kinase [16,69,72,73]. The glucose-enhanced activity of AtTOR was evidenced by the stimulation of root meristem activity [74]. Inversely, specific inhibitors of AtTOR reduced root growth. TOR activates glycolysis to enhance carbon skeleton production, which is further needed for amino acid and protein synthesis. AtTOR interaction with the RAPTOR protein is involved in the regulation of the ribosomal protein kinase S6K1, which represses the cell cycle by phosphorylating the Retino-Blastoma-Related (RBR) protein under unfavorable conditions [75]. Furthermore, it has been suggested that RBR is involved in the transition from heterotrophic to autotrophic plant development, which requires the expression-inhibition of cell cycle genes, and the persistent inactivation of late embryonic genes through the modification of the epigenetic landscape, namely the trimethylation of lysine 27 of histone H3 (H3K27met3) [76].

Both the SnRK1 and TOR-kinase regulators act antagonistically. Energy and nutrient (C and N) scarcity activates SnRK1 to promote energy-saving and nutrient remobilization processes, while TOR is active under favorable conditions, when nutrients are available to enhance growth, development, and the anabolic metabolism. Such a crosstalk between TOR-kinase and SnRK1 is central for plants to adapt protein synthesis and metabolism to the available resources [77–79]. TOR and SnRK1 act downstream of sugar sensing and their activities are modulated by the sugar status of plants (Figure 1) [16]. T6P potentially inhibits AtSnRK1, supporting the model that T6P reflects cell sugar availability and promotes growth by repressing SnRK1 activity in sink tissues [31,32,35,80–83].

### 2.3.3. The OPPP: The Oxidative Pentose Phosphate Pathway

Specific investigations of sugar sensing, downstream of HXK, highlighted the occurrence of the OPPP in plants (Figure 1). This pathway seems to govern nitrogen and sulfur acquisition in response to the carbon status of the plant [84]. This integration would be critical for the coordination of amino-acid biosynthesis with the availability of these three important components.

### 2.4. Sugar Signaling in the Regulation of Sugar Transporters

*AtSTP1* (*Arabidopsis thaliana* sugar transporter 1) was the earliest-discovered sugar transporter gene regulated by light [85]. Two other STP genes (*AtSTP13* and *AtSTP14*) have been reported to be sensitive to light conditions. They display diurnal regulation, which may result from a direct light effect or from the sensing of photosynthesis-derived sugars [86]. As sugar sensing plays a significant role in the establishment of different developmental stages, sugar transport and signaling appear crucial for these transitions. The latter assumption is corroborated by the changes in the transcriptional control of many sugar transporter genes in distinct mutants such as the *Arabidopsis* mutant “sweetie”, which is strongly affected in carbohydrate metabolism and displays an upregulated *STP1* gene [87]. The tight connection between sugar signaling and the regulation of sugar transporters fits with the impact of SnRK1 alteration on the expression of several *STPs* (*AtSTP1*, *AtSTP3*, *AtSTP4*, *AtSTP7*, and *AtSTP14*) by transient expression in mesophyll protoplasts [61].

Glucose-dependent down-regulation has been suggested for several STP genes (*STP1*, *STP4*, *STP13*, and *STP14*), but there appears to be different pathways for sugar control of *STP* expression [4,86,88–90]. Based on the demonstrated down-regulation of *STP4* and *STP10* in two independent hexokinase1 mutants, it has been suggested that their transcriptional control requires the glucose sensor HXK1. Inversely, *STP1*, one of the genes most repressed by sugars as revealed by large-scale genome analyses, displays glucose-dependent regulation independent of HXK1 [89]. The high responsiveness of *STP1* to sugars is corroborated by the rapid modulation of its expression in response to minor fluctuations of sugar levels (5 mM glucose) [4,88].



### 3. Molecular Mechanisms Involved in Regulation by Sugars

#### 3.1. Epigenetic Regulation

Epigenetic mechanisms (DNA methylation, histone posttranslational modifications), as well as small RNAs, histone variants, chromatin remodeling, and higher-order chromatin organization control chromatin structure and thereby influence gene expression. Combinations of these epigenetic marks reflect the active (accessible) and repressive (inaccessible) chromatin state according to the “histone code hypothesis” [91]. A growing body of evidence from yeast and mammals suggests that metabolic signals also play crucial roles in determining chromatin structure [92]. In plants, histones act as metabolic sensors and may affect sensitivity/resistance to glucose and sucrose in link with germination. In *Arabidopsis*, the enzyme encoded by HISTONE ACETYLTRANSFERASE1 (HAC1), was efficiently involved in histone acetylation and protein–protein interactions required for transcriptional activation of gene expression [93–95]. Mutations in HAC1 cause a sugar-response defect, and lead to decreased expression of genes, *AtPV42a* and *AtPV42b*, which encode cystathionine- $\beta$ -synthase (CBS) domain-containing proteins that belong to the PV42 class of  $\gamma$ -type subunits of the plant SnRK1 complexes [96]. This pioneer finding resulted from a screen for sugar-insensitive mutants. It highlights the fact that *hac1* mutants are resistant to high glucose and sucrose concentrations. The authors discussed the possible role of this histone acetyltransferase in the plant sugar response through long-term effects of the nutritional status on the expression of a specific set of genes. The detailed phenotyping of these mutants revealed delayed flowering times possibly related to the indirectly increased expression of the central floral repressor FLC (FLOWERING LOCUS C) by HAC1 [97,98], and a low productivity, namely a reduced number of seeds per silique [96]. The importance of sugar levels for the induction of flowering [99–101] suggests a putative involvement of HAC1 in the link between the sugar response and flowering time.

The fine-tuning of the cell fate between proliferation and differentiation in shoot and root apices relies on the balance of antagonistic effects of auxin and cytokinins, but also on glucose and light. All these signals are integrated by TOR kinase. Furthermore, the mutation of transcriptional corepressor TOPLESS, which is required to repress root formation at the shoot pole in late embryogenesis, may be suppressed by a mutation in HAC1. These data suggest that the stable switching-off of auxin-inducible genes (i.e., prevention of their activation), needs to be done through chromatin remodeling [102]. We may also speculate that epigenetic regulation seems required in the complex interplay between metabolic and hormonal signaling. New data arguing in favor of this statement concerns a small family of proteins interacting with ABA INSENSITIVE 5 (ABI5), named (ABI5)-binding proteins AFPs. They may interact with the TOPLESS co-repressor to inhibit ABA- and stress-responses, conferring strong resistance to ABA-mediated inhibition of germination in *Arabidopsis* overexpressing lines [103]. Using a yeast two-hybrid system, the authors demonstrated the direct interaction of AFP2 with histone deacetylase (HDAC) subunits and thereby suggested the possible involvement of some AFPs in the regulation of gene expression through chromatin remodeling.

A new histone modification was reported recently, the *N*-acetylglucosamine (GlcNAc) can be O-linked to the serine 112 of H2B by the enzyme O-GlcNAc transferase (OGT) and produces the O-GlcNAcylation mark [104]. The activated sugar UDP-GlcNAc (Uridine diphosphate *N*-acetylglucosamine) acting as co-substrate, is synthesized from extracellular glucose via the hexosamine biosynthesis pathway. For a first time, the activity of a histone-modifying enzyme is directly linked to the extracellular glucose concentration. Fujiki et al. demonstrated that O-GlcNAcylation of histone H2B at Ser112 fluctuates in response to extracellular glucose. Through a genome-wide analysis, they revealed that H2B Ser112 O-GlcNAcylation was frequently located nearby transcribed genes, suggesting that histone H2B O-GlcNAcylation facilitates gene transcription [104]. GlcNAc is a key signaling metabolite that can coordinate the glucose and glutamine metabolisms in cells through glycosylation of growth factor receptors [105]. Although the transcriptional implication of histone GlcNAcylation remains to be fully elucidated, it is likely that a flux through the hexosamine

biosynthesis pathway affects the levels of this novel epigenetic mark. Therefore, nutrient sensing by OGT may be pivotal in the modulation of chromatin remodeling and in the regulation of gene expression [106,107].

In *Drosophila melanogaster*, OGTs act as part of chromatin-remodeling complexes (CRCs) called polycomb group (PcG) proteins [108,109]. Switch/Sucrose-Nonfermenting-(SWI/SNF) type CRCs are constituted of a central Snf2-type ATPase associated with several non-catalytic core subunits evolutionarily conserved in eukaryotes. In *Arabidopsis*, the BRAHMA (BRM) ATPase and SWI3C CRC subunits act within a common complex to fulfill most of their functions, i.e., regulation of transcription, DNA replication and repair, and cell cycling. In addition, the *swi3c* mutation inhibits DELLA-dependent transcriptional activation of GIBBERELLIN-INSENSITIVE DWARF1 (GID1) GA-receptor and GA3ox (active GA biosynthesis) genes [110]. SWI3C also interacts with the O-GlcNAc transferase SPINDLY (SPY) required for the functioning of DELLAs in the GA-response pathway. Physical protein–protein interactions of SWI3C with DELLA and SPY have been demonstrated and further supposed to be required for certain DELLA-mediated effects such as transcriptional activation of the GID1 and GA3ox genes. The established pivotal role of DELLA proteins as a hub in the hormonal crosstalk between gibberellins, auxins, abscisic acid, ethylene, and brassinosteroids has been further supported by their direct physical interaction with SWI/SNF-type CRCs [111]. In the same context, it appears tantalizing to decipher the roles of sugar signaling because it interacts so tightly with hormone signaling. Moreover, it is possibly involved in the linking of the energy metabolism with epigenetic regulation through the expression of specific sets of genes in plant growth, development, and stress responses.

### 3.2. Transcriptional Regulation

Sugars affect the expression level of many genes in plants. Approximately 10% of *Arabidopsis* genes are sugar-responsive [4,112]. Based on the functional characterization of many sugar-regulated plant promoters, different cis-acting elements have emerged as crucial components of sugar-regulated gene expression. Such cis-acting elements transduce signals of sugar starvation [113,114] or sugar supply [115–119]. The GC-box (GGAGAACCGG), G-box (CTACGTG), TA-box (TATCAA), and their variants are associated with sugar starvation promoting the expression of  $\alpha$ -Amy3 ( $\alpha$ -amylase 3, an endo-amylolytic enzyme catalyzing starch degradation in higher plants) [113, 114]. By contrast, Sporamin Promoters 8 [SP8a (ACTGTGTA) and SP8b (TACTATT)] and SUGAR RESPONSIVE-elements SURE1 (AATAGAAA) and SURE2 (AATACTAAT) are involved in sugar induction of sporamin and patatin expression, respectively [117,120]. Other cis-acting elements such as the B-box (GCTAAACAAT), the CGACG element, the TGGACGG element, and the W-box (TGACT), S box (CACCTCCA), and TTATC element also participate in plant sugar signaling [117–119,121]. Sugar-responsive transcription factors include members of the ERF/AP2 [122], MYB [123], WRKY [124], and bZIP [125] families (Table 1). The first to be identified were SPF8 and SUSIBA2 (SUGAR SIGNALING IN BARLEY) [120,124], two members of the plant-specific WRKY family [126]. SUSIBA2 has a high relevance in plant sugar signaling because it is specifically sugar inducible, binds to SURE and W-box elements of the isoamylase (*iso1*) promoter, a key amylopectin-synthesizing enzyme, and induces carbohydrate accumulation in barley endosperm [124]. This regulation is biologically important, and makes the activity of SUSIBA2 a major component of the high sink strength of seeds. In agreement with this, SUSIBA2-expressing rice preferentially reallocates photosynthates towards aboveground tissues (stem and seeds); this offers sustainable means of increasing starch contents for food production and limits root-related greenhouse gas emission during rice cultivation [127]. In barley leaves, SUSIBA1 and SUSIBA2 are involved in an antagonistic SUSIBA regulatory network that ultimately leads to the coordination of starch and fructan synthesis in response to sugar availability [128]. Low sucrose concentrations generally upregulate SUSIBA1 expression, which acts as a repressor of both fructan synthesis and SUSIBA2 expression, while high sucrose levels induce SUSIBA2 expression, which stimulates starch accumulation in leaves but represses SUSIBA1 expression. This intertwined regulation

shows that SUSIBA2 expression depends on the competitive binding of SUSIBA1 (repressor)/SUSIBA2 (inducer) to the target site (W-box) of the SUSIBA2 promoter, building up an autoregulatory system for the sequential regulation of starch and fructan synthesis [128]. Noteworthy, we do not know as yet whether the SUSIBA-related function in sugar signaling is evolutionarily conserved in eudicots. Besides the WRKY family, transcription factors from the bZIP and MYB families are also involved in sugar-regulated gene expression. bZIP is one of the largest transcription factor families in higher plants, characterized by a leucine zipper and a basic region necessary for their specific binding activity to various ACGT elements in plant promoters [129]. This bZIP family regulates the expression of genes involved in an array of plant biological processes and environmental stresses [130–136]. Early investigations based on transcriptomic analysis identified 10 sugar-responsive bZIP transcription factors in *Arabidopsis*. Amongst them, *AtbZIP1* is transcriptionally and post-translationally repressed by glucose through a hexokinase-dependent pathway [4], which explains its high expression under conditions of sugar and energy depletion [137]. Besides its negative role in early seedling growth, *bZIP1* acts as a master regulator gene for the sugar-signaling pathway: most of the genes identified as *AtbZIP1*-regulated are also sugar sensitive, and it could probably mediate sugar signaling by binding to the C- or G-boxes in the promoters of its target genes [125,137]. Unlike SUSIBA2, *AtbZIP1* is involved in other signaling pathways, especially those elicited by light, nutrients, and stress signaling [125,138]. Some transcription factors of the MYB family also mediate sugar signaling, as shown for sugar-induced anthocyanin biosynthesis. Out of the transcription factors involved in this process, MYB71/PAP1, whose expression is upregulated by sucrose availability [139], stimulates the anthocyanin biosynthesis pathway [140,141] through sugar signaling. In fact, the *myb71/pap1* mutant is defective in sucrose-induced DRF (dihydroflavonol reductase) expression; DRF encodes a key enzymatic function in anthocyanin accumulation, and the alteration of MYB71/PAP1 protein-binding activity related to natural variation in *Arabidopsis* accessions impairs sugar inducibility [13]. Other MYB transcription factors contribute to the sugar-dependent regulation of  $\alpha$ -amylase expression. In rice suspension cells and barley aleurone, three structurally related OsMYB transcription factors (OsMYB1, OsMYB2, and OsMYB3) bind to the same target site (a TA-box), share overlapping sequences, but display different biological functions, with a prominent role of OsMYB1 in sugar-starvation-induced  $\alpha$ -amylase gene expression [123]. These OsMYBs are also involved in GA-induced expression of  $\alpha$ -amylase. This raises the question of their multifunctional roles in many signaling pathways [123]. More recently, Chen et al. (2017) identified two homologs of OsMYB1 in *Arabidopsis* (MYB1 and MYB2) that also recognize the sugar-response element TA-box, but play opposite roles in glucose signaling in *Arabidopsis* [142].

### 3.3. Post-Transcriptional Level

Gene post-transcriptional regulation plays a determining role in plant growth and represents a powerful strategy for plants to flexibly adapt their growth and development to endogenous and exogenous stimuli. This could involve regulation of the rate of mRNA turnover. Extensive investigations have reported that RNA-binding proteins (RBPs) regulate many aspects of RNA processing [143]. In rice cell cultures, nuclear run-on transcription. and mRNA half-life analyses revealed that sugar starvation led to reduced mRNA transcription rates and stability of a large set of genes [144]. Using microarray experiments, Nicolai et al. (2006) identified 268 mRNAs and 224 mRNAs under transcriptional and post-transcriptional regulation, respectively, in response to sugar starvation [145]. Most of them were sugar-starvation-repressed and related to the plant cell cycle and plant cell growth, supporting a rapid adaptability of cell metabolic activity to a low sugar status. Another example that links sugar availability to mRNA destabilization resides in the sugar-induced instability of  $\alpha$ -Amy3 [146], probably through the 3'UTR sequence of  $\alpha$ -Amy3 RNA [147,148]. Although such post-transcriptional regulation is involved in sugar-controlled mRNA stability, much remains to be understood about the molecular mechanisms involved in this process. UPF RNA helicase, a key component of NMD (nonsense-mediated RNA decay) in *Arabidopsis*,



takes part in the sugar-signaling pathway [149], as demonstrated by the low- $\beta$ -amylase1 (*lba1*) phenotype of the AtUP-1 RNA helicase mutant [150]. Consistently, many sugar-inducible genes were upregulated when the *lba1* mutant was complemented with the wild type AtUPF1, suggesting that AtUPF RNA helicase might optimize sugar inducibility [149]. Similarly, AtTZF1, which encodes an *Arabidopsis thaliana* tandem zinc finger protein, is sugar responsive and might confer sugar-dependent post-transcriptional regulation [151]. This family of proteins plays a critical role in plant growth, development, and stress responses, probably via regulation RNA processing [152].

An emerging process behind sugar-dependent post-transcriptional regulation is mediated by miRNA. miRNAs are regarded as the most important gene regulators that hinder much of gene expression [153]. Many studies have demonstrated that sugars induced the juvenile-to-adult transition by repressing the levels of two members of miR156 (miR156A and miR156C) in *Arabidopsis* seedlings [154,155]. miR156 is known to promote leaf juvenility by impeding the function of SPL (SQUAMOSA PROMOTER BINDING PROTEIN-Like) transcription factor [156]. This sugar effect implies the AtHXK1 signaling pathway and T6P [154,157], and occurs cooperatively with the Mediator Cyclin-Dependent Kinase 8 (CDK8) module [158]. All these findings indicate that sugar-dependent post-transcriptional regulation is far from being a neglected mechanism, but rather involves a diversity of complex processes that requires more investment to decipher the regulatory molecular network.

#### 3.4. Translational and Post-Translational Regulation

Regulation of mRNA translation can operate at multiple stages, including through regulatory elements in the 5' and 3' untranslated regions (UTRs) of mRNA. Upstream of the open reading frame (uORF), 30% to 40% of eukaryotic mRNAs are located in the 5'UTR [159] and involved in many developmental and growth-related processes [160,161]. Such regulation concerns the *Arabidopsis* basic leucine zipper *AtbZIP11*, which orchestrates metabolic reprogramming in response to cellular sugar status and energy deprivation conditions [162–165]. Under high sucrose conditions, *AtbZIP11* is induced at the transcriptional level, while it is repressed at the translational level [4,112,166,167]. This translational regulation requires the second uORF of *bZIP11* mRNA, named sucrose-induced repression of translation (SIRT), which is evolutionarily conserved among all groups of S1 members [167–171]. Data from frame-shift mutation and amino-acid substitution indicate that sucrose specifically causes ribosome stalling during translation of the second uORF, impeding the translation of the bZIP main ORF [167]. Using a cell-free translation model, Yamashita et al. (2017) demonstrated that SIRT was critical for specific sucrose-induced ribosome stalling, and probably acted as an intracellular sensor of sucrose [172]. In heterotrophic maize suspension cells, Cheng et al. (1999) ascribed a determining role to the length of the 3'UTR sequence of *Incw1*, a cell wall invertase, in sugar-mediated translational control [173]. *Incw1* encodes two transcripts that only diverge in the length of their 3'UTR (*Incw1*-Small RNA and *Incw1*-Large RNA) and are differentially regulated by sugars. The 3'UTR of the *Incw1* genes may act as a regulatory sensor of carbon starvation and as a link between sink metabolism and cellular translation in plants.

Sugar signaling can also be mediated by different mechanisms of post-translational regulation. The 14-3-3 proteins are phosphoserine-binding proteins that regulate a wide array of targets via direct protein–protein interactions [174]. They are involved in sugar-mediated post-translational regulation. In suspension-cultured cell models, sugar supply promotes both protein phosphorylation and their interaction with 14-3-3 proteins, while sugar depletion induces the dissociation of this protein complex, ultimately leading to selective degradation of these 14-3-3-regulated proteins [175]. This coordinated post-translational regulation could establish a new steady-state balance of metabolic activity adapted to sugar starvation conditions. Energy depletion (sugar starvation) due to the application of 2-deoxyglucose, a powerful blocker of the glycolysis pathway [74], led to the inhibition of key metabolic enzymes [60] related to their coordinated phosphorylation by SnRK1 and recognition by 14-3-3 proteins [57,59,60]. More recently, Okumura et al. (2016) demonstrated that sugar accumulation in photosynthetic leaves induced the activation of the plasma membrane H<sup>+</sup>-ATPase

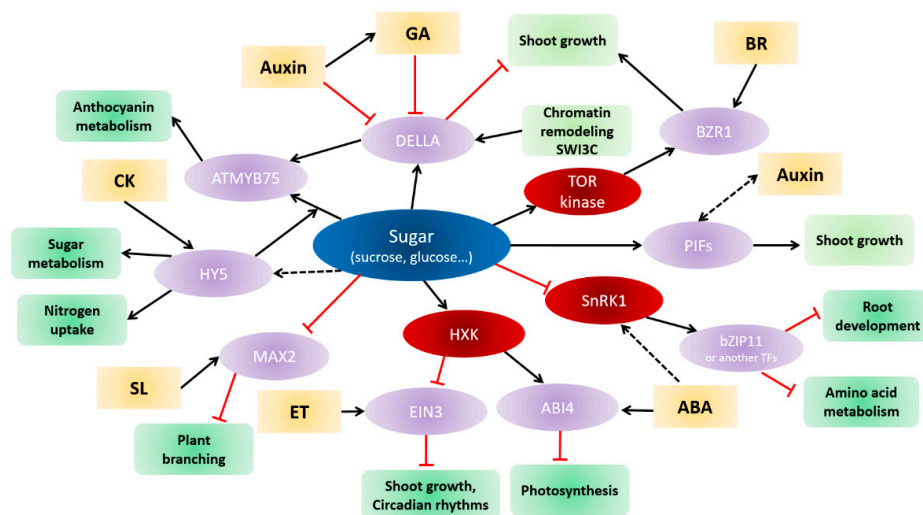
through the phosphorylation of the penultimate threonine of the C-terminal region and the binding of 14-3-3 proteins [176,177]. Accordingly, light-induced phosphorylation of H<sup>+</sup>-ATPase was strongly suppressed in mutants impaired in endogenous sugar accumulation. Such activation of H<sup>+</sup>-ATPase may stimulate sucrose export from leaves and thereby avoid inhibition of photosynthesis by high sugar accumulation [178,179]. Additional mechanisms of sugar-elicited posttranslational regulation come from the regulation of AGPase (ADP gluco-pyrophosphorylase), a key enzyme of the starch biosynthesis pathway [180]. Starch synthesis can increase via allosteric activation of AGPase, as a result of a higher 3PGA (3-phosphoglycerate) to Pi (inorganic phosphate) ratio [181] and/or through its post-translational redox activation in response to light or high sugar treatment in *Arabidopsis* [182–185]. This latter regulation is dependent on T6P [186,187]. All these findings show that post-transcriptional regulation is prevalent for sugar signaling, and extensive investigations are required to get more information about the molecular mechanisms and the relevance of additional post-transcriptional mechanisms such as sumoylation, protein–protein interactions, or unfolded cytoplasmic proteins.

#### 4. Crosstalk between Sugar and Hormone Signaling

##### 4.1. Sugars and Auxin

Auxin has been chemically identified as indole-3-acetic acid (IAA). It plays a pivotal role in almost all processes of plant growth and development [188–190]. Growing evidence suggests a crosstalk between sugar and auxin that involves metabolism [191–193], transport [194–197], and signaling pathways [198–201]. The first link between sugar and auxin came from *Arabidopsis* hypocotyl explants of *hvk/gin2*, which is insensitive to auxin induction of cell proliferation and root formation [42]. Accordingly, auxin-resistant mutants (*axr1*, *axr2*, *tir1*) are insensitive to high glucose concentrations [42]. Sugar and auxin represent a highly complex and central signaling network in various aspects of plant development, including cell proliferation, cell expansion, cell differentiation, hypocotyl elongation, or anther development [179,202–206]. A novel allele of the *hookless1* gene (*hls1*) was found resistant to both sugar and auxin responses in excised leaf petioles, suggesting that it may be part of the negative effects of auxin on sugar-responsive gene expression [199]. One of the best examples is their major contributing role in root system architecture, whereby sugar works individually or cooperatively with auxin [200,203,207–209]. Transcriptomic experiments on seedling roots revealed that glucose regulates the expression of many auxin-related genes (e.g., YUCCA, TIR1); more interestingly, a number of these genes are insensitive to glucose alone, but become glucose-responsive in the presence of auxin (e.g., AUX/IAA) [200]. In addition, exogenous glucose supply enhances defects in the induction of lateral root growth, root hair elongation, and gravitropism in mutants of auxin sensing (*tir1*) and signaling (*axr2* and *axr3*), suggesting that glucose-regulated root architecture may occur through auxin-based signal transduction [200]. Gonzali et al. (2005) showed that auxin and turanose, a non-metabolizable analogue of sucrose, regulated the expression of the WOX5 transcription factor, a Wushel-related homeobox gene required for sustaining local auxin maxima in the root apical meristem [198]. Additional insights into the interactions between auxin and sugar come from the elegant work conducted in *Arabidopsis* by Weiste et al. (2017): they demonstrated a new function of S<sub>1</sub>bZIP11-related TFs (bZIP1,-11 and -44) as negative regulators of auxin-mediated primary root growth (Figure 2) [165]. These transcription factors are downregulated by sugar and upregulated by low energy levels through SnRK1 kinase activity [61,162,167,170,171,210,211]. In this context, bZIP11 and closely related TFs directly up-regulate the expression of IAA3/SHY2, a key negative regulator of root growth. By repressing transcription of PIN1 and PIN3—major auxin efflux facilitators—IAA3/SHY2 restricts polar auxin transport (PAT) to the root apical meristem and thereby blocks auxin-driven primary root growth. These findings support that *bZIP11* and closely related transcription factors are a gateway for integrating low-energy-related stimuli into auxin-mediated root growth responses [165]. A close interaction between bZIP11 and auxin signaling was also demonstrated when the highly homologous bZIP11-related TFs were found to quantitatively modulate auxin-responsive gene

expression by recruiting the histone acetylation machinery to target promoters [212]. Repression of PIN1 accumulation and consequently reduction of PAT in roots explains the inhibition of root elongation in response to high glucose concentrations, through *ABI5* (ABA insensitive 5) [213]. Part of the glucose and auxin interplay in root growth and development is thought to result from the glucose-dependent activation of the heterotrimeric G-protein [214] and the auxin-activated TOR-kinase signaling pathway [215]. Based on genetic analysis, Raya-González et al. (2017) proposed a new mechanism involving MED12 or MED13, two subunits of the MEDIATOR complex responsible for the connection of RNA polymerase II to specific transcription factors [216], and thus controlling gene transcription [217]. The loss-of-function mutants *med12* and *med13* displayed short and thin primary roots associated with decreased auxin responsiveness and a reduction of cell proliferation and elongation in primary roots. This behavior was fully alleviated by exogenous sugar. Further analysis supports that MED12 and MED13 can operate as positive linkers of sugar sensing to the auxin response pathway, and that MED12 acts upstream of AUXIN RESISTANT 1 (*AUX1*), an auxin influx carrier central for the spatio-temporal transport of auxin within the root tissue. An interesting connection between sugar signaling and polar auxin transport also results from hypocotyl elongation; it involves the PIF (Phytochrome interacting family) transcriptional regulators (Figure 2). PIFs (e.g., PIF4) induces the expression of many auxin biosynthesis genes (e.g., *YUCCA*) by binding to their promoter [218], and its upregulation by sucrose leads to auxin accumulation and thereby to hypocotyl elongation [195]. The regulation mechanism between sugar and PIF seems to be complex: other works showed that PIFs could act as negative regulators of sugar-induced IAA biosynthesis [196], and that the auxin response acts upstream of PIFs [197]. Additionally, the role of PIFs in linking sugar signaling to auxin accumulation is central during another development in response to high temperature [204]. Although the sugar and auxin interplay plays a coordinated role in the control of many plant developmental processes, extensive investigations are still required to understand whether these so-far described pathways are interconnected or correlated with each other.



**Figure 2.** Schematic representation of the crosstalk between the sugar and hormone signaling pathways (orange frame) in the regulation of certain physiological processes (green frame). Light-purple circles represent hub regulators, including transcription factors (*ABI4*: ABA insensitive 4; *ATMYB75/PAP1*; *bZIP11*; *EIN3*: ETHYLENE-INSENSITIVE 3; *HY5*: Elongated Hypocotyl 5; *PIFs*: Phytochrome interacting factors), F-box (*MAX2*: MORE AXILLARY 2) and key regulators of the hormone signaling pathways (*DELLA* and *BZR1*: BRASSINAZOLE RESISTANT). Red circles represent glucose sensors (*HXK*: hexokinase) and energy sensors (*SnRK1*: Sucrose non-fermenting related kinase 1; *TOR*-kinase: Target of Rapamycin kinase). *ABA*: Abscisic acid; *BR*: Brassinosteroid; *CK*: Cytokinin; *GA*: Gibberellin; *SL*: Strigolactone. Black arrows indicate stimulating effects and red blunts indicate repressing effects.

#### 4.2. Sugar and Cytokinins

Cytokinins (CKs) are underlying factors of the regulation of plant development. They influence many central processes including cell proliferation, source/sink relationships, leaf senescence, apical dominance, root growth, nutritional signaling, and responses to abiotic and biotic stresses [219–223]. Many examples indicate that CKs and sugars can cross-influence their metabolism and transport [193,222,224–229], which may impinge on signaling pathways. Based on transcript profiling of *Arabidopsis* seedlings after glucose and cytokinin treatment, Kushwah and Laxmi (2014) showed that glucose and CKs acted both agonistically and antagonistically on gene expression, and glucose had a strong effect on genes involved in cytokinin metabolism and signaling [229]. The first direct interplay between sugar and CKs came from the characterization of the *hvk1/gin2* mutant, which displays decreased sensitivity to sugar and increased sensitivity to CKs [42], suggesting an antagonistic effect of CKs. In accordance with this, a constitutive CK response mutant was insensitive to high glucose-dependent seedling development repression [230], and a CK receptor mutant (*ahk3*) exhibited CK resistance but increased sucrose sensitivity during plant growth assays [231]. The cytokinin-resistant (*cnr1*) mutant exhibited a number of altered auxin responses as well as hypersensitivity to sugars, as evidenced by high levels of chlorophyll and anthocyanins as compared to the wild type [232]. Further proof came from the fact that sucrose downregulates WPK4, that is activated by CK and encodes a putative protein kinase belonging to the SnF1 kinase subfamily [233,234]. Other responses rather revealed synergistic effects. In *Arabidopsis* seedlings, CKs and glucose positively regulate root elongation via an HXK1-dependent pathway [235], involving *Arabidopsis* cytokinin receptor AHK4 (ARABIDOPSIS HISTIDINE KINASE 4) and three *Arabidopsis* type-B response regulators (ARR1, ARR10, and ARR11) [235,236]. In that case, glucose only boosts CK-dependent root elongation, which occurs upstream of the effect of auxin on root development [235,236]. CKs and sugar also play important roles in the regulation of different cell cycle phases, including the G1/S transition via the sucrose induction of *cycD3* expression [15] and the G2/M transition [237]. Another synergistic action between CKs and glucose resides in their combinatorial effect on anthocyanin accumulation in *Arabidopsis* leaves: sugar-induced anthocyanin biosynthesis is enhanced by CKs via the redundant action of three type-B ARR (ARR1, ARR10, and ARR12) [238]. This signaling cascade involves transcriptional upregulation of MYB75/PAP1 by LONG HYPOCOTYL 5 (HY5) (Figure 2) [239].

In *Arabidopsis*, a balance between the antagonistic effects of auxin—which mediates cell division—and CKs—which mediate cell differentiation—establishes the root meristem [240]. Inversely, in the shoot meristem, CKs seem to promote the proliferation of stem cells and inhibit their differentiation, whereas auxin triggers organ primordia initiation [102]. It is noteworthy that the activation of root and shoot apical meristems relies on distinct glucose and light signals [241]. The authors provide arguments that glucose is required and sufficient to activate TOR kinase in the root apex, whereas neither glucose nor light alone can efficiently activate this central integrator of the cell nutrient and energy status in the shoot apex.

#### 4.3. Sugars and Strigolactones

Strigolactones (SLs) were first considered as rhizosphere-signaling molecules that promote the germination of root-parasitic weeds and the symbiotic interactions between plants and soil microorganisms [242–244]. Since then, SLs have been revealed as mobile phytohormones controlling plant development and plant adaptation to environmental stress [245–253]. In addition, genes involved in SL biosynthesis and signaling are known in many plants [254]. Only a few studies have addressed how sugar signaling and SL signaling interplay to regulate plant functioning. Wu et al. (2017) showed that an *smxl4/smxl5* double mutant of *Arabidopsis* caused defective phloem transport of sugar and enhanced starch accumulation [255]. Li et al. (2016) reported that both mutants of *MAX1* and *MAX2*, involved in SL biosynthesis and signaling, respectively, were hyposensitive to glucose repression of seedling establishment; this suggests that this repression is under the cooperative effect of SLs and glucose, probably via the hexokinase-independent pathway [256]. Conversely,



an antagonistic effect between the sugar- and SL-signaling pathways has been reported for plant branching. In that case, SLs act as inhibitors while sugars act as inducers [257]. In accordance with this, *Arabidopsis* plants overexpressing cyanobacterial fructose-1,6-bisphosphatase-II in the cytosol exhibited an over-branching phenotype associated with high sugar contents and repression of *MAX1* and *MAX4*, two SL-biosynthesis genes [258]. These findings fit with those reported by Barbier et al. (2015) in *Rosa* sp. buds, in which both metabolizable and non-metabolizable analogs of sucrose or hexoses down-regulated *MAX2* expression, and this effect coincided with the ability of buds to grow out [193]. Further investigations should be led to ascertain the components through which these two signals interact.

#### 4.4. Sugars and Gibberellins

Gibberellins (GAs) constitute a large group of molecules with a tetracyclic diterpenoid structure. They function as plant hormones and influence photosynthesis, the carbohydrate metabolism, plant growth (cell and stem length elongation) and development processes (germination, flowering etc.), and responses to biotic and abiotic stresses [259–268]. GAs directly regulate the plant carbon status through their effect on photosynthetic activity [269–271] and sugar metabolic activity [272–279]. Sugar can also affect the GA metabolism in different biological contexts [49,280]. A first direct interaction between sugar and GA signaling was revealed by the sugar-insensitive1 (*sis1*) mutant, which was also insensitive to gibberellins during seed germination [281], suggesting a cooperative effect between sugars and GAs. However, other data provide evidence for an antagonistic crosstalk. Sugar and GA signaling compete to regulate the expression of  $\alpha$ -amylase in many cereal seeds [282–285], which involves spatiotemporal transcriptional regulation of *GAMYB* [285,286]. Li et al. (2014) reported that sucrose stabilizes DELLA proteins [287], supporting the importance of GAs in dark-induced hypocotyl elongation [288] and their negative effect on the sucrose-dependent induction of the anthocyanin biosynthesis pathway [289]. DELLA proteins are central repressors of the GA response [290]. In this context, Loreti et al. (2008) showed that GA repressed the expression of several sucrose-induced genes involved in anthocyanin synthesis, and this repressive effect was noticeably absent in *gai*, a mutant expressing a stabilized DELLA protein [289]. DELLA acts by inducing the upregulation of *PAP1/MYB75* [291], a sucrose-induced transcription factor that mediates anthocyanin synthesis (Figure 2) [13]. DELLA proteins could be one of the main convergent actors of the hormonal and sucrose-dependent molecular networks.

#### 4.5. Sugars and Ethylene

Ethylene regulates a host of plant processes, ranging from seed germination to organ senescence and plant responses to biotic and abiotic cues [292–294]. In higher plants, the pathways of ethylene metabolism and signaling are well established [295]. As evidenced by genetic and phenotypic analyses of many *Arabidopsis* mutants, there is a tight, but generally antagonistic, interaction between sugar and ethylene signaling. Mutants displaying nonfunctional ethylene receptors (*etr1*, *ein4*) or alteration of signal transduction proteins (*ein2* and *ein3*), are hypersensitive to sugar-mediated photosynthesis repression, while constitutive triple response 1 (*ctr1*), a negative regulator of ethylene signaling, is glucose insensitive [281,296–298]. Consistently, the ethylene-insensitive *etr1* and *ein2* mutants both exhibit *glo* (glucose-oversensitive) phenotypes, whereas the constitutive ethylene signaling mutant *ctr1* is allelic to *gin4*, a glucose-insensitive mutant [296,299]. Such an antagonistic interaction explains the ability of glucose to stimulate the degradation of ETHYLENE-INSENSITIVE3 (*EIN3*), a key positive transcriptional regulator in ethylene signaling, through the hexokinase-signaling pathway, and thereby promote plant growth [298]. The antagonistic interplay between the sucrose and ethylene pathways is involved in sustaining sugar-dependent circadian rhythms in darkness through post-transcriptional regulation of the circadian oscillator *GIGANTEA* (*GI*) [300]. According to these authors, sugars maintain circadian rhythms in the evening/night transition by stabilizing the *GIGANTEA* (*GI*) protein depending on the activity of the F-Box protein *ZEITLUPE* (*ZTL*), and by destabilizing



EIN3 (Figure 2) [300]. The ethylene- and sugar-signaling pathways can also work cooperatively: both ethylene-insensitive (*ein2-1*) and ethylene-constitutive response (*sis1/ctr1*) mutants displayed only a slight modification of sugar-dependent chlorophyll accumulation and growth, but higher impairment of the sugar-induced tolerance to atrazine (an inhibitor of electron transport in photosystem-II photosynthesis) [301]. It appears that the mechanism of sucrose-dependent protection against atrazine requires active ethylene signaling and may rather involve a hexokinase-independent pathway.

#### 4.6. Sugars and Abscisic Acid

Abscisic Acid (ABA) regulates many plant adaptive responses to environmental constraints [302–304]. Among plant hormones, ABA is one of major importance in the interaction with sugar signals since many mutations affecting sugar sensing and signaling are allelic to genes encoding components of the ABA synthesis or ABA transduction pathways. In *Arabidopsis*, ABA-deficient (*aba2*, *aba3*) and ABA-insensitive (*abi4*) mutants are allelic to glucose insensitive1 (*gin1*)/impaired sucrose induction 4 (*isi4*)/sugar insensitive1 (*sis1*) [305,306], and *gin6/isi3/sis5/sun6* [122], respectively. The *abi8* mutants are resistant to glucose-mediated developmental arrest of wild-type seedlings [307]. The crosstalk between sugar and ABA can involve synergistic effects with ApL3 (ADP pyrophosphorylase large subunit) [306,308], ASR (ABA, stress and ripening-induced protein) in grape [309] and many photosynthesis-related genes [121,310,311]; but it can also involve agonistic effects, e.g., on the expression of Rab16A [312], Amy3D [115], and OsTIP3.1, a tonoplast intrinsic protein [313]. ABI4, a transcription factor of the AP2/ERF family, plays a prominent role in glucose and ABA signaling [121,122,314,315]. Many investigations underline the key role of SnRK1 in glucose and ABA signaling, since plants over-expressing SnRK1.1 displayed hypersensitivity to glucose and ABA during early seedling development [316], and SnRK1 was required for ABA-mediated maturation of pea seeds [317]. In addition, mutants disrupted in the three SnRK1 subunits displayed full ABA insensitivity, supporting that SnRK-mediated protein phosphorylation is necessary for all aspects of ABA functioning [318]. Exogenous ABA application resulted in the fine-tuning of SnRK1 activity [319]. Overlapping between the ABA and sucrose pathways was also confirmed by the phenotype of *aip* (a null mutant of AIP1), a member of group A PP2C serving as a positive actor in ABA signaling. This mutant exhibited lower sensitivity to ABA and glucose during seed germination and early seedling development [320]. More recently, Carvalho et al. (2016) identified a negative regulator of the glucose signaling pathway corresponding to the plant-specific SR45, belonging to the highly conserved family of serine/arginine-rich (SR) proteins [321]. Phenotypic and molecular characterization of the *sr45-1* mutant revealed hypersensitivity to glucose during early seedling growth, and over-induction of ABA-biosynthesis and ABA-signaling genes in response to glucose as compared to the wild type.

#### 4.7. Sugars and Brassinosteroids

Brassinosteroids (BRs) are a class of polyhydroxylated sterol derivatives that regulate many plant growth processes [322–326]. Glucose affects BR biosynthesis, perception, transduction, and homeostasis [327–329]. On the other hand, BRs influence CO<sub>2</sub> assimilation, metabolism, and sugar fluxes [330–339]. BRs and sugars interplay cooperatively to regulate certain developmental processes, including etiolated hypocotyl elongation and LR development in *Arabidopsis* seedlings [340–342]. Analysis of glucose and BR sensitivity in both hexokinase-dependent and hexokinase-independent pathways complete this picture, providing evidence that glucose and BRs act via HXK1 pathway and BRs act downstream of this glucose sensor [329,341,342]. BZR1 (BRASSINAZOLE RESISTANT 1) protein can represent a converging hub between sugar and BR signaling (Figure 2) [341,343], and its stability is positively and synergistically controlled by TOR-dependent and BR signaling pathways in hypocotyls [343]. According to these authors, such TOR-mediated regulation allows carbon availability to control the hormonal growth promotion programs, ensuring a supply-demand balance in plant growth. Synergetic overlapping between sugar and BR signaling might also take place in the regulation of floral signal transduction, with a downstream effect of BZR1 and BZR2 [263]. This assumption

is linked to the fact that many BR-deficient mutants (*brs1*, *det2*, *cpd*, *bls1*) display a late-flowering phenotype, and the *bls1* (*brassinosteroid, light and sugar1*) mutant is hypersensitive to sugars [344].

#### 4.8. Crosstalk between Sugar and Nitrate Signaling

##### 4.8.1. Interactions between Sugars and Nitrogen

The control of C and N interactions involves various endogenous signals,  $\text{NO}_3^-$  and  $\text{NH}_4^+$  ions, amino acids, as well as sugars issued from the carbon metabolism [345–349]. Nitrate acts as a positive signal for the induction of proper sugar uptake and assimilation, while the metabolites resulting from sugar assimilation—e.g., glutamate, glutamine, aspartate, and to a lesser extent glycine and serine—serve as negative signals [350–356]. NR (nitrate reductase) and PEPc (phosphoenolpyruvate carboxylase) are two enzymes that link primary N and C assimilation in plants [357]. The interdependence of the C and N metabolisms supports their roles in the regulation of gene expression that can occur at the cell, organ, or whole plant levels [358]. Furthermore, nitrate uptake is enhanced by the  $\text{CO}_2$  level through the availability of carbohydrates, and inversely a reduction of carbon storage by defoliation impairs nitrate uptake [345,349,359–363]. In line with this, the dark-dependent decrease of N uptake is reversed by addition of sucrose, which transcriptionally affects high- and low-affinity nitrate transporters [364]. Moreover, the regulation of nitrate uptake by light and sucrose is strongly linked [365], and NR gene expression appears to be regulated by photosynthesis through glucose synthesis [366]. Taken together, these results strongly suggest that the C/N ratio affects NR and NiR gene expression as well as the related enzyme activities. Nitrogen starvation of wheat seedlings significantly decreased both the transcript levels and enzyme activities of NR, NiR, GS, and GOGAT, while potassium nitrate and ammonium nitrate restored gene expression and the catalytic activities of these enzymes [367]. In *Brassica juncea*, the expression of most of the N-pathway genes is significantly modulated under exogenous supply of sucrose or of sucrose and nitrogen [368]. These data emphasize the importance of C/N ratio signaling in the regulation of gene expression.

##### 4.8.2. C/N Regulation

Many transcription factors—bZIP, Dof, Nin-like protein 7—as well as proteins such as kinases/phosphorylases are involved in regulating both the carbon and nitrogen metabolisms. Besides TOR kinases, other regulatory hubs between sugars and the nitrogen metabolism have been identified in plants. Among them, Elongated Hypocotyl 5 (HY5) is a bZIP transcription factor involved in a great number of signaling pathways such as hormonal, metabolic, or abiotic stress pathways [369]. It may operate in combination with the circadian rhythm to adjust levels of photosynthetic gene expression in the daytime [370]. HY5 is a shoot-to-root phloem-mobile signal and it mediates the regulation of root growth and nitrate uptake by light [369,371,372]. In the shoot, HY5 promotes carbon assimilation and translocation, whereas in the root it mediates the activation *NRT2.1* expression, supporting the fact that it coordinates plant nutrition and growth in response to fluctuating light environments (Figure 2). Furthermore, HY5 regulates the sucrose metabolism and sucrose movement into phloem cells for shoot-to-root translocation by increasing the expression levels of *SWEET11* and *SWEET12*, two genes encoding sucrose efflux transporters required for sucrose phloem loading [371,373]. Taken together, all these results strongly suggest that HY5 mediates the homeostatic regulation of the whole-plant C status versus the whole-plant N status [371]. Furthermore, the master clock control gene *CCA1* targets the transcription factor bZIP1, which itself targets *ASN1* involved in asparagine synthesis, and the nitrate transporter 2.1 (*NRT2.1*) [4,138]. SnRK1 phosphorylates NR [374,375] supporting the impact of both SnRK1 and bZIP1 on nitrogen signaling. Dröge-Laser and Weiste (2018) recently highlighted the importance of bZIPs in the control of metabolic gene expression according to the plant nutritional status [376].

The Dof1 (DNA binding with one finger) transcription factor from maize (*ZmDof1*) up-regulates the expression of PEPc and thereby modulates the C/N network. Overexpression of *ZmDof1* in *Arabidopsis* and potato was accompanied by the promotion of nitrogen assimilation and plant growth under low nitrogen conditions [377–379], and up-regulation of multiple genes involved in carbon skeleton synthesis [378]. In agreement with this, expression of *ZmDof1* regulates the expression of genes involved in organic acid metabolism, leading to the accumulation of amino acids and to increased growth under N-limiting conditions. These effects suggest that nitrogen use efficiency (NUE) could also be improved by manipulating the carbon metabolism pathways [363]. An analysis of the *cis*-regulatory element in the promoter of *AtSUC2*, which encodes a companion-cell-specific proton-sucrose symporter, identified a putative binding site for HD-Zip and a binding site for DOF transcription factors [380]. Furthermore, Skirycz et al. (2006) reported the phloem-specific localization of a member of the DOF transcription factor family [381]. In *Oryza sativa*, OsDOF11 modulates sugar transport by regulating the expression of SUT (SUT1, 3, 4, and 5) and SWEET (SWEET11 and SWEET14) genes [382].

Proteins from the Nodule inception-like protein (NIN-Like Protein—NLP) family appear as master regulators of nitrate signaling. NLP7 and NLP6 bind and activate the promoters of several nitrate-induced genes [78,383–386]. The only known actor of the signaling mechanisms involved in the induction of *NRT2.1* and *NRT1.1* expression by carbon is the OPPP [84,387,388]. Otherwise, NLP7 is involved in the regulation of the gene coding for 6-phosphogluconate dehydrogenase, a key enzyme of the OPPP [385]. Glucose increases *NRT2.1* protein levels and transport activity independently of its hexokinase1-mediated stimulation of *NRT2.1* expression, demonstrating another possible post-transcriptional mechanism influencing nitrate uptake [387]. These authors also established that photosynthate availability in the form of glucose is coupled to nitrate uptake and assimilation through glucose metabolism by HXK1 in the OPPP, transcriptional control of *NRT2.1*, and post-translational regulation of *NRT2.1* protein levels and transport activities [387].

**Table 1.** The transcription factors that are involved in sugar signaling in *Arabidopsis thaliana*.

| Gene ID   | Gene Symbol | Transcription Factor Family | Main Process/Function  | Binding Site                           | References                |
|-----------|-------------|-----------------------------|--|--|---------------------------|
| AT1G69780 | ATHB13      | HD-ZIP                      | Response to sugar signaling pathways. Control cotyledon and leaf morphogenesis   | 5'-CAATNATTG-3'                        | [100,389–391]             |
| AT5G28770 | AtbZIP63    | bZIP                        | Response to glucose and ABA signaling pathways   | 5'-CACGTG-3' *                         | [392,393]                 |
| AT1G45249 | ABF2        | bZIP                        | Involved in ABA and glucose signaling pathways. Response to salt stress  | 5'-CACGTG-3'; 5'-ACGTGKC-3'            | [394–399]                 |
| AT2G40220 | ABI4        | AP2/ERF                     | Response to ABA, ethylene, cytokinin, and sugar signaling pathways. Involved in osmotic stress, defense response and root development, and stomatal movement   | 5'-CACTTCCA-3'                         | [121,311,400–405]         |
| AT5G24800 | AtbZIP9     | bZIP                        | Response to sugar signaling pathway  | 5'-CACGTG-3'                           | [406,407]                 |
| AT4G34590 | AtbZIP11    | bZIP                        | Involved in sugar, auxin signaling pathways. Affect root growth and amino acid metabolism  | 5'-CACGTG-3'                           | [162,165,167,212,408]     |
| AT3G20770 | AtEIN3      | EIL                         | Response to ethylene and sugar signaling pathways  | 5'-GGATTCAAGGGGCA TGTATCTTGAATCC-3'    | [298,409–411]             |
| AT2G28350 | ARF10       | ARF                         | Involved in auxin, and ABA signaling pathways. Control cell division, seed germination and developmental growth, and root cap development  | 5'-TGTCTC-3' *                         | [412–418]                 |
| AT1G56650 | AtMYB75     | MYB                         | Response to sugar, jasmonic acid, auxin, ethylene signaling pathways. Regulation of anthocyanin biosynthetic process and removal of superoxide radicals. Involved in cell wall formation                               | 5'-CACGTG-3', 5'-ACACGT-3'             | [13,239,289,419–425]      |
| AT2G36270 | ABI5        | bZIP                        | Involved in ABA, sugar signaling pathways during seed germination  | 5'-CACGTG-3'                           | [103,122,289,426–431]     |
| AT2G30470 | HSI2        | B3                          | Repressor of the sugar-inducible genes involved in the seed maturation. Plays an essential role in regulating the transition from seed maturation to seedling growth. Involved in embryonic pathways and ABA signaling | 5'-CATGCA-3'                           | [432–437]                 |
| AT5G49450 | AtbZIP1     | bZIP                        | Involved in sugar (nutrients) signaling pathway. Response to salt and osmotic stress   | 5'-CACGTG-3'                           | [125,136,138,210,406,438] |
| AT3G23210 | bHLH34      | bHLH                        | Response to glucose and ABA signaling  | 5'-(GA) <sub>n</sub> -3'; 5'-CANNTG-3' | [107,406]                 |

Table 1. Cont.

| Gene ID   | Gene Symbol | Transcription Factor Family | Main Process/Function  | Binding Site             | References |
|-----------|-------------|-----------------------------|--|--------------------------|------------|
| AT3G44290 | NAC060      | NAC                         | Response to sugar-and ABA signaling cascade  | Unknown                  | [315,439]  |
| AT4G00238 | AtSTKL1     | GeBP                        | Involved in mediating certain glucose responses  | 5'-GCCT-3'               | [440]      |
| AT5G08790 | ATAF2       | NAC                         | Response to sugar, jasmonic signaling pathways. Seedling photomorphogenesis and leaf senescence  | 5'-RTKVCGTR-3' *         | [441–446]  |
| AT5G56860 | GATA21      | GATA                        | Response to Gibberellic acid and sugar signaling pathways. Involved in regulation of nitrogen compound metabolic process, flower development, cell differentiation, and chlorophyll biosynthetic process | 5'-GATA-3'               | [447–452]  |
| AT3G54320 | AtWRI1      | AP2/ERF                     | Response to sugar signaling pathway. Involved in triglyceride biosynthetic process, lipid metabolic process, regulation of glycolytic process, and seed development                                      | 5'-CACRNTHCCRADG-3' *    | [453–459]  |
| AT4G14410 | bHLH104     | bHLH                        | Response to sugar signaling pathway and iron homeostasis   | 5'-(GA) <sub>n</sub> -3' | [460–462]  |
| AT5G64750 | ABR1        | AP2/ERF                     | Involved in ABA and sugar signaling pathways. Response to osmotic stress and salt  | 5'-GCCGCC-3'             | [463–465]  |
| AT4G00250 | ATSTKL2     | GeBP                        | Response to sugar signaling  | 5'-GCCT-3'               | [440]      |

The code of bind site follows the IUPAC role. \* The binding sites are predicted by PlantPAN database (<http://plantpan2.itps.ncku.edu.tw/index.html>) [466].



## 5. Conclusions

The complex processes of plant growth and development rely on the integration of inputs about nutrient availability, the energy status, and the hormonal balance under variable conditions at the level of whole organisms. Sugar signaling downstream of signal-specific sensors (e.g., hexokinase, RGS1, fructose 1,6 biphosphatase, O-GlcNAc transferase) converge to hub regulators of the nutrient and energy status (SnRK1 and TOR kinase). These key integrators might mediate the balance between the anabolic and catabolic metabolisms, as well as accumulation of reserves versus remobilization of reserves through epigenetic reprogramming, transcriptional/post-transcriptional regulation, ribosome biogenesis, translational activity, and protein modifications. Extensive investigations are required to identify additional hub regulators with original/unexpected functions. In this regard, the relevance of “non-canonical” sensors including histone modifiers, microRNAs, transcription factors, and many others (small peptides etc.) should not be overlooked. The complexity of sugar-responsiveness processes further requires the approaches of systems biology. The diversity of sugar sensors and the emerging transduction pathways are tightly interconnected with the hormone and nitrate signaling networks. At present, there is still a knowledge gap about the interconnections between all these signal transduction pathways, while the identity of the molecular actors involved in convergence points remains mostly unknown.

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## References

1. Chiariello, N.R.; Mooney, H.A.; Williams, K. Growth, carbon allocation and cost of plant tissues. In *Plant Physiological Ecology*; Springer Netherlands: New York, NY, USA, 2000; pp. 327–365.
2. Sheen, J.; Zhou, L.; Jang, J.C. Sugars as signaling molecules. *Curr. Opin. Plant Biol.* **1999**, *2*, 410–418. [[CrossRef](#)]
3. Eastmond, P.J.; Graham, I.A. Trehalose metabolism: A regulatory role for trehalose-6-phosphate? *Curr. Opin. Plant Biol.* **2003**, *6*, 231–235. [[CrossRef](#)]
4. Price, J.; Laxmi, A.; Martin, S.K.S.; Jang, J.C. Global transcription profiling reveals multiple sugar signal transduction mechanisms in *Arabidopsis*. *Plant Cell* **2004**, *16*, 2128–2150. [[CrossRef](#)] [[PubMed](#)]
5. Wind, J.; Smeekens, S.; Hanson, J. Sucrose: Metabolite and signaling molecule. *Phytochemistry* **2010**, *71*, 1610–1614. [[CrossRef](#)] [[PubMed](#)]
6. Li, L.; Sheen, J. Dynamic and diverse sugar signaling. *Curr. Opin. Plant Biol.* **2016**, *33*, 116–125. [[CrossRef](#)] [[PubMed](#)]
7. Funk, J.L.; Glenwinkel, L.A.; Sack, L. Differential Allocation to Photosynthetic and Non-Photosynthetic Nitrogen Fractions among Native and Invasive Species. *PLoS ONE* **2013**, *8*, E64502. [[CrossRef](#)] [[PubMed](#)]
8. Zhang, X.; Li, K.; Xing, R.; Liu, S.; Li, P. Metabolite profiling of wheat seedlings induced by chitosan: Revelation of the enhanced carbon and nitrogen metabolism. *Front. Plant Sci.* **2017**, *8*. [[CrossRef](#)] [[PubMed](#)]
9. Ljung, K.; Nemhauser, J.L.; Perata, P. New mechanistic links between sugar and hormone signalling networks. *Curr. Opin. Plant Biol.* **2015**, *25*, 130–137. [[CrossRef](#)] [[PubMed](#)]
10. Chiou, T.J.; Bush, D.R. Sucrose is a signal molecule in assimilate partitioning. *Proc. Natl. Acad. Sci. USA* **1998**, *95*, 4784–4788. [[CrossRef](#)] [[PubMed](#)]
11. Loreti, E.; Alpi, A.; Perata, P. Glucose and disaccharide-sensing mechanisms modulate the expression of  $\alpha$ -amylase in barley embryos. *Plant Physiol.* **2000**, *123*, 939–948. [[CrossRef](#)] [[PubMed](#)]
12. Fernie, A.R.; Roscher, A.; Ratcliffe, R.G.; Kruger, N.J. Fructose 2, 6-bisphosphate activates pyrophosphate: Fructose-6-phosphate 1-phosphotransferase and increases triose phosphate to hexose phosphate cycling in heterotrophic cells. *Planta* **2001**, *212*, 250–263. [[CrossRef](#)] [[PubMed](#)]

13. Teng, S.; Keurentjes, J.; Bentsink, L.; Koornneef, M.; Smeekens, S. Sucrose-specific induction of anthocyanin biosynthesis in *Arabidopsis* requires the MYB75/PAP1 gene. *Plant Physiol.* **2005**, *139*, 1840–1852. [[CrossRef](#)] [[PubMed](#)]
14. Roldán, M.; Gómez-Mena, C.; Ruiz-García, L.; Salinas, J.; Martínez-Zapater, J.M. Sucrose availability on the aerial part of the plant promotes morphogenesis and flowering of *Arabidopsis* in the dark. *Plant J.* **1999**, *20*, 581–590. [[CrossRef](#)] [[PubMed](#)]
15. Riou-Khamlichi, C.; Menges, M.; Healy, J.S.; Murray, J.A. Sugar control of Plant Cell cycle: Differential regulation of *Arabidopsis* D-type cyclin gene expression. *Mol. Cell. Biol.* **2000**, *20*, 4513–4521. [[CrossRef](#)] [[PubMed](#)]
16. Lastdrager, J.; Hanson, J.; Smeekens, S. Sugar signals and the control of plant growth and development. *J. Exp. Bot.* **2014**, *65*, 799–807. [[CrossRef](#)] [[PubMed](#)]
17. Ruan, Y.L. Sucrose metabolism: Gateway to diverse carbon use and sugar signaling. *Annu. Rev. Plant Biol.* **2014**, *65*, 33–67. [[CrossRef](#)] [[PubMed](#)]
18. Mason, M.G.; Ross, J.J.; Babst, B.A.; Wienclaw, B.N.; Beveridge, C.A. Sugar demand, not auxin, is the initial regulator of apical dominance. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 6092–6097. [[CrossRef](#)] [[PubMed](#)]
19. Barker, L.; Kühn, C.; Weise, A.; Schulz, A.; Gebhardt, C.; Hirner, B.; Hellmann, H.; Schulze, W.; Ward, J.M.; Frommer, W.B. SUT2, a putative sucrose sensor in sieve elements. *Plant Cell* **2000**, *12*, 1153–1164. [[CrossRef](#)] [[PubMed](#)]
20. Li, Y.; Li, L.L.; Fan, R.C.; Peng, C.C.; Sun, H.L.; Zhu, S.Y.; Wang, X.F.; Zhang, L.Y.; Zhang, D.P. *Arabidopsis* sucrose transporter SUT4 interacts with cytochrome b5-2 to regulate seed germination in response to sucrose and glucose. *Mol. Plant* **2012**, *5*, 1029–1041. [[CrossRef](#)] [[PubMed](#)]
21. Vitrac, X.; Larronde, F.; Krisa, S.; Decendit, A.; Deffieux, G.; Mérillon, J.M. Sugar sensing and Ca<sup>2+</sup>-calmodulin requirement in *Vitis vinifera* cells producing anthocyanins. *Phytochemistry* **2000**, *53*, 659–665. [[CrossRef](#)]
22. Martinez-Noel, G.; Tognetti, J.A.; Salerno, G.; Horacio, P. Sugar signaling of fructan metabolism: New insights on protein phosphatases in sucrose-fed wheat leaves. *Plant Signal. Behav.* **2010**, *5*, 311–313. [[CrossRef](#)] [[PubMed](#)]
23. Nguyen, D.M.; Zhang, Z.; Doherty, W.O. Degradation of hydroxycinnamic acid mixtures in aqueous sucrose solutions by the Fenton process. *J. Agric. Food Chem.* **2015**, *63*, 1582–1592. [[CrossRef](#)] [[PubMed](#)]
24. Soyk, S.; Šimková, K.; Zürcher, E.; Luginbühl, L.; Brand, L.H.; Vaughan, C.K.; Wanke, D.; Zeeman, S.C. The enzyme-like domain of *Arabidopsis* nuclear  $\beta$ -amylases is critical for DNA sequence recognition and transcriptional activation. *Plant Cell* **2014**, *26*, 1746–1763. [[CrossRef](#)] [[PubMed](#)]
25. Cabib, E.; Leloir, L.F. The biosynthesis of trehalose phosphate. *J. Biol. Chem.* **1958**, *231*, 259–275. [[PubMed](#)]
26. Leyman, B.; Van Dijck, P.; Thevelein, J.M. An unexpected plethora of trehalose biosynthesis genes in *Arabidopsis thaliana*. *Trends Plant Sci.* **2001**, *6*, 510–513. [[CrossRef](#)]
27. Ramon, M.; De Smet, I.V.E.; Vandesteene, L.; Naudts, M.; Leyman, B.; Van Dijck, P.; Rolland, F.; Beeckman, T.; Thevelein, J.M. Extensive expression regulation and lack of heterologous enzymatic activity of the Class II trehalose metabolism proteins from *Arabidopsis thaliana*. *Plant Cell Environ.* **2009**, *32*, 1015–1032. [[CrossRef](#)] [[PubMed](#)]
28. Vandesteene, L.; López-Galvis, L.; Vanneste, K.; Feil, R.; Maere, S.; Lammens, W.; Rolland, F.; Lunn, J.E.; Avonce, N.; Beeckman, T.; et al. Expansive evolution of the trehalose-6-phosphate phosphatase gene family in *Arabidopsis*. *Plant Physiol.* **2012**, *160*, 884–896. [[CrossRef](#)] [[PubMed](#)]
29. Vandesteene, L.; Ramon, M.; Le Roy, K.; Van Dijck, P.; Rolland, F. A single active trehalose-6-P synthase (TPS) and a family of putative regulatory TPS-like proteins in *Arabidopsis*. *Mol. Plant* **2010**, *3*, 406–419. [[CrossRef](#)] [[PubMed](#)]
30. Paul, M.J.; Primavesi, L.F.; Jhurreea, D.; Zhang, Y. Trehalose metabolism and signaling. *Annu. Rev. Plant Biol.* **2008**, *59*, 417–441. [[CrossRef](#)] [[PubMed](#)]
31. Yadav, U.P.; Ivakov, A.; Feil, R.; Duan, G.Y.; Walther, D.; Giavalisco, P.; Piques, M.; Carillo, P.; Hubberten, H.M.; Stitt, M.; et al. The sucrose–trehalose 6-phosphate (Tre6P) nexus: Specificity and mechanisms of sucrose signalling by Tre6P. *J. Exp. Bot.* **2014**, *65*, 1051–1068. [[CrossRef](#)] [[PubMed](#)]
32. Figueroa, C.M.; Lunn, J.E. A tale of two sugars: Trehalose 6-phosphate and sucrose. *Plant Physiol.* **2016**, *172*, 7–27. [[CrossRef](#)] [[PubMed](#)]

33. 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. Trehalose 6-phosphate is involved in triggering axillary bud outgrowth in garden pea (*Pisum sativum* L.). *Plant J.* **2017**, *92*, 611–623. [[CrossRef](#)] [[PubMed](#)]
34. Carillo, P.; Feil, R.; Gibon, Y.; Satoh-Nagasawa, N.; Jackson, D.; Bläsing, O.E.; Stitt, M.; Lunn, J.E. A fluorometric assay for trehalose in the picomole range. *Plant Methods* **2013**, *9*, 21. [[CrossRef](#)] [[PubMed](#)]
35. Lunn, J.E.; Delorge, I.; Figueroa, C.M.; Van Dijck, P.; Stitt, M. Trehalose metabolism in plants. *Plant J.* **2014**, *79*, 544–567. [[CrossRef](#)] [[PubMed](#)]
36. Phan, N.; Urano, D.; Srba, M.; Fischer, L.; Jones, A.M. Sugar-induced endocytosis of plant 7TM-RGS proteins. *Plant Signal. Behav.* **2013**, *8*, e22814. [[CrossRef](#)] [[PubMed](#)]
37. Grigston, J.C.; Osuna, D.; Scheible, W.R.; Liu, C.; Stitt, M.; Jones, A.M. D-Glucose sensing by a plasma membrane regulator of G signaling protein, AtRGS1. *FEBS Lett.* **2008**, *582*, 3577–3584. [[CrossRef](#)] [[PubMed](#)]
38. Urano, D.; Phan, N.; Jones, J.C.; Yang, J.; Huang, J.; Grigston, J.; Taylor, J.P.; Jones, A.M. Endocytosis of the seven-transmembrane RGS1 protein activates G-protein-coupled signalling in *Arabidopsis*. *Nat. Cell Biol.* **2012**, *14*, 1079–1088. [[CrossRef](#)] [[PubMed](#)]
39. Fu, Y.; Lim, S.; Urano, D.; Tunc-Ozdemir, M.; Phan, N.G.; Elston, T.C.; Jones, A.M. Reciprocal encoding of signal intensity and duration in a glucose-sensing circuit. *Cell* **2014**, *156*, 1084–1095. [[CrossRef](#)] [[PubMed](#)]
40. Jang, J.C.; Sheen, J. Sugar sensing in higher plants. *Plant Cell* **1994**, *6*, 1665–1679. [[CrossRef](#)] [[PubMed](#)]
41. Jang, J.C.; León, P.; Zhou, L.; Sheen, J. Hexokinase as a sugar sensor in higher plants. *Plant Cell* **1997**, *9*, 5–19. [[CrossRef](#)] [[PubMed](#)]
42. Moore, B.; Zhou, L.; Rolland, F.; Hall, Q.; Cheng, W.H.; Liu, Y.X.; Hwang, I.; Jones, T.; Sheen, J. Role of the *Arabidopsis* glucose sensor HXK1 in nutrient, light, and hormonal signaling. *Science* **2003**, *300*, 332–336. [[CrossRef](#)] [[PubMed](#)]
43. Cho, Y.H.; Yoo, S.D.; Sheen, J. Regulatory functions of nuclear hexokinase1 complex in glucose signaling. *Cell* **2006**, *127*, 579–589. [[CrossRef](#)] [[PubMed](#)]
44. Granot, D.; Kelly, G.; Stein, O.; David-Schwartz, R. Substantial roles of hexokinase and fructokinase in the effects of sugars on Plant Physiology and development. *J. Exp. Bot.* **2013**, *65*, 809–819. [[CrossRef](#)] [[PubMed](#)]
45. Veramendi, J.; Fernie, A.R.; Leisse, A.; Willmitzer, L.; Trethewey, R.N. Potato hexokinase 2 complements transgenic *Arabidopsis* plants deficient in hexokinase 1 but does not play a key role in tuber carbohydrate metabolism. *Plant Mol. Biol.* **2002**, *49*, 491–501. [[CrossRef](#)] [[PubMed](#)]
46. Cho, J.I.; Ryoo, N.; Hahn, T.R.; Jeon, J.S. Evidence for a role of hexokinases as conserved glucose sensors in both monocot and dicot plant species. *Plant Signal. Behav.* **2009**, *4*, 908–910. [[CrossRef](#)] [[PubMed](#)]
47. Karve, A.; Moore, B.D. Function of *Arabidopsis* hexokinase-like1 as a negative regulator of plant growth. *J. Exp. Bot.* **2009**, *60*, 4137–4149. [[CrossRef](#)] [[PubMed](#)]
48. Karve, A.; Xia, X.; Moore, B.D. *Arabidopsis* Hexokinase-Like1 and Hexokinase1 form a critical node in mediating plant glucose and ethylene responses. *Plant Physiol.* **2012**, *158*, 1965–1975. [[CrossRef](#)] [[PubMed](#)]
49. Zhang, Y.; Liu, Z.; Wang, L.; Zheng, S.; Xie, J.; Bi, Y. Sucrose-induced hypocotyl elongation of *Arabidopsis* seedlings in darkness depends on the presence of gibberellins. *J. Plant Physiol.* **2010**, *167*, 1130–1136. [[CrossRef](#)] [[PubMed](#)]
50. Fukumoto, T.; Kano, A.; Ohtani, K.; Inoue, M.; Yoshihara, A.; Izumori, K.; Tajima, S.; Shigematsu, Y.; Tanaka, K.; Ohkouchi, T.; et al. Phosphorylation of d-allose by hexokinase involved in regulation of *OsABF1* expression for growth inhibition in *Oryza sativa* L. *Planta* **2013**, *237*, 1379–1391. [[CrossRef](#)] [[PubMed](#)]
51. Bruggeman, Q.; Prunier, F.; Mazubert, C.; de Bont, L.; Garmier, M.; Lugan, R.; Benhamed, M.; Bergounioux, C.; Raynaud, C.; Delarue, M. Involvement of *Arabidopsis* hexokinase1 in cell death mediated by myo-inositol accumulation. *Plant Cell* **2015**. [[CrossRef](#)] [[PubMed](#)]
52. Cho, Y.H.; Yoo, S.D. Signaling role of fructose mediated by FINS1/FBP in *Arabidopsis thaliana*. *PLoS Genet.* **2011**, *7*, e1001263. [[CrossRef](#)] [[PubMed](#)]
53. Li, P.; Wind, J.J.; Shi, X.; Zhang, H.; Hanson, J.; Smeeckens, S.C.; Teng, S. Fructose sensitivity is suppressed in *Arabidopsis* by the transcription factor ANAC089 lacking the membrane-bound domain. *Proc. Natl. Acad. Sci. USA* **2011**, *108*, 3436–3441. [[CrossRef](#)] [[PubMed](#)]
54. Gilkerson, J.; Perez-Ruiz, J.M.; Chory, J.; Callis, J. The plastid-localized pfkB-type carbohydrate kinases FRUCTOKINASE-LIKE 1 and 2 are essential for growth and development of *Arabidopsis thaliana*. *BMC Plant Biol.* **2012**, *12*, 102. [[CrossRef](#)] [[PubMed](#)]

55. Broeckx, T.; Hulsmans, S.; Rolland, F. The plant energy sensor: Evolutionary conservation and divergence of SnRK1 structure, regulation, and function. *J. Exp. Bot.* **2016**, *67*, 6215–6252. [[CrossRef](#)] [[PubMed](#)]
56. Simon, N.M.; Sawkins, E.; Dodd, A.N. Involvement of the SnRK1 subunit KIN10 in sucrose-induced hypocotyl elongation. *Plant Signal. Behav.* **2018**. [[CrossRef](#)] [[PubMed](#)]
57. Polge, C.; Thomas, M. SNF1/AMPK/SnRK1 kinases, global regulators at the heart of energy control? *Trends Plant Sci.* **2007**, *12*, 20–28. [[CrossRef](#)] [[PubMed](#)]
58. Alderson, A.; Sabelli, P.A.; Dickinson, J.R.; Cole, D.; Richardson, M.; Kreis, M.; Halford, N.G. Complementation of *snf1*, a mutation affecting global regulation of carbon metabolism in yeast, by a plant protein kinase cDNA. *Proc. Natl. Acad. Sci. USA* **1991**, *88*, 8602–8605. [[CrossRef](#)] [[PubMed](#)]
59. Sugden, C.; Crawford, R.M.; Halford, N.G.; Hardie, D.G. Regulation of spinach SNF1-related (SnRK1) kinases by protein kinases and phosphatases is associated with phosphorylation of the T loop and is regulated by 5'-AMP. *Plant J.* **1999**, *19*, 433–439. [[CrossRef](#)] [[PubMed](#)]
60. Harthill, J.E.; Meek, S.E.; Morrice, N.; Pegg, M.W.; Borch, J.; Wong, B.H.; MacKintosh, C. Phosphorylation and 14-3-3 binding of *Arabidopsis* trehalose-phosphate synthase 5 in response to 2-deoxyglucose. *Plant J.* **2006**, *47*, 211–223. [[CrossRef](#)] [[PubMed](#)]
61. Baena-González, E.; Rolland, F.; Thevelein, J.M.; Sheen, J. A central integrator of transcription networks in plant stress and energy signalling. *Nature* **2007**, *448*, 938–942. [[CrossRef](#)] [[PubMed](#)]
62. Coello, P.; Hey, S.J.; Halford, N.G. The sucrose non-fermenting-1-related (SnRK) family of protein kinases: Potential for manipulation to improve stress tolerance and increase yield. *J. Exp. Bot.* **2010**, *62*, 883–893. [[CrossRef](#)] [[PubMed](#)]
63. Hey, S.J.; Byrne, E.; Halford, N.G. The interface between metabolic and stress signalling. *Ann. Bot.* **2009**, *105*, 197–203. [[CrossRef](#)] [[PubMed](#)]
64. Rodrigues, A.; Adamo, M.; Crozet, P.; Margalha, L.; Confraria, A.; Martinho, C.; Elias, A.; Rabissi, A.; Lumberras, V.; González-Guzmán, M.; et al. ABI1 and PP2CA phosphatases are negative regulators of Snf1-related protein kinase1 signaling in *Arabidopsis*. *Plant Cell* **2013**. [[CrossRef](#)] [[PubMed](#)]
65. Confraria, A.; Martinho, C.S.D.S.; Elias, A.; Rubio-Somoza, I.; Baena-González, E. miRNAs mediate SnRK1-dependent energy signaling in *Arabidopsis*. *Front. Plant Sci.* **2013**, *4*, 197. [[CrossRef](#)] [[PubMed](#)]
66. Kravchenko, A.; Citerne, S.; Jéhanno, I.; Bersimbaev, R.I.; Veit, B.; Meyer, C.; Leprince, A.S. Mutations in the *Arabidopsis* Lst8 and Raptor genes encoding partners of the TOR complex, or inhibition of TOR activity decrease abscisic acid (ABA) synthesis. *Biochem. Biophys. Res. Commun.* **2015**, *467*, 992–997. [[CrossRef](#)] [[PubMed](#)]
67. Menand, B.; Desnos, T.; Nussaume, L.; Berger, F.; Bouchez, D.; Meyer, C.; Robaglia, C. Expression and disruption of the *Arabidopsis* TOR (target of rapamycin) gene. *Proc. Natl. Acad. Sci. USA* **2002**, *99*, 6422–6427. [[CrossRef](#)] [[PubMed](#)]
68. Liu, Y.; Bassham, D.C. TOR is a negative regulator of autophagy in *Arabidopsis thaliana*. *PLoS ONE* **2010**, *5*, e11883. [[CrossRef](#)] [[PubMed](#)]
69. Dobrenel, T.; Marchive, C.; Sormani, R.; Moreau, M.; Mozzo, M.; Montané, M.H.; Menand, B.; Robaglia, C.; Meyer, C. Regulation of plant growth and metabolism by the TOR kinase. *Biochem. Soc. Trans.* **2011**, *39*, 477–481. [[CrossRef](#)] [[PubMed](#)]
70. Xiong, Y.; Sheen, J. TOR signaling networks in plant growth and metabolism. *Plant Physiol.* **2014**. [[CrossRef](#)] [[PubMed](#)]
71. Dobrenel, T.; Marchive, C.; Azzopardi, M.; Clément, G.; Moreau, M.; Sormani, R.; Robaglia, C.; Meyer, C. Sugar metabolism and the plant target of rapamycin kinase: A sweet opera TOR? *Front. Plant Sci.* **2013**, *4*, 93. [[CrossRef](#)] [[PubMed](#)]
72. Robaglia, C.; Thomas, M.; Meyer, C. Sensing nutrient and energy status by SnRK1 and TOR kinases. *Curr. Opin. Plant Biol.* **2012**, *15*, 301–307. [[CrossRef](#)] [[PubMed](#)]
73. Ren, M.; Venglat, P.; Qiu, S.; Feng, L.; Cao, Y.; Wang, E.; Xiang, D.; Wang, J.; Alexander, D.; Chalivendra, S.; et al. Target of rapamycin signaling regulates metabolism, growth, and life span in *Arabidopsis*. *Plant Cell* **2012**, *24*, 4850–4874. [[CrossRef](#)] [[PubMed](#)]
74. Xiong, Y.; McCormack, M.; Li, L.; Hall, Q.; Xiang, C.; Sheen, J. Glucose–TOR signalling reprograms the transcriptome and activates meristems. *Nature* **2013**, *496*, 181–186. [[CrossRef](#)] [[PubMed](#)]



75. Henriques, R.; Magyar, Z.; Monardes, A.; Khan, S.; Zalejski, C.; Orellana, J.; Szabados, L.; Torre, C.; Koncz, C.; Bögre, L. *Arabidopsis* S6 kinase mutants display chromosome instability and altered RBR1–E2F pathway activity. *EMBO J.* **2010**, *29*, 2979–2993. [[CrossRef](#)] [[PubMed](#)]
76. Gutzat, R.; Borghi, L.; Fütterer, J.; Bischof, S.; Laizet, Y.H.; Hennig, L.; Feil, R.; Lunn, J.; Gruitsem, W. Retinoblastoma-Related Protein controls the transition to autotrophic plant development. *Development* **2011**, *138*, 2977–2986. [[CrossRef](#)] [[PubMed](#)]
77. Baena-González, E. Energy signaling in the regulation of gene expression during stress. *Mol. Plant* **2010**, *3*, 300–313. [[CrossRef](#)] [[PubMed](#)]
78. Krapp, A.; David, L.C.; Chardin, C.; Girin, T.; Marmagne, A.; Leprince, A.S.; Chaillou, S.; Ferrario-Méry, S.; Meyer, C.; Daniel-Vedele, F. Nitrate transport and signalling in *Arabidopsis*. *J. Exp. Bot.* **2014**, *65*, 789–798. [[CrossRef](#)] [[PubMed](#)]
79. Baena-González, E.; Hanson, J. Shaping plant development through the SnRK1–TOR metabolic regulators. *Curr. Opin. Plant Biol.* **2017**, *35*, 152–157. [[CrossRef](#)] [[PubMed](#)]
80. Zhang, Y.; Primavesi, L.F.; Jhurrea, D.; Andralojc, P.J.; Mitchell, R.A.; Powers, S.J.; Schlupepmann, H.; Delatte, T.; Wingler, A.; Paul, M.J. Inhibition of SNF1-related protein kinase1 activity and regulation of metabolic pathways by trehalose-6-phosphate. *Plant Physiol.* **2009**, *149*, 1860–1871. [[CrossRef](#)] [[PubMed](#)]
81. Paul, M.J.; Jhurrea, D.; Zhang, Y.; Primavesi, L.F.; Delatte, T.; Schlupepmann, H.; Wingler, A. Up-regulation of biosynthetic processes associated with growth by trehalose 6-phosphate. *Plant Signal. Behav.* **2010**, *5*, 386–392. [[CrossRef](#)] [[PubMed](#)]
82. Smeekens, S.; Ma, J.; Hanson, J.; Rolland, F. Sugar signals and molecular networks controlling plant growth. *Curr. Opin. Plant Biol.* **2010**, *13*, 273–278. [[CrossRef](#)] [[PubMed](#)]
83. O'hara, L.E.; Paul, M.J.; Wingler, A. How do sugars regulate plant growth and development? New insight into the role of trehalose-6-phosphate. *Mol. Plant* **2013**, *6*, 261–274. [[CrossRef](#)] [[PubMed](#)]
84. Lejay, L.; Wirth, J.; Pervent, M.; Cross, J.M.F.; Tillard, P.; Gojon, A. Oxidative pentose phosphate pathway-dependent sugar sensing as a mechanism for regulation of root ion transporters by photosynthesis. *Plant Physiol.* **2008**, *146*, 2036–2053. [[CrossRef](#)] [[PubMed](#)]
85. Stadler, R.; Büttner, M.; Ache, P.; Hedrich, R.; Ivashikina, N.; Melzer, M.; Shearson, S.M.; Smith, S.M.; Sauer, N. Diurnal and light-regulated expression of *AtSTP1* in guard cells of *Arabidopsis*. *Plant Physiol.* **2003**, *133*, 528–537. [[CrossRef](#)] [[PubMed](#)]
86. Büttner, M. The *Arabidopsis* sugar transporter (AtSTP) family: An update. *Plant Biol.* **2010**, *12*, 35–41. [[CrossRef](#)] [[PubMed](#)]
87. Veyres, N.; Danon, A.; Aono, M.; Galliot, S.; Karibasappa, Y.B.; Diet, A.; Grandmottet, F.; Tamaoki, M.; Lesur, D.; Pilard, S.; et al. The *Arabidopsis* sweetie mutant is affected in carbohydrate metabolism and defective in the control of growth, development and senescence. *Plant J.* **2008**, *55*, 665–686. [[CrossRef](#)] [[PubMed](#)]
88. Villadsen, D.; Smith, S. Identification of more than 200 glucose-responsive *Arabidopsis* genes none of which responds to 3-O-methylglucose or 6-deoxyglucose. *Plant Mol. Biol.* **2004**, *55*, 467–477. [[CrossRef](#)] [[PubMed](#)]
89. Cordoba, E.; Aceves-Zamudio, D.L.; Hernández-Bernal, A.F.; Ramos-Vega, M.; León, P. Sugar regulation of SUGAR TRANSPORTER PROTEIN 1 (*STP1*) expression in *Arabidopsis thaliana*. *J. Exp. Bot.* **2014**, *66*, 147–159. [[CrossRef](#)] [[PubMed](#)]
90. Rottmann, T.; Zierer, W.; Subert, C.; Sauer, N.; Stadler, R. *STP10* encodes a high-affinity monosaccharide transporter and is induced under low-glucose conditions in pollen tubes of *Arabidopsis*. *J. Exp. Bot.* **2016**, *67*, 2387–2399. [[CrossRef](#)] [[PubMed](#)]
91. Strahl, B.D.; Allis, C.D. The language of covalent histone modifications. *Nature* **2000**, *403*, 41–45. [[CrossRef](#)] [[PubMed](#)]
92. Lu, C.; Thompson, C.B. Metabolic regulation of epigenetics. *Cell Metab.* **2012**, *16*, 9–17. [[CrossRef](#)] [[PubMed](#)]
93. Bordoli, L.; Netsch, M.; Lüthi, U.; Lutz, W.; Eckner, R. Plant orthologs of p300/CBP: Conservation of a core domain in metazoan p300/CBP acetyltransferase-related proteins. *Nucleic Acids Res.* **2001**, *29*, 589–597. [[CrossRef](#)] [[PubMed](#)]
94. Pandey, R.; MuÈller, A.; Napoli, C.A.; Selinger, D.A.; Pikaard, C.S.; Richards, E.J.; Bender, J.; Mount, D.; Jorgensen, R.A. Analysis of histone acetyltransferase and histone deacetylase families of *Arabidopsis thaliana* suggests functional diversification of chromatin modification among multicellular eukaryotes. *Nucleic Acids Res.* **2002**, *30*, 5036–5055. [[CrossRef](#)] [[PubMed](#)]



95. Bharti, K.; von Koskull-Döring, P.; Bharti, S.; Kumar, P.; Tintschl-Körbitzer, A.; Treuter, E.; Nover, L. Tomato heat stress transcription factor HsfB1 represents a novel type of general transcription coactivator with a histone-like motif interacting with the plant CREB binding protein ortholog HAC1. *Plant Cell* **2004**, *16*, 1521–1535. [[CrossRef](#)] [[PubMed](#)]
96. Heisel, T.J.; Li, C.Y.; Grey, K.M.; Gibson, S.I. Mutations in HISTONE ACETYLTRANSFERASE1 affect sugar response and gene expression in *Arabidopsis*. *Front. Plant Sci.* **2013**, *4*, 245. [[CrossRef](#)] [[PubMed](#)]
97. Deng, W.; Liu, C.; Pei, Y.; Deng, X.; Niu, L.; Cao, X. Involvement of the histone acetyltransferase AtHAC1 in the regulation of flowering time via repression of FLOWERING LOCUS C in *Arabidopsis*. *Plant Physiol.* **2007**, *143*, 1660–1668. [[CrossRef](#)] [[PubMed](#)]
98. Han, S.K.; Song, J.D.; Noh, Y.S.; Noh, B. Role of plant CBP/p300-like genes in the regulation of flowering time. *Plant J.* **2007**, *49*, 103–114. [[CrossRef](#)] [[PubMed](#)]
99. Corbesier, L.; Lejeune, P.; Bernier, G. The role of carbohydrates in the induction of flowering in *Arabidopsis thaliana*: Comparison between the wild type and a starchless mutant. *Planta* **1998**, *206*, 131–137. [[CrossRef](#)] [[PubMed](#)]
100. Gibson, S.I. Control of plant development and gene expression by sugar signaling. *Curr. Opin. Plant Biol.* **2005**, *8*, 93–102. [[CrossRef](#)] [[PubMed](#)]
101. Xing, L.B.; Zhang, D.; Li, Y.M.; Shen, Y.W.; Zhao, C.P.; Ma, J.J.; An, N.; Han, M.Y. Transcription profiles reveal sugar and hormone signaling pathways mediating flower induction in apple (*Malus domestica* Borkh.). *Plant Cell Physiol.* **2015**, *56*, 2052–2068. [[CrossRef](#)] [[PubMed](#)]
102. Wolters, H.; Jürgens, G. Survival of the flexible: Hormonal growth control and adaptation in plant development. *Nat. Rev. Genet.* **2009**, *10*, 305–317. [[CrossRef](#)] [[PubMed](#)]
103. Lynch, T.J.; Erickson, B.J.; Miller, D.R.; Finkelstein, R.R. ABI5-binding proteins (ABFs) alter transcription of ABA-induced genes via a variety of interactions with chromatin modifiers. *Plant Mol. Biol.* **2017**, *93*, 403–418. [[CrossRef](#)] [[PubMed](#)]
104. Fujiki, R.; Hashiba, W.; Sekine, H.; Yokoyama, A.; Chikanishi, T.; Ito, S.; Imai, Y.; Kim, J.; He, H.H.; Igarashi, K.; et al. GlcNAcylation of histone H2B facilitates its monoubiquitination. *Nature* **2011**, *480*, 557–560. [[CrossRef](#)] [[PubMed](#)]
105. Wellen, K.E.; Hatzivassiliou, G.; Sachdeva, U.M.; Bui, T.V.; Cross, J.R.; Thompson, C.B. ATP-citrate lyase links cellular metabolism to histone acetylation. *Science* **2009**, *324*, 1076–1080. [[CrossRef](#)] [[PubMed](#)]
106. Dehennaut, V.; Leprince, D.; Lefebvre, T. O-GlcNAcylation, an epigenetic mark. Focus on the histone code, TET family proteins, and polycomb group proteins. *Front. Endocrinol.* **2014**, *5*, 155. [[CrossRef](#)] [[PubMed](#)]
107. Wu, D.; Cai, Y.; Jin, J. Potential coordination role between O-GlcNAcylation and epigenetics. *Protein Cell* **2017**, *8*, 713–723. [[CrossRef](#)] [[PubMed](#)]
108. Gambetta, M.C.; Oktaba, K.; Müller, J. Essential role of the glycosyltransferase *sxc/Ogt* in polycomb repression. *Science* **2009**, *325*, 93–96. [[CrossRef](#)] [[PubMed](#)]
109. Sinclair, D.A.; Syrzycka, M.; Macauley, M.S.; Rastgardani, T.; Komljenovic, I.; Vocadlo, D.J.; Brock, H.W.; Honda, B.M. Drosophila O-GlcNAc transferase (OGT) is encoded by the Polycomb group (PcG) gene, super sex combs (*sxc*). *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 13427–13432. [[CrossRef](#)] [[PubMed](#)]
110. Sarnowska, E.A.; Rolicka, A.T.; Bucior, E.; Cwiek, P.; Tohge, T.; Fernie, A.R.; Jikumaru, Y.; Kamiya, Y.; Franzen, R.; Schmelzer, E.; et al. DELLA-interacting SWI3C core subunit of SWI/SNF chromatin remodeling complex modulates gibberellin responses and hormonal crosstalk in *Arabidopsis*. *Plant Physiol.* **2013**, *163*, 305–317. [[CrossRef](#)] [[PubMed](#)]
111. Sarnowska, E.; Gratkowska, D.M.; Sacharowski, S.P.; Cwiek, P.; Tohge, T.; Fernie, A.R.; Siedlecki, J.A.; Koncz, C.; Sarnowski, T.J. The role of SWI/SNF chromatin remodeling complexes in hormone crosstalk. *Trends Plant Sci.* **2016**, *21*, 594–608. [[CrossRef](#)] [[PubMed](#)]
112. Bläsing, O.E.; Gibon, Y.; Günther, M.; Höhne, M.; Morcuende, R.; Osuna, D.; Thimm, O.; Usadel, B.; Scheible, R.; Stitt, M. Sugars and circadian regulation make major contributions to the global regulation of diurnal gene expression in *Arabidopsis*. *Plant Cell* **2005**, *17*, 3257–3281. [[CrossRef](#)] [[PubMed](#)]
113. Lu, C.A.; Lim, E.K.; Yu, S.M. Sugar response sequence in the promoter of a rice  $\alpha$ -amylase gene serves as a transcriptional enhancer. *J. Biol. Chem.* **1998**, *273*, 10120–10131. [[CrossRef](#)] [[PubMed](#)]
114. Chen, W.; Provart, N.J.; Glazebrook, J.; Katagiri, F.; Chang, H.S.; Eulgem, T.; Mauch, F.; Luan, S.; Zou, G.; Whitham, S.A.; et al. Expression profile matrix of *Arabidopsis* transcription factor genes suggests their putative functions in response to environmental stresses. *Plant Cell* **2002**, *14*, 559–574. [[CrossRef](#)] [[PubMed](#)]

115. Hwang, Y.S.; Karrer, E.E.; Thomas, B.R.; Chen, L.; Rodriguez, R.L. Three cis-elements required for rice  $\alpha$ -amylase *Amy3D* expression during sugar starvation. *Plant Mol. Biol.* **1998**, *36*, 331–341. [[CrossRef](#)] [[PubMed](#)]
116. Ishiguro, S.; Nakamura, K. The nuclear factor SP8BF binds to the 5'-upstream regions of three different genes coding for major proteins of sweet potato tuberous roots. *Plant Mol. Biol.* **1992**, *18*, 97–108. [[CrossRef](#)] [[PubMed](#)]
117. Grierson, C.; Du, J.S.; De Torres Zabala, M.; Beggs, K.; Smith, C.; Holdsworth, M.; Bevan, M. Separate cis sequences and trans factors direct metabolic and developmental regulation of a potato tuber storage protein gene. *Plant J.* **1994**, *5*, 815–826. [[CrossRef](#)] [[PubMed](#)]
118. Maeo, K.; Tomiya, T.; Hayashi, K.; Akaike, M.; Morikami, A.; Ishiguro, S.; Nakamura, K. Sugar-responsible elements in the promoter of a gene for  $\beta$ -amylase of sweet potato. *Plant Mol. Biol.* **2001**, *46*, 627–637. [[CrossRef](#)] [[PubMed](#)]
119. Zourelidou, M.; De Torres-Zabala, M.; Smith, C.; Bevan, M.W. Storekeeper defines a new class of plant-specific DNA-binding proteins and is a putative regulator of patatin expression. *Plant J.* **2002**, *30*, 489–497. [[CrossRef](#)] [[PubMed](#)]
120. Ishiguro, S.; Nakamura, K. Characterization of a cDNA encoding a novel DNA-binding protein, SPF1, that recognizes SP8 sequences in the 5' upstream regions of genes coding for sporamin and  $\beta$ -amylase from sweet potato. *Mol. Gen. Genet.* **1994**, *244*, 563–571. [[CrossRef](#)] [[PubMed](#)]
121. Acevedo-Hernández, G.J.; León, P.; Herrera-Estrella, L.R. Sugar and ABA responsiveness of a minimal RBCS light-responsive unit is mediated by direct binding of ABI4. *Plant J.* **2005**, *43*, 506–519. [[CrossRef](#)] [[PubMed](#)]
122. Arenas-Huertero, F.; Arroyo, A.; Zhou, L.; Sheen, J.; Leon, P. Analysis of *Arabidopsis* glucose insensitive mutants, *gin5* and *gin6*, reveals a central role of the plant hormone ABA in the regulation of plant vegetative development by sugar. *Genes Dev.* **2000**, *14*, 2085–2096. [[PubMed](#)]
123. Lu, C.A.; Ho, T.H.D.; Ho, S.L.; Yu, S.M. Three novel MYB proteins with one DNA binding repeat mediate sugar and hormone regulation of  $\alpha$ -amylase gene expression. *Plant Cell* **2002**, *14*, 1963–1980. [[CrossRef](#)] [[PubMed](#)]
124. Sun, C.; Palmqvist, S.; Olsson, H.; Borén, M.; Ahlandsberg, S.; Jansson, C. A novel WRKY transcription factor, SUSIBA2, participates in sugar signaling in barley by binding to the sugar-responsive elements of the *iso1* promoter. *Plant Cell* **2003**, *15*, 2076–2092. [[CrossRef](#)] [[PubMed](#)]
125. Kang, S.G.; Price, J.; Lin, P.C.; Hong, J.C.; Jang, J.C. The *Arabidopsis* bZIP1 transcription factor is involved in sugar signaling, protein networking, and DNA binding. *Mol. Plant* **2010**, *3*, 361–373. [[CrossRef](#)] [[PubMed](#)]
126. Eulgem, T.; Rushton, P.J.; Robatzek, S.; Somssich, I.E. The WRKY superfamily of plant transcription factors. *Trends Plant Sci.* **2000**, *5*, 199–206. [[CrossRef](#)]
127. Su, J.; Hu, C.; Yan, X.; Jin, Y.; Chen, Z.; Guan, Q.; Wang, Y.; Zhong, D.; Jansson, C.; Wang, F.; et al. Expression of barley SUSIBA2 transcription factor yields high-starch low-methane rice. *Nature* **2015**, *523*, 602–606. [[CrossRef](#)] [[PubMed](#)]
128. Jin, Y.; Fei, M.; Rosenquist, S.; Jin, L.; Gohil, S.; Sandström, C.; Olsson, H.; Persson, C.; Höglund, A.; Fransson, G.; et al. A dual-promoter gene orchestrates the sucrose-coordinated synthesis of starch and fructan in barley. *Mol. Plant* **2017**, *10*, 1556–1570. [[CrossRef](#)] [[PubMed](#)]
129. Izawa, T.; Foster, R.; Chua, N.H. Plant bZIP protein DNA binding specificity. *J. Mol. Biol.* **1993**, *230*, 1131–1144. [[CrossRef](#)] [[PubMed](#)]
130. Jakoby, M.; Weisshaar, B.; Dröge-Laser, W.; Vicente-Carbajosa, J.; Tiedemann, J.; Kroj, T.; Parcy, F. bZIP transcription factors in *Arabidopsis*. *Trends Plant Sci.* **2002**, *7*, 106–111. [[CrossRef](#)]
131. Kim, S.Y. The role of ABF family bZIP class transcription factors in stress response. *Physiol. Plant.* **2006**, *126*, 519–527. [[CrossRef](#)]
132. Alves, M.S.; Dadalto, S.P.; Gonçalves, A.B.; De Souza, G.B.; Barros, V.A.; Fietto, L.G. Plant bZIP transcription factors responsive to pathogens: A review. *Int. J. Mol. Sci.* **2013**, *14*, 7815–7828. [[CrossRef](#)] [[PubMed](#)]
133. Lockhart, J. Frenemies: Antagonistic bHLH/bZIP transcription factors integrate light and reactive oxygen species signaling in *Arabidopsis*. *Plant Cell* **2013**. [[CrossRef](#)] [[PubMed](#)]
134. Sun, L.; Yang, Z.T.; Song, Z.T.; Wang, M.J.; Sun, L.; Lu, S.J.; Liu, J.X. The plant-specific transcription factor gene *NAC103* is induced by bZIP60 through a new cis-regulatory element to modulate the unfolded protein response in *Arabidopsis*. *Plant J.* **2013**, *76*, 274–286. [[PubMed](#)]

135. Cookson, S.J.; Yadav, U.P.; Klie, S.; Morcuende, R.; Usadel, B.; Lunn, J.E.; Stitt, M. Temporal kinetics of the transcriptional response to carbon depletion and sucrose readdition in *Arabidopsis* seedlings. *Plant Cell Environ.* **2016**, *39*, 768–786. [[CrossRef](#)] [[PubMed](#)]
136. Dash, M.; Yordanov, Y.S.; Georgieva, T.; Tschaplinski, T.J.; Yordanova, E.; Busov, V. Poplar *PtabZIP1-like* enhances lateral root formation and biomass growth under drought stress. *Plant J.* **2017**, *89*, 692–705. [[CrossRef](#)] [[PubMed](#)]
137. Dietrich, K.; Weltmeier, F.; Ehlert, A.; Weiste, C.; Stahl, M.; Harter, K.; Dröge-Laser, W. Heterodimers of the *Arabidopsis* transcription factors bZIP1 and bZIP53 reprogram amino acid metabolism during low energy stress. *Plant Cell* **2011**. [[CrossRef](#)] [[PubMed](#)]
138. Para, A.; Li, Y.; Marshall-Colón, A.; Varala, K.; Francoeur, N.J.; Moran, T.M.; Edwards, M.B.; Hackley, C.; Bargmann, B.O.; Birnbaum, K.D.; et al. Hit-and-run transcriptional control by bZIP1 mediates rapid nutrient signaling in *Arabidopsis*. *Proc. Natl. Acad. Sci. USA* **2014**. [[CrossRef](#)] [[PubMed](#)]
139. Kranz, H.D.; Denekamp, M.; Greco, R.; Jin, H.; Leyva, A.; Meissner, R.C.; Petroni, K.; Urzainqui, A.; Bevan, M.; Martin, C.; et al. Towards functional characterisation of the members of the R2R3-MYB gene family from *Arabidopsis thaliana*. *Plant J.* **1998**, *16*, 263–276. [[CrossRef](#)] [[PubMed](#)]
140. Borevitz, J.O.; Xia, Y.; Blount, J.; Dixon, R.A.; Lamb, C. Activation tagging identifies a conserved MYB regulator of phenylpropanoid biosynthesis. *Plant Cell* **2000**, *12*, 2383–2393. [[CrossRef](#)] [[PubMed](#)]
141. Tohge, T.; Nishiyama, Y.; Hirai, M.Y.; Yano, M.; Nakajima, J.I.; Awazuhara, M.; Inoue, E.; Takahashi, H.; Goodenowe, D.B.; Kitayama, M.; et al. Functional genomics by integrated analysis of metabolome and transcriptome of *Arabidopsis* plants over-expressing an MYB transcription factor. *Plant J.* **2005**, *42*, 218–235. [[CrossRef](#)] [[PubMed](#)]
142. Chen, Y.S.; Chao, Y.C.; Tseng, T.W.; Huang, C.K.; Lo, P.C.; Lu, C.A. Two MYB-related transcription factors play opposite roles in sugar signaling in *Arabidopsis*. *Plant Mol. Biol.* **2017**, *93*, 299–311. [[CrossRef](#)] [[PubMed](#)]
143. Wang, M.; Ogé, L.; Perez-Garcia, M.D.; Hamama, L.; Sakr, S. The PUF Protein Family: Overview on PUF RNA targets, biological functions, and post transcriptional regulation. *Int. J. Mol. Sci.* **2018**, *19*, 410. [[CrossRef](#)] [[PubMed](#)]
144. Ho, S.L.; Chao, Y.C.; Tong, W.F.; Yu, S.M. Sugar coordinately and differentially regulates growth-and stress-related gene expression via a complex signal transduction network and multiple control mechanisms. *Plant Physiol.* **2001**, *125*, 877–890. [[CrossRef](#)] [[PubMed](#)]
145. Nicolai, M.; Roncato, M.A.; Canoy, A.S.; Rouquie, D.; Sarda, X.; Freyssinet, G.; Robaglia, C. Large-scale analysis of mRNA translation states during sucrose starvation in *Arabidopsis* cells identifies cell proliferation and chromatin structure as targets of translational control. *Plant Physiol.* **2006**, *141*, 663–673. [[CrossRef](#)] [[PubMed](#)]
146. Sheu, J.J.; Jan, S.P.; Lee, H.T.; Yu, S.M. Control of transcription and mRNA turnover as mechanisms of metabolic repression of  $\alpha$ -amylase gene expression. *Plant J.* **1994**, *5*, 655–664. [[CrossRef](#)]
147. Chan, M.T.; Yu, S.M. The 3' untranslated region of a rice  $\alpha$ -amylase gene functions as a sugar-dependent mRNA stability determinant. *Proc. Natl. Acad. Sci. USA* **1998**, *95*, 6543–6547. [[CrossRef](#)] [[PubMed](#)]
148. Chan, M.T.; Yu, S.M. The 3' untranslated region of a rice  $\alpha$ -amylase gene mediates sugar-dependent abundance of mRNA. *Plant J.* **1998**, *15*, 685–695. [[CrossRef](#)] [[PubMed](#)]
149. Yoine, M.; Ohto, M.A.; Onai, K.; Mita, S.; Nakamura, K. The lba1 mutation of UPF1 RNA helicase involved in nonsense-mediated mRNA decay causes pleiotropic phenotypic changes and altered sugar signalling in *Arabidopsis*. *Plant J.* **2006**, *47*, 49–62. [[CrossRef](#)] [[PubMed](#)]
150. Mita, S.; Murano, N.; Akaike, M.; Nakamura, K. Mutants of *Arabidopsis thaliana* with pleiotropic effects on the expression of the gene for  $\beta$ -amylase and on the accumulation of anthocyanin that are inducible by sugars. *Plant J.* **1997**, *11*, 841–851. [[CrossRef](#)] [[PubMed](#)]
151. Pomeranz, M.C.; Hah, C.; Lin, P.C.; Kang, S.G.; Finer, J.J.; Blackshear, P.J.; Jang, J.C. The *Arabidopsis* tandem zinc finger protein AtTZF1 traffics between the nucleus and cytoplasmic foci and binds both DNA and RNA. *Plant Physiol.* **2010**, *152*, 151–165. [[CrossRef](#)] [[PubMed](#)]
152. Bogamuwa, S.P.; Jang, J.C. Tandem CCCH zinc finger proteins in plant growth, development and stress response. *Plant Cell Physiol.* **2014**, *55*, 1367–1375. [[CrossRef](#)] [[PubMed](#)]
153. Barrera-Figueroa, B.E.; Gao, L.; Wu, Z.; Zhou, X.; Zhu, J.; Jin, H.; Liu, L.; Zhu, J.K. High throughput sequencing reveals novel and abiotic stress-regulated microRNAs in the inflorescences of rice. *BMC Plant Biol.* **2012**, *12*, 132. [[CrossRef](#)] [[PubMed](#)]

154. Yang, L.; Xu, M.; Koo, Y.; He, J.; Poethig, R.S. Sugar promotes vegetative phase change in *Arabidopsis thaliana* by repressing the expression of *MIR156A* and *MIR156C*. *eLife* **2013**, *2*, e00260. [[CrossRef](#)] [[PubMed](#)]
155. Yu, S.; Cao, L.; Zhou, C.M.; Zhang, T.Q.; Lian, H.; Sun, Y.; Wu, J.; Huang, J.; Wang, G.; Wang, J.W. Sugar is an endogenous cue for juvenile-to-adult phase transition in plants. *eLife* **2013**, *2*, e00269. [[CrossRef](#)] [[PubMed](#)]
156. Yamaguchi, A.; Wu, M.F.; Yang, L.; Wu, G.; Poethig, R.S.; Wagner, D. The microRNA-regulated SBP-Box transcription factor SPL3 is a direct upstream activator of *LEAFY*, *FRUITFULL*, and *APETALA1*. *Dev. Cell* **2009**, *17*, 268–278. [[CrossRef](#)] [[PubMed](#)]
157. Wahl, V.; Ponnu, J.; Schlereth, A.; Arrivault, S.; Langenecker, T.; Franke, A.; Feil, R.; Lunn, J.E.; Stitt, M.; Schmid, M. Regulation of flowering by trehalose-6-phosphate signaling in *Arabidopsis thaliana*. *Science* **2013**, *339*, 704–707. [[CrossRef](#)] [[PubMed](#)]
158. Buendía-Monreal, M.; Gillmor, C.S. Convergent repression of miR156 by sugar and the CDK8 module of *Arabidopsis* mediator. *Dev. Biol.* **2017**, *423*, 19–23. [[CrossRef](#)] [[PubMed](#)]
159. Churbanov, A.; Rogozin, I.B.; Babenko, V.N.; Ali, H.; Koonin, E.V. Evolutionary conservation suggests a regulatory function of AUG triplets in 5'-UTRs of eukaryotic genes. *Nucleic Acids Res.* **2005**, *33*, 5512–5520. [[CrossRef](#)] [[PubMed](#)]
160. Von Arnim, A.G.; Jia, Q.; Vaughn, J.N. Regulation of plant translation by upstream open reading frames. *Plant Sci.* **2014**, *214*, 1–12. [[CrossRef](#)] [[PubMed](#)]
161. Wethmar, K. The regulatory potential of upstream open reading frames in eukaryotic gene expression. *Wiley Interdiscip. Rev. RNA* **2014**, *5*, 765–768. [[CrossRef](#)] [[PubMed](#)]
162. Hanson, J.; Hanssen, M.; Wiese, A.; Hendriks, M.M.; Smeekens, S. The sucrose regulated transcription factor bZIP11 affects amino acid metabolism by regulating the expression of *ASPARAGINE SYNTHETASE1* and *PROLINE DEHYDROGENASE2*. *Plant J.* **2008**, *53*, 935–949. [[CrossRef](#)] [[PubMed](#)]
163. Ma, J.; Hanssen, M.; Lundgren, K.; Hernández, L.; Delatte, T.; Ehlert, A.; Liu, C.M.; Schluempmann, H.; Dröge-Laser, W.; Moritz, T.; et al. The sucrose-regulated *Arabidopsis* transcription factor bZIP11 reprograms metabolism and regulates trehalose metabolism. *New Phytol.* **2011**, *191*, 733–745. [[CrossRef](#)] [[PubMed](#)]
164. Juntawong, P.; Girke, T.; Bazin, J.; Bailey-Serres, J. Translational dynamics revealed by genome-wide profiling of ribosome footprints in *Arabidopsis*. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, E203–E212. [[CrossRef](#)] [[PubMed](#)]
165. Weiste, C.; Pedrotti, L.; Selvanayagam, J.; Muralidhara, P.; Fröschel, C.; Novák, O.; Ljung, K.; Hanson, J.; Dröge-Laser, W. The *Arabidopsis* bZIP11 transcription factor links low-energy signalling to auxin-mediated control of primary root growth. *PLoS Genet.* **2017**, *13*, e1006607. [[CrossRef](#)] [[PubMed](#)]
166. Thum, K.E.; Shin, M.J.; Palenchar, P.M.; Kouranov, A.; Coruzzi, G.M. Genome-wide investigation of light and carbon signaling interactions in *Arabidopsis*. *Genome Biol.* **2004**, *5*, R10. [[CrossRef](#)] [[PubMed](#)]
167. Rahmani, F.; Hummel, M.; Schuurmans, J.; Wiese-Klinkenberg, A.; Smeekens, S.; Hanson, J. Sucrose control of translation mediated by an upstream open reading frame-encoded peptide. *Plant Physiol.* **2009**, *150*, 1356–1367. [[CrossRef](#)] [[PubMed](#)]
168. Wiese, A.; Elzinga, N.; Wobbes, B.; Smeekens, S. A conserved upstream open reading frame mediates sucrose-induced repression of translation. *Plant Cell* **2004**, *16*, 1717–1729. [[CrossRef](#)] [[PubMed](#)]
169. Wiese, A.; Elzinga, N.; Wobbes, B.; Smeekens, S. Sucrose-induced translational repression of plant bZIP-type transcription factors. *Biochem. Soc. Trans.* **2005**, *33*, 272–275. [[CrossRef](#)] [[PubMed](#)]
170. Hummel, M.; Rahmani, F.; Smeekens, S.; Hanson, J. Sucrose-mediated translational control. *Ann. Bot.* **2009**, *104*, 1–7. [[CrossRef](#)] [[PubMed](#)]
171. Weltmeier, F.; Rahmani, F.; Ehlert, A.; Dietrich, K.; Schütze, K.; Wang, X.; Chaban, C.; Hanson, J.; Teige, M.; Harter, K.; et al. Expression patterns within the *Arabidopsis* C/S1 bZIP transcription factor network: Availability of heterodimerization partners controls gene expression during stress response and development. *Plant Mol. Biol.* **2009**, *69*, 107–119. [[CrossRef](#)] [[PubMed](#)]
172. Yamashita, Y.; Takamatsu, S.; Glasbrenner, M.; Becker, T.; Naito, S.; Beckmann, R. Sucrose sensing through nascent peptide-mediated ribosome stalling at the stop codon of *Arabidopsis* bZIP11 uORF2. *FEBS Lett.* **2017**, *591*, 1266–1277. [[CrossRef](#)] [[PubMed](#)]
173. Cheng, W.H.; Taliercio, E.W.; Chourey, P.S. Sugars modulate an unusual mode of control of the cell-wall invertase gene (*Incw1*) through its 3' untranslated region in a cell suspension culture of maize. *Proc. Natl. Acad. Sci. USA* **1999**, *96*, 10512–10517. [[CrossRef](#)] [[PubMed](#)]
174. Camoni, L.; Visconti, S.; Aducci, P.; Marra, M. 14-3-3 proteins in plant hormone signaling: Doing several things at once. *Front. Plant Sci.* **2018**, *9*, 297. [[CrossRef](#)] [[PubMed](#)]



175. Moorhead, G.; Douglas, P.; Cotelle, V.; Harthill, J.; Morrice, N.; Meek, S.; Deiting, U.; Stitt, M.; Scarabel, M.; Aitken, A.; et al. Phosphorylation-dependent interactions between enzymes of plant metabolism and 14-3-3 proteins. *Plant J.* **1999**, *18*, 1–12. [[CrossRef](#)] [[PubMed](#)]
176. Okumura, M.; Inoue, S.I.; Kuwata, K.; Kinoshita, T. Photosynthesis activates plasma membrane H<sup>+</sup>-ATPase via sugar accumulation in *Arabidopsis* leaves. *Plant Physiol.* **2016**. [[CrossRef](#)] [[PubMed](#)]
177. Fuglsang, A.T.; Visconti, S.; Drumm, K.; Jahn, T.; Stensballe, A.; Mattei, B.; Jensen, O.N.; Aducci, P.; Palmgren, M.G. Binding of 14-3-3 protein to the plasma membrane H<sup>+</sup>-ATPase AHA2 involves the three C-terminal residues Tyr946-Thr-Val and requires phosphorylation of Thr947. *J. Biol. Chem.* **1999**, *274*, 36774–36780. [[CrossRef](#)] [[PubMed](#)]
178. Lemoine, R.; La Camera, S.; Atanassova, R.; Dédaldéchamp, F.; Allario, T.; Pourtau, N.; Bonnemain, J.L.; Laloi, M.; Coutos-Thévenot, P.; Maurousset, L.; et al. Source-to-sink transport of sugar and regulation by environmental factors. *Front. Plant Sci.* **2013**, *4*, 272. [[CrossRef](#)] [[PubMed](#)]
179. Wang, L.; Ruan, Y.L. Regulation of cell division and expansion by sugar and auxin signaling. *Front. Plant Sci.* **2013**, *4*, 163. [[CrossRef](#)] [[PubMed](#)]
180. Saripalli, G.; Gupta, P.K. AGPase: Its role in crop productivity with emphasis on heat tolerance in cereals. *Theor. Appl. Genet.* **2015**, *128*, 1893–1916. [[CrossRef](#)] [[PubMed](#)]
181. Preiss, J. Biosynthesis of starch and its regulation. *Biochem. Plants* **1988**, *14*, 181–254.
182. Hendriks, J.H.; Kolbe, A.; Gibon, Y.; Stitt, M.; Geigenberger, P. ADP-glucose pyrophosphorylase is activated by posttranslational redox-modification in response to light and to sugars in leaves of *Arabidopsis* and other plant species. *Plant Physiol.* **2003**, *133*, 838–849. [[CrossRef](#)] [[PubMed](#)]
183. Tiessen, A.; Prescha, K.; Branscheid, A.; Palacios, N.; McKibbin, R.; Halford, N.G.; Geigenberger, P. Evidence that SNF1-related kinase and hexokinase are involved in separate sugar-signalling pathways modulating post-translational redox activation of ADP-glucose pyrophosphorylase in potato tubers. *Plant J.* **2003**, *35*, 490–500. [[CrossRef](#)] [[PubMed](#)]
184. Gibson, S.I. Sugar and phytohormone response pathways: Navigating a signalling network. *J. Exp. Bot.* **2004**, *55*, 253–264. [[CrossRef](#)] [[PubMed](#)]
185. Geigenberger, P.; Kolbe, A.; Tiessen, A. Redox regulation of carbon storage and partitioning in response to light and sugars. *J. Exp. Bot.* **2005**, *56*, 1469–1479. [[CrossRef](#)] [[PubMed](#)]
186. Kolbe, A.; Tiessen, A.; Schluempmann, H.; Paul, M.; Ulrich, S.; Geigenberger, P. Trehalose 6-phosphate regulates starch synthesis via posttranslational redox activation of ADP-glucose pyrophosphorylase. *Proc. Natl. Acad. Sci. USA* **2005**, *102*, 11118–11123. [[CrossRef](#)] [[PubMed](#)]
187. Lunn, J.E.; Feil, R.; Hendriks, J.H.; Gibon, Y.; Morcuende, R.; Osuna, D.; Scheible, W.; Carillo, P.; Hajirezaei, M.R.; Stitt, M. Sugar-induced increases in trehalose 6-phosphate are correlated with redox activation of ADPglucose pyrophosphorylase and higher rates of starch synthesis in *Arabidopsis thaliana*. *Biochem. J.* **2006**, *397*, 139–148. [[CrossRef](#)] [[PubMed](#)]
188. Olatunji, D.; Geelen, D.; Verstraeten, I. Control of endogenous auxin levels in plant root development. *Int. J. Mol. Sci.* **2017**, *18*, 2587. [[CrossRef](#)] [[PubMed](#)]
189. Majda, M.; Robert, S. The role of auxin in cell wall expansion. *Int. J. Mol. Sci.* **2018**, *19*, 951. [[CrossRef](#)] [[PubMed](#)]
190. Tian, H.; Lv, B.; Ding, T.; Bai, M.; Ding, Z. Auxin-BR interaction regulates plant growth and development. *Front. Plant Sci.* **2018**, *8*, 2256. [[CrossRef](#)] [[PubMed](#)]
191. LeClere, S.; Schmelz, E.A.; Chourey, P.S. Sugar levels regulate tryptophan-dependent auxin biosynthesis in developing maize kernels. *Plant Physiol.* **2010**, *153*, 306–318. [[CrossRef](#)] [[PubMed](#)]
192. Sagar, M.; Chervin, C.; Mila, I.; Hao, Y.; Roustan, J.P.; Benichou, M.; Gibon, Y.; Biaies, B.; Maury, P.; Latche, A.; et al. SIARF4, an auxin response factor involved in the control of sugar metabolism during tomato fruit development. *Plant Physiol.* **2013**, *161*, 1362–1374. [[CrossRef](#)] [[PubMed](#)]
193. Barbier, F.; Péron, T.; Lecerf, M.; Perez-Garcia, M.D.; Barrière, Q.; Rolčik, J.; Boutet-Mercey, S.; Citerne, S.; Lemoine, R.; Porcheron, B.; et al. Sucrose is an early modulator of the key hormonal mechanisms controlling bud outgrowth in *Rosa hybrida*. *J. Exp. Bot.* **2015**, *66*, 2569–2582. [[CrossRef](#)] [[PubMed](#)]
194. Long, J.C.; Zhao, W.; Rashotte, A.M.; Muday, G.K.; Huber, S.C. Gravity-stimulated changes in auxin and invertase gene expression in maize pulvinal cells. *Plant Physiol.* **2002**, *128*, 591–602. [[CrossRef](#)] [[PubMed](#)]
195. Stewart, J.L.; Maloof, J.N.; Nemhauser, J.L. PIF genes mediate the effect of sucrose on seedling growth dynamics. *PLoS ONE* **2011**, *6*, e19894. [[CrossRef](#)] [[PubMed](#)]



196. Sairanen, I.; Novák, O.; Pěňčík, A.; Ikeda, Y.; Jones, B.; Sandberg, G.; Ljung, K. Soluble carbohydrates regulate auxin biosynthesis via PIF proteins in *Arabidopsis*. *Plant Cell* **2012**. [[CrossRef](#)] [[PubMed](#)]
197. Lilley, J.L.; Gee, C.W.; Sairanen, I.; Ljung, K.; Nemhauser, J.L. An endogenous carbon-sensing pathway triggers increased auxin flux and hypocotyl elongation. *Plant Physiol.* **2012**. [[CrossRef](#)] [[PubMed](#)]
198. Gonzali, S.; Novi, G.; Loreti, E.; Paolicchi, F.; Poggi, A.; Alpi, A.; Perata, P. A turanose-insensitive mutant suggests a role for WOX5 in auxin homeostasis in *Arabidopsis thaliana*. *Plant J.* **2005**, *44*, 633–645. [[CrossRef](#)] [[PubMed](#)]
199. Ohto, M.A.; Hayashi, S.; Sawa, S.; Hashimoto-Ohta, A.; Nakamura, K. Involvement of HLS1 in sugar and auxin signaling in *Arabidopsis* leaves. *Plant Cell Physiol.* **2006**, *47*, 1603–1611. [[CrossRef](#)] [[PubMed](#)]
200. Mishra, B.S.; Singh, M.; Aggrawal, P.; Laxmi, A. Glucose and auxin signaling interaction in controlling *Arabidopsis thaliana* seedlings root growth and development. *PLoS ONE* **2009**, *4*, e4502. [[CrossRef](#)] [[PubMed](#)]
201. Lin, X.Y.; Ye, Y.Q.; Fan, S.K.; Jin, C.W.; Zheng, S.J. Increased sucrose accumulation regulates iron-deficiency responses by promoting auxin signaling in *Arabidopsis* plants. *Plant Physiol.* **2016**, *170*, 907–920. [[CrossRef](#)] [[PubMed](#)]
202. Altman, A.; Wareing, P.F. The Effect of IAA on Sugar Accumulation and Basipetal Transport of <sup>14</sup>C-labelled Assimilates in Relation to Root Formation in *Phaseolus vulgaris* Cuttings. *Physiol. Plant.* **1975**, *33*, 32–38. [[CrossRef](#)]
203. Eveland, A.L.; Jackson, D.P. Sugars, signalling, and plant development. *J. Exp. Bot.* **2011**, *63*, 3367–3377. [[CrossRef](#)] [[PubMed](#)]
204. Min, L.; Li, Y.; Hu, Q.; Zhu, L.; Gao, W.; Wu, Y.; Ding, Y.; Liu, S.; Yang, X.; Zhang, X.; et al. Sugar and auxin signaling pathways respond to high temperature stress during anther development as revealed by transcript profiling analysis in cotton. *Plant Physiol.* **2014**. [[CrossRef](#)] [[PubMed](#)]
205. Li, G.; Ma, J.; Tan, M.; Mao, J.; An, N.; Sha, G.; Zhang, D.; Zhao, C.; Han, M. Transcriptome analysis reveals the effects of sugar metabolism and auxin and cytokinin signaling pathways on root growth and development of grafted apple. *BMC Genom.* **2016**, *17*, 150. [[CrossRef](#)] [[PubMed](#)]
206. Moreno-Ortega, B.; Chandezon, E.; Fort, G.; Guédon, Y.; Muller, B.L. Why is lateral root growth so variable? A framework to analyze growth variability among lateral roots and the possible roles of auxin and carbon. In Proceedings of the 7th International Symposium on Root Development, Weimar, Germany, 15–19 September 2014.
207. Jain, A.; Poling, M.D.; Karthikeyan, A.S.; Blakeslee, J.J.; Peer, W.A.; Titapiwatanakun, B.; Murphy, A.S.; Raghothama, K.G. Differential effects of sucrose and auxin on localized phosphate deficiency-induced modulation of different traits of root system architecture in *Arabidopsis*. *Plant Physiol.* **2007**, *144*, 232–247. [[CrossRef](#)] [[PubMed](#)]
208. MacGregor, D.R.; Deak, K.I.; Ingram, P.A.; Malamy, J.E. Root system architecture in *Arabidopsis* grown in culture is regulated by sucrose uptake in the aerial tissues. *Plant Cell* **2008**, *20*, 2643–2660. [[CrossRef](#)] [[PubMed](#)]
209. Kircher, S.; Schopfer, P. Photosynthetic sucrose acts as cotyledon-derived long-distance signal to control root growth during early seedling development in *Arabidopsis*. *Proc. Natl. Acad. Sci. USA* **2012**, *109*, 11217–11221. [[CrossRef](#)] [[PubMed](#)]
210. Hartmann, L.; Pedrotti, L.; Weiste, C.; Fekete, A.; Schierstaedt, J.; Göttler, J.; Kempa, S.; Krischke, M.; Dietrich, K.; Mueller, M.J.; et al. Crosstalk between two bZIP signaling pathways orchestrates salt-induced metabolic reprogramming in *Arabidopsis* roots. *Plant Cell* **2015**. [[CrossRef](#)] [[PubMed](#)]
211. Mair, A.; Pedrotti, L.; Wurzinger, B.; Anrather, D.; Simeunovic, A.; Weiste, C.; Valerio, C.; Dietrich, K.; Kirchler, T.; Nagele, T.; et al. SnRK1-triggered switch of bZIP63 dimerization mediates the low-energy response in plants. *eLife* **2015**, *4*, e05828. [[CrossRef](#)] [[PubMed](#)]
212. Weiste, C.; Dröge-Laser, W. The *Arabidopsis* transcription factor bZIP11 activates auxin-mediated transcription by recruiting the histone acetylation machinery. *Nat. Commun.* **2014**, *5*, 3883. [[CrossRef](#)] [[PubMed](#)]
213. Yuan, T.T.; Xu, H.H.; Zhang, K.X.; Guo, T.T.; Lu, Y.T. Glucose inhibits root meristem growth via ABA INSENSITIVE 5, which represses PIN1 accumulation and auxin activity in *Arabidopsis*. *Plant Cell Environ.* **2014**, *37*, 1338–1350. [[CrossRef](#)] [[PubMed](#)]
214. Booker, K.S.; Schwarz, J.; Garrett, M.B.; Jones, A.M. Glucose attenuation of auxin-mediated bimodality in lateral root formation is partly coupled by the heterotrimeric G protein complex. *PLoS ONE* **2010**, *5*, e12833. [[CrossRef](#)] [[PubMed](#)]

215. Barrada, A.; Montané, M.H.; Robaglia, C.; Menand, B. Spatial regulation of root growth: Placing the plant TOR pathway in a developmental perspective. *Int. J. Mol. Sci.* **2015**, *16*, 19671–19697. [[CrossRef](#)] [[PubMed](#)]
216. Raya-González, J.; López-Bucio, J.S.; Prado-Rodríguez, J.C.; Ruiz-Herrera, L.F.; Guevara-García, Á.A.; López-Bucio, J. The MEDIATOR genes *MED12* and *MED13* control *Arabidopsis* root system configuration influencing sugar and auxin responses. *Plant Mol. Biol.* **2017**, *95*, 141–156. [[CrossRef](#)] [[PubMed](#)]
217. Malik, S.; Roeder, R.G. The metazoan Mediator co-activator complex as an integrative hub for transcriptional regulation. *Nat. Rev. Genet.* **2010**, *11*, 761. [[CrossRef](#)] [[PubMed](#)]
218. Franklin, K.A.; Lee, S.H.; Patel, D.; Kumar, S.V.; Spartz, A.K.; Gu, C.; Ye, S.; Yu, P.; Breen, G.; Cohen, J.D.; et al. Phytochrome-interacting factor 4 (PIF4) regulates auxin biosynthesis at high temperature. *Proc. Natl. Acad. Sci. USA* **2011**, *108*, 20231–20235. [[CrossRef](#)] [[PubMed](#)]
219. Kuiper, D. Sink strength: Established and regulated by plant growth regulators. *Plant Cell Environ.* **1993**, *16*, 1025–1026. [[CrossRef](#)]
220. Hirose, N.; Takei, K.; Kuroha, T.; Kamada-Nobusada, T.; Hayashi, H.; Sakakibara, H. Regulation of cytokinin biosynthesis, compartmentalization and translocation. *J. Exp. Bot.* **2007**, *59*, 75–83. [[CrossRef](#)] [[PubMed](#)]
221. Eviatar-Ribak, T.; Shalit-Kaneh, A.; Chappell-Maor, L.; Amsellem, Z.; Eshed, Y.; Lifschitz, E. A cytokinin-activating enzyme promotes tuber formation in tomato. *Curr. Biol.* **2013**, *23*, 1057–1064. [[CrossRef](#)] [[PubMed](#)]
222. Wang, G.; Zhang, G.; Wu, M. CLE peptide signaling and crosstalk with phytohormones and environmental stimuli. *Front. Plant Sci.* **2016**, *6*, 1211. [[CrossRef](#)] [[PubMed](#)]
223. Kieber, J.J.; Schaller, G.E. Cytokinin signaling in plant development. *Development* **2018**, *145*, dev149344. [[CrossRef](#)] [[PubMed](#)]
224. Lara, M.E.B.; Garcia, M.C.G.; Fatima, T.; Ehneß, R.; Lee, T.K.; Proels, R.; Tanner, T.; Roitsch, T. Extracellular invertase is an essential component of cytokinin-mediated delay of senescence. *Plant Cell* **2004**, *16*, 1276–1287. [[CrossRef](#)] [[PubMed](#)]
225. Werner, T.; Holst, K.; Pörs, Y.; Guivarch, A.; Muströph, A.; Chriqui, D.; Grimm, B.; Schmülling, T. Cytokinin deficiency causes distinct changes of sink and source parameters in tobacco shoots and roots. *J. Exp. Bot.* **2008**, *59*, 2659–2672. [[CrossRef](#)] [[PubMed](#)]
226. Lefebvre, R.; Vasseur, J.; Backoula, E.; Coullerot, J.P. Participation of carbohydrate metabolism in the organogenic orientation of *Chicorium intybus* tissues cultivated in vitro. *Can. J. Bot.* **1992**, *70*, 1897–1902. [[CrossRef](#)]
227. Reguera, M.; Peleg, Z.; Abdel-Tawab, Y.M.; Tumimbang, E.; Delatorre, C.A.; Blumwald, E. Stress-Induced CK Synthesis Increases Drought Tolerance through the Coordinated Regulation of Carbon and Nitrogen Assimilation in Rice. *Plant Physiol.* **2013**. [[CrossRef](#)] [[PubMed](#)]
228. Albacete, A.; Cantero-Navarro, E.; Balibrea, M.E.; Großkinsky, D.K.; de la Cruz González, M.; Martínez-Andújar, C.; Smigocki, A.C.; Roitsch, T.; Pérez-Alfocea, F. Hormonal and metabolic regulation of tomato fruit sink activity and yield under salinity. *J. Exp. Bot.* **2014**, *65*, 6081–6095. [[CrossRef](#)] [[PubMed](#)]
229. Kushwah, S.; Laxmi, A. The interaction between glucose and cytokinin signal transduction pathway in *Arabidopsis thaliana*. *Plant Cell Environ.* **2014**, *37*, 235–253. [[CrossRef](#)] [[PubMed](#)]
230. Rolland, F.; Baena-Gonzalez, E.; Sheen, J. Sugar sensing and signaling in plants: Conserved and novel mechanisms. *Annu. Rev. Plant Biol.* **2006**, *57*, 675–709. [[CrossRef](#)] [[PubMed](#)]
231. Franco-Zorrilla, J.M.; Martín, A.C.; Leyva, A.; Paz-Ares, J. Interaction between phosphate-starvation, sugar, and cytokinin signaling in *Arabidopsis* and the roles of cytokinin receptors CRE1/AHK4 and AHK3. *Plant Physiol.* **2005**, *138*, 847–857. [[CrossRef](#)] [[PubMed](#)]
232. Laxmi, A.; Paul, L.K.; Raychaudhuri, A.; Peters, J.L.; Khurana, J.P. *Arabidopsis* cytokinin-resistant mutant, *cnr1*, displays altered auxin responses and sugar sensitivity. *Plant Mol. Biol.* **2006**, *62*, 409–425. [[CrossRef](#)] [[PubMed](#)]
233. Sano, H.; Youssefian, S. Light and nutritional regulation of transcripts encoding a wheat protein kinase homolog is mediated by cytokinins. *Proc. Natl. Acad. Sci. USA* **1994**, *91*, 2582–2586. [[CrossRef](#)] [[PubMed](#)]
234. Ikeda, Y.; Koizumi, N.; Kusano, T.; Sano, H. Sucrose and cytokinin modulation of WPK4, a gene encoding a SNF1-related protein kinase from wheat. *Plant Physiol.* **1999**, *121*, 813–820. [[CrossRef](#)] [[PubMed](#)]
235. Kushwah, S.; Jones, A.M.; Laxmi, A. Cytokinin interplay with ethylene, auxin and glucose signaling controls *Arabidopsis* seedling root directional growth. *Plant Physiol.* **2011**. [[CrossRef](#)] [[PubMed](#)]

236. Kushwah, S.; Laxmi, A. The interaction between glucose and cytokinin signaling in controlling *Arabidopsis thaliana* seedling root growth and development. *Plant Signal. Behav.* **2017**, *12*, e1312241. [[CrossRef](#)] [[PubMed](#)]
237. Dewitte, W.; Riou-Khamlichi, C.; Scofield, S.; Healy, J.S.; Jacqmard, A.; Kilby, N.J.; Murray, J.A. Altered cell cycle distribution, hyperplasia, and inhibited differentiation in *Arabidopsis* caused by the D-type cyclin CYCD3. *Plant Cell* **2003**, *15*, 79–92. [[CrossRef](#)] [[PubMed](#)]
238. Das, P.K.; Shin, D.H.; Choi, S.B.; Yoo, S.D.; Choi, G.; Park, Y.I. Cytokinins enhance sugar-induced anthocyanin biosynthesis in *Arabidopsis*. *Mol. Cells* **2012**. [[CrossRef](#)] [[PubMed](#)]
239. Shin, D.H.; Choi, M.; Kim, K.; Bang, G.; Cho, M.; Choi, S.B.; Choi, G.; Park, Y.I. HY5 regulates anthocyanin biosynthesis by inducing the transcriptional activation of the MYB75/PAP1 transcription factor in *Arabidopsis*. *FEBS Lett.* **2013**, *587*, 1543–1547. [[CrossRef](#)] [[PubMed](#)]
240. Ioio, R.D.; Linhares, F.S.; Scacchi, E.; Casamitjana-Martinez, E.; Heidstra, R.; Costantino, P.; Sabatini, S. Cytokinins determine *Arabidopsis* root-meristem size by controlling cell differentiation. *Curr. Biol.* **2007**, *17*, 678–682. [[CrossRef](#)] [[PubMed](#)]
241. Li, C.; Wang, H.; Ming, J.; Liu, M.; Fang, P. Hydrogen generation by photocatalytic reforming of glucose with heterostructured CdS/MoS<sub>2</sub> composites under visible light irradiation. *Int. J. Hydrogen Energy* **2017**, *42*, 16968–16978. [[CrossRef](#)]
242. Xie, X.; Yoneyama, K.; Yoneyama, K. The strigolactone story. *Annu. Rev. Phytopathol.* **2010**, *48*. [[CrossRef](#)] [[PubMed](#)]
243. Czarnecki, O.; Yang, J.; Weston, D.J.; Tuskan, G.A.; Chen, J.G. A dual role of strigolactones in phosphate acquisition and utilization in plants. *Int. J. Mol. Sci.* **2013**, *14*, 7681–7701. [[CrossRef](#)] [[PubMed](#)]
244. Smith, S.M.; Li, J. Signalling and responses to strigolactones and karrikins. *Curr. Opin. Plant Biol.* **2014**, *21*, 23–29. [[CrossRef](#)] [[PubMed](#)]
245. Gomez-Roldan, V.; Fermas, S.; Brewer, P.B.; Puech-Pagès, V.; Dun, E.A.; Pillot, J.P.; Letisse, F.; Matusova, R.; Danoun, S.; Portais, J.; et al. Strigolactone inhibition of shoot branching. *Nature* **2008**, *455*, 189–194. [[CrossRef](#)] [[PubMed](#)]
246. Umehara, M.; Hanada, A.; Yoshida, S.; Akiyama, K.; Arite, T.; Takeda-Kamiya, N.; Magome, H.; Kamiya, Y.; Shirasu, K.; Yoneyama, K.; et al. Inhibition of shoot branching by new terpenoid plant hormones. *Nature* **2008**, *455*, 195–200. [[CrossRef](#)] [[PubMed](#)]
247. Koltai, H. Strigolactones are regulators of root development. *New Phytol.* **2011**, *190*, 545–549. [[CrossRef](#)] [[PubMed](#)]
248. Ruyter-Spira, C.; Al-Babili, S.; Van Der Krol, S.; Bouwmeester, H. The biology of strigolactones. *Trends Plant Sci.* **2013**, *18*, 72–83. [[CrossRef](#)] [[PubMed](#)]
249. Van Ha, C.; Leyva-González, M.A.; Osakabe, Y.; Tran, U.T.; Nishiyama, R.; Watanabe, Y.; Tanaka, M.; Seki, M.; Yamaguchi, S.; Dong, N.V.; et al. Positive regulatory role of strigolactone in plant responses to drought and salt stress. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 851–856.
250. Kapulnik, Y.; Koltai, H. Strigolactone involvement in root development, response to abiotic stress and interactions with the biotic soil environment. *Plant Physiol.* **2014**. [[CrossRef](#)] [[PubMed](#)]
251. Saeed, W.; Naseem, S.; Ali, Z. Strigolactones biosynthesis and their role in abiotic stress resilience in plants: A critical review. *Front. Plant Sci.* **2017**, *8*, 1487. [[CrossRef](#)] [[PubMed](#)]
252. Hu, Q.; Zhang, S.; Huang, B. Strigolactones and interaction with auxin regulating root elongation in tall fescue under different temperature regimes. *Plant Sci.* **2018**, *271*, 34–39. [[CrossRef](#)] [[PubMed](#)]
253. Luo, L.; Wang, H.; Liu, X.; Hu, J.; Zhu, X.; Pan, S.; Qin, R.; Wang, Y.; Zhao, P.; Fan, X.; et al. Strigolactones affect the translocation of nitrogen in rice. *Plant Sci.* **2018**, *270*, 190–197. [[CrossRef](#)] [[PubMed](#)]
254. Waters, M.T.; Gutjahr, C.; Bennett, T.; Nelson, D.C. Strigolactone signaling and evolution. *Annu. Rev. Plant Biol.* **2017**, *68*, 291–322. [[CrossRef](#)] [[PubMed](#)]
255. Wu, Y.Y.; Hou, B.H.; Lee, W.C.; Lu, S.H.; Yang, C.J.; Vaucheret, H.; Chen, H.M. DCL2- and RDR6-dependent transitive silencing of SMXL4 and SMXL5 in *Arabidopsis dcl4* mutants causes defective phloem transport and carbohydrate over-accumulation. *Plant J.* **2017**, *90*, 1064–1078. [[CrossRef](#)] [[PubMed](#)]
256. Li, G.D.; Pan, L.N.; Jiang, K.; Takahashi, I.; Nakamura, H.; Xu, Y.W.; Asami, T.; Shen, R.F. Strigolactones are involved in sugar signaling to modulate early seedling development in *Arabidopsis*. *Plant Biotechnol.* **2016**, *33*, 87–97. [[CrossRef](#)]
257. Rameau, C.; Bertheloot, J.; Leduc, N.; Andrieu, B.; Foucher, F.; Sakr, S. Multiple pathways regulate shoot branching. *Front. Plant Sci.* **2015**, *5*, 741. [[CrossRef](#)] [[PubMed](#)]

258. Otori, K.; Tamoi, M.; Tanabe, N.; Shigeoka, S. Enhancements in sucrose biosynthesis capacity affect shoot branching in *Arabidopsis*. *Biosci. Biotechnol. Biochem.* **2017**, *81*, 1470–1477. [[CrossRef](#)] [[PubMed](#)]
259. Richards, D.E.; King, K.E.; Ait-ali, T.; Harberd, N.P. How gibberellin regulates plant growth and development: A molecular genetic analysis of gibberellin signaling. *Annu. Rev. Plant Biol.* **2001**, *52*, 67–88. [[CrossRef](#)] [[PubMed](#)]
260. Biemelt, S.; Tschiersch, H.; Sonnewald, U. Impact of altered gibberellin metabolism on biomass accumulation, lignin biosynthesis, and photosynthesis in transgenic tobacco plants. *Plant Physiol.* **2004**, *135*, 254–265. [[CrossRef](#)] [[PubMed](#)]
261. Ueguchi-Tanaka, M.; Nakajima, M.; Motoyuki, A.; Matsuoka, M. Gibberellin receptor and its role in gibberellin signaling in plants. *Annu. Rev. Plant Biol.* **2007**, *58*, 183–198. [[CrossRef](#)] [[PubMed](#)]
262. Huerta, L.; Forment, J.; Gadea, J.; Fagoaga, C.; Peña, L.; Pérez-Amador, M.A.; García-Martínez, J.L. Gene expression analysis in citrus reveals the role of gibberellins on photosynthesis and stress. *Plant Cell Environ.* **2008**, *31*, 1620–1633. [[CrossRef](#)] [[PubMed](#)]
263. Matsoukas, I.G. Interplay between sugar and hormone signaling pathways modulate floral signal transduction. *Front. Genet.* **2014**, *5*, 218. [[CrossRef](#)] [[PubMed](#)]
264. Xu, H.; Liu, Q.; Yao, T.; Fu, X. Shedding light on integrative GA signaling. *Curr. Opin. Plant Biol.* **2014**, *21*, 89–95. [[CrossRef](#)] [[PubMed](#)]
265. Ševčíková, H.; Mašková, P.; Tarkovská, D.; Mašek, T.; Lipavská, H. Carbohydrates and gibberellins relationship in potato tuberization. *J. Plant Physiol.* **2017**, *214*, 53–63. [[CrossRef](#)] [[PubMed](#)]
266. Wang, B.; Wei, H.; Xue, Z. The role of gibberellin in iron homeostasis in rice. *Ann. Bot.* **2017**, *119*, 945–956. [[PubMed](#)]
267. Conti, L. Hormonal control of the floral transition: Can one catch them all? *Dev. Biol.* **2017**, *430*, 288–301. [[CrossRef](#)] [[PubMed](#)]
268. Shu, K.; Zhou, W.; Yang, W. APETALA 2-domain-containing transcription factors: Focusing on abscisic acid and gibberellins antagonism. *New Phytol.* **2018**, *217*, 977–983. [[CrossRef](#)] [[PubMed](#)]
269. Yuan, L.; Xu, D.Q. Stimulation effect of gibberellic acid short-term treatment on leaf photosynthesis related to the increase in Rubisco content in broad bean and soybean. *Photosynth. Res.* **2001**, *68*, 39–47. [[CrossRef](#)] [[PubMed](#)]
270. Tuna, A.L.; Kaya, C.; Dikilitas, M.; Higgs, D. The combined effects of gibberellic acid and salinity on some antioxidant enzyme activities, plant growth parameters and nutritional status in maize plants. *Environ. Exp. Bot.* **2008**, *62*, 1–9. [[CrossRef](#)]
271. Jiang, X.; Li, H.; Wang, T.; Peng, C.; Wang, H.; Wu, H.; Wang, X. Gibberellin indirectly promotes chloroplast biogenesis as a means to maintain the chloroplast population of expanded cells. *Plant J.* **2012**, *72*, 768–780. [[CrossRef](#)] [[PubMed](#)]
272. Miyamoto, K.; Ueda, J.; Kamisaka, S. Gibberellin-enhanced sugar accumulation in growing subhooks of etiolated *Pisum sativum* seedlings. Effects of gibberellic acid, indoleacetic acid and cycloheximide on invertase activity, sugar accumulation and growth. *Physiol. Plant.* **1993**, *88*, 301–306. [[CrossRef](#)]
273. Chen, W.S.; Liu, H.Y.; Liu, Z.H.; Yang, L.; Chen, W.H. Gibberellin and temperature influence carbohydrate content and flowering in *Phalaenopsis*. *Physiol. Plant.* **1994**, *90*, 391–395. [[CrossRef](#)]
274. Mehouchi, J.; Tadeo, F.R.; Zaragoza, S.; Primo-Millo, E.; Talon, M. Effects of gibberellic acid and paclobutrazol on growth and carbohydrate accumulation in shoots and roots of citrus rootstock seedlings. *J. Hortic. Sci.* **1996**, *71*, 747–754. [[CrossRef](#)]
275. Miyamoto, K.; Ito, E.; Yamamoto, H.; Ueda, J.; Kamisaka, S. Gibberellin-enhanced growth and sugar accumulation in growing subhooks of etiolated *Pisum sativum* seedlings: Effects of actinomycin D on invertase activity, soluble sugars and stem elongation. *J. Plant Physiol.* **2000**, *156*, 449–453. [[CrossRef](#)]
276. Ranwala, A.P.; Miller, W.B. Gibberellin-mediated changes in carbohydrate metabolism during flower stalk elongation in tulips. *Plant Growth Regul.* **2008**, *55*, 241–248. [[CrossRef](#)]
277. Choubane, D.; Rabot, A.; Mortreau, E.; Legourriec, J.; Péron, T.; Foucher, F.; AHCÈNE, Y.; Pelleschi-Travier, S.; Leduc, N.; Hamama, L.; et al. Photocontrol of bud burst involves gibberellin biosynthesis in *Rosa* sp. *J. Plant Physiol.* **2012**, *169*, 1271–1280. [[CrossRef](#)] [[PubMed](#)]



278. Liu, S.S.; Chen, J.; Li, S.C.; Zeng, X.; Meng, Z.X.; Guo, S.X. Comparative transcriptome analysis of genes involved in GA-GID1-DELLA regulatory module in symbiotic and asymbiotic seed germination of *Anoectochilus roxburghii* (Wall.) Lindl. (Orchidaceae). *Int. J. Mol. Sci.* **2015**, *16*, 30190–30203. [[CrossRef](#)] [[PubMed](#)]
279. Machado, R.A.; Baldwin, I.T.; Erb, M. Herbivory-induced jasmonates constrain plant sugar accumulation and growth by antagonizing gibberellin signaling and not by promoting secondary metabolite production. *New Phytol.* **2017**, *215*, 803–812. [[CrossRef](#)] [[PubMed](#)]
280. Paparelli, E.; Parlanti, S.; Gonzali, S.; Novi, G.; Mariotti, L.; Ceccarelli, N.; Dongen, J.T.; Kölling, K.; Zeeman, S.C.; Perata, P. Nighttime sugar starvation orchestrates gibberellin biosynthesis and plant growth in *Arabidopsis*. *Plant Cell* **2013**. [[CrossRef](#)] [[PubMed](#)]
281. Gibson, S.I.; Laby, R.J.; Kim, D. The *sugar-insensitive1* (*sis1*) mutant of *Arabidopsis* is allelic to *ctr1*. *Biochem. Biophys. Res. Commun.* **2001**, *280*, 196–203. [[CrossRef](#)] [[PubMed](#)]
282. Karrer, E.E.; Rodriguez, R.L. Metabolic regulation of rice  $\alpha$ -amylase and sucrose synthase genes in *planta*. *Plant J.* **1992**, *2*, 517–523. [[PubMed](#)]
283. Perata, P.; Matsukura, C.; Vernieri, P.; Yamaguchi, J. Sugar repression of a gibberellin-dependent signaling pathway in barley embryos. *Plant Cell* **1997**, *9*, 2197–2208. [[CrossRef](#)] [[PubMed](#)]
284. Morita, A.; Umemura, T.A.; Kuroyanagi, M.; Futsuhara, Y.; Perata, P.; Yamaguchi, J. Functional dissection of a sugar-repressed  $\alpha$ -amylase gene (RAmy1A) promoter in rice embryos. *FEBS Lett.* **1998**, *423*, 81–85. [[CrossRef](#)]
285. Chen, P.W.; Chiang, C.M.; Tseng, T.H.; Yu, S.M. Interaction between rice MYBGA and the gibberellin response element controls tissue-specific sugar sensitivity of  $\alpha$ -amylase genes. *Plant Cell* **2006**, *18*, 2326–2340. [[CrossRef](#)] [[PubMed](#)]
286. Gubler, F.; Kalla, R.; Roberts, J.K.; Jacobsen, J.V. Gibberellin-regulated expression of a myb gene in barley aleurone cells: Evidence for Myb transactivation of a high-pI  $\alpha$ -amylase gene promoter. *Plant Cell* **1995**, *7*, 1879–1891. [[CrossRef](#)] [[PubMed](#)]
287. Li, Y.; Van den Ende, W.; Rolland, F. Sucrose induction of anthocyanin biosynthesis is mediated by DELLA. *Mol. Plant* **2014**, *7*, 570–572. [[CrossRef](#)] [[PubMed](#)]
288. Alabadi, D.; Gil, J.; Blázquez, M.A.; García-Martínez, J.L. Gibberellins repress photomorphogenesis in darkness. *Plant Physiol.* **2004**, *134*, 1050–1057. [[CrossRef](#)] [[PubMed](#)]
289. Loreti, E.; Povero, G.; Novi, G.; Solfanelli, C.; Alpi, A.; Perata, P. Gibberellins, jasmonate and abscisic acid modulate the sucrose-induced expression of anthocyanin biosynthetic genes in *Arabidopsis*. *New Phytol.* **2008**, *179*, 1004–1016. [[CrossRef](#)] [[PubMed](#)]
290. Davière, J.M.; Achard, P. A pivotal role of DELLAs in regulating multiple hormone signals. *Mol. Plant* **2016**, *9*, 10–20. [[CrossRef](#)] [[PubMed](#)]
291. Gallego-Bartolomé, J.; Alabadi, D.; Blázquez, M.A. DELLA-induced early transcriptional changes during etiolated development in *Arabidopsis thaliana*. *PLoS ONE* **2011**, *6*, e23918. [[CrossRef](#)] [[PubMed](#)]
292. Yin, C.C.; Zhao, H.; Ma, B.; Chen, S.Y.; Zhang, J.S. Diverse roles of ethylene in regulating agronomic traits in rice. *Front. Plant Sci.* **2017**, *8*, 1676. [[CrossRef](#)] [[PubMed](#)]
293. Dubois, M.; Van den Broeck, L.; Inzé, D. The pivotal role of ethylene in plant growth. *Trends Plant Sci.* **2018**, *23*, 311–323. [[CrossRef](#)] [[PubMed](#)]
294. Nascimento, F.X.; Rossi, M.J.; Glick, B.R. Ethylene and 1-Aminocyclopropane-1-carboxylate (ACC) in plant–bacterial interactions. *Front. Plant Sci.* **2018**, *9*, 114. [[CrossRef](#)] [[PubMed](#)]
295. Larsen, P.B. Mechanisms of ethylene biosynthesis and response in plants. *Essays Biochem.* **2015**, *58*, 61–70. [[CrossRef](#)] [[PubMed](#)]
296. Zhou, L.; Jang, J.C.; Jones, T.L.; Sheen, J. Glucose and ethylene signal transduction crosstalk revealed by an *Arabidopsis* glucose-insensitive mutant. *Proc. Natl. Acad. Sci. USA* **1998**, *95*, 10294–10299. [[CrossRef](#)] [[PubMed](#)]
297. León, P.; Sheen, J. Sugar and hormone connections. *Trends Plant Sci.* **2003**, *8*, 110–116. [[CrossRef](#)]
298. Yanagisawa, S.; Yoo, S.D.; Sheen, J. Differential regulation of EIN3 stability by glucose and ethylene signalling in plants. *Nature* **2003**, *425*, 521–525. [[CrossRef](#)] [[PubMed](#)]
299. Cheng, W.H.; Endo, A.; Zhou, L.; Penney, J.; Chen, H.C.; Arroyo, A.; Leon, P.; Nambara, E.; Asami, T.; Seo, M.; et al. A unique short-chain dehydrogenase/reductase in *Arabidopsis* glucose signaling and abscisic acid biosynthesis and functions. *Plant Cell* **2002**, *14*, 2723–2743. [[CrossRef](#)] [[PubMed](#)]



300. Haydon, M.J.; Mielczarek, O.; Frank, A.; Román, Á.; Webb, A.A. Sucrose and ethylene signaling interact to modulate the circadian clock. *Plant Physiol.* **2017**, 00592. [[CrossRef](#)] [[PubMed](#)]
301. Sulmon, C.; Gouesbet, G.; El Amrani, A.; Couée, I. Involvement of the ethylene-signalling pathway in sugar-induced tolerance to the herbicide atrazine in *Arabidopsis thaliana* seedlings. *J. Plant Physiol.* **2007**, *164*, 1083–1092. [[CrossRef](#)] [[PubMed](#)]
302. Rohde, A.; Kurup, S.; Holdsworth, M. ABI3 emerges from the seed. *Trends Plant Sci.* **2000**, *5*, 418–419. [[CrossRef](#)]
303. Finkelstein, R.R.; Gampala, S.S.; Rock, C.D. Abscisic acid signaling in seeds and seedlings. *Plant Cell* **2002**, *14* (Suppl. 1), S15–S45. [[CrossRef](#)]
304. Vishwakarma, K.; Upadhyay, N.; Kumar, N.; Yadav, G.; Singh, J.; Mishra, R.K.; Kumar, V.; Verma, R.; Upadhyay, R.G.; Pandey, M.; et al. Abscisic acid signaling and abiotic stress tolerance in plants: A review on current knowledge and future prospects. *Front. Plant Sci.* **2017**, *8*, 161. [[CrossRef](#)] [[PubMed](#)]
305. Laby, R.J.; Kincaid, M.S.; Kim, D.; Gibson, S.I. The *Arabidopsis* sugar-insensitive mutants *sis4* and *sis5* are defective in abscisic acid synthesis and response. *Plant J.* **2000**, *23*, 587–596. [[CrossRef](#)] [[PubMed](#)]
306. Rook, F.; Corke, F.; Card, R.; Munz, G.; Smith, C.; Bevan, M.W. Impaired sucrose-induction mutants reveal the modulation of sugar-induced starch biosynthetic gene expression by abscisic acid signalling. *Plant J.* **2001**, *26*, 421–433. [[CrossRef](#)] [[PubMed](#)]
307. Brocard-Gifford, I.; Lynch, T.J.; Garcia, M.E.; Malhotra, B.; Finkelstein, R.R. The *Arabidopsis thaliana* *ABSCISIC ACID-INSENSITIVE 8* locus encodes a novel protein mediating abscisic acid and sugar responses essential for growth. *Plant Cell* **2004**, *16*, 406–421. [[CrossRef](#)] [[PubMed](#)]
308. Akihiro, T.; Mizuno, K.; Fujimura, T. Gene expression of ADP-glucose pyrophosphorylase and starch contents in rice cultured cells are cooperatively regulated by sucrose and ABA. *Plant Cell Physiol.* **2005**, *46*, 937–946. [[CrossRef](#)] [[PubMed](#)]
309. Çakir, B.; Agasse, A.; Gaillard, C.; Saumonneau, A.; Delrot, S.; Atanassova, R. A grape ASR protein involved in sugar and abscisic acid signaling. *Plant Cell* **2003**, *15*, 2165–2180. [[CrossRef](#)] [[PubMed](#)]
310. Susek, R.E.; Ausubel, F.M.; Chory, J. Signal transduction mutants of *Arabidopsis* uncouple nuclear *CAB* and *RBCS* gene expression from chloroplast development. *Cell* **1993**, *74*, 787–799. [[CrossRef](#)]
311. Huijser, C.; Kortstee, A.; Pego, J.; Weisbeek, P.; Wisman, E.; Smeekens, S. The *Arabidopsis* *SUCROSE UNCOUPLED-6* gene is identical to *ABSCISIC ACID INSENSITIVE-4*: Involvement of abscisic acid in sugar responses. *Plant J.* **2000**, *23*, 577–585. [[CrossRef](#)] [[PubMed](#)]
312. Toyofuku, K.; Loreti, E.; Vernieri, P.; Alpi, A.; Perata, P.; Yamaguchi, J. Glucose modulates the abscisic acid-inducible *Rab16A* gene in cereal embryos. *Plant Mol. Biol.* **2000**, *42*, 451–460. [[CrossRef](#)] [[PubMed](#)]
313. Han, C.S.; Kim, S.; Lee, S.E.; Choi, S.; Kim, S.H.; sun Yoon, I.; Hwang, Y.S. Cross-talk between ABA and sugar signaling is mediated by the ACGT core and CE1 element reciprocally in *OsTIP3;1* promoter. *J. Plant Physiol.* **2018**, *224*, 103–111. [[CrossRef](#)] [[PubMed](#)]
314. Wind, J.J.; Peviani, A.; Snel, B.; Hanson, J.; Smeekens, S.C. ABI4: Versatile activator and repressor. *Trends Plant Sci.* **2013**, *18*, 125–132. [[CrossRef](#)] [[PubMed](#)]
315. Li, P.; Zhou, H.; Shi, X.; Yu, B.; Zhou, Y.; Chen, S.; Wang, Y.; Peng, Y.; Meyer, R.C.; Smeekens, S.C.; et al. The ABI4-induced *Arabidopsis* ANAC060 transcription factor attenuates ABA signaling and renders seedlings sugar insensitive when present in the nucleus. *PLoS Genet.* **2014**, *10*, e10. [[CrossRef](#)] [[PubMed](#)]
316. Jossier, M.; Bouly, J.P.; Meimoun, P.; Arjmand, A.; Lessard, P.; Hawley, S.; Hardie, D.G.; Thomas, M. SnRK1 (SNF1-related kinase 1) has a central role in sugar and ABA signalling in *Arabidopsis thaliana*. *Plant J.* **2009**, *59*, 316–328. [[CrossRef](#)] [[PubMed](#)]
317. Radchuk, R.; Emery, R.N.; Weier, D.; Vigeolas, H.; Geigenberger, P.; Lunn, J.E.; Feil, R.; Weschke, W.; Weber, H. Sucrose non-fermenting kinase 1 (SnRK1) coordinates metabolic and hormonal signals during pea cotyledon growth and differentiation. *Plant J.* **2010**, *61*, 324–338. [[CrossRef](#)] [[PubMed](#)]
318. Fujii, H.; Zhu, J.K. *Arabidopsis* mutant deficient in 3 abscisic acid-activated protein kinases reveals critical roles in growth, reproduction, and stress. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 8380–8385. [[CrossRef](#)] [[PubMed](#)]
319. Coello, P.; Hirano, E.; Hey, S.J.; Muttucumaru, N.; Martinez-Barajas, E.; Parry, M.A.; Halford, N.G. Evidence that abscisic acid promotes degradation of SNF1-related protein kinase (SnRK) 1 in wheat and activation of a putative calcium-dependent SnRK2. *J. Exp. Bot.* **2011**, *63*, 913–924. [[CrossRef](#)] [[PubMed](#)]

320. Lim, C.W.; Kim, J.H.; Baek, W.; Kim, B.S.; Lee, S.C. Functional roles of the protein phosphatase 2C, AtAIP1, in abscisic acid signaling and sugar tolerance in *Arabidopsis*. *Plant Sci.* **2012**, *187*, 83–88. [[CrossRef](#)] [[PubMed](#)]
321. Carvalho, R.F.; Szakonyi, D.; Simpson, C.G.; Barbosa, I.C.; Brown, J.W.; Baena-González, E.; Duque, P. The *Arabidopsis* SR45 splicing factor, a negative regulator of sugar signaling, modulates SNF1-related protein kinase 1 (SnRK1) stability. *Plant Cell* **2016**. [[CrossRef](#)] [[PubMed](#)]
322. Bajguz, A. Metabolism of brassinosteroids in plants. *Plant Physiol. Biochem.* **2007**, *45*, 95–107. [[CrossRef](#)] [[PubMed](#)]
323. Wang, Z.Y. Brassinosteroids modulate plant immunity at multiple levels. *Proc. Natl. Acad. Sci. USA* **2012**, *109*, 7–8. [[CrossRef](#)] [[PubMed](#)]
324. Wang, W.; Bai, M.Y.; Wang, Z.Y. The brassinosteroid signaling network—a paradigm of signal integration. *Curr. Opin. Plant Biol.* **2014**, *21*, 147–153. [[CrossRef](#)] [[PubMed](#)]
325. Nolan, T.M.; Brennan, B.; Yang, M.; Chen, J.; Zhang, M.; Li, Z.; Wang, X.; Bassham, D.C.; Walley, J.; Yin, Y. Selective autophagy of BES1 mediated by DSK2 balances plant growth and survival. *Dev. Cell* **2017**, *41*, 33–46. [[CrossRef](#)] [[PubMed](#)]
326. Li, Z.; Ou, Y.; Zhang, Z.; Li, J.; He, Y. Brassinosteroid signaling recruits histone 3 lysine-27 demethylation activity to FLOWERING LOCUS C chromatin to inhibit the floral transition in *Arabidopsis*. *Mol. Plant.* **2018**. [[CrossRef](#)] [[PubMed](#)]
327. Szekeres, M.; Németh, K.; Koncz-Kálmán, Z.; Mathur, J.; Kauschmann, A.; Altmann, T.; Rédei, G.P.; Nagy, F.; Schell, J.; Koncz, C. Brassinosteroids rescue the deficiency of CYP90, a cytochrome P450, controlling cell elongation and de-etiolation in *Arabidopsis*. *Cell* **1996**, *85*, 171–182. [[CrossRef](#)]
328. Smeekens, S. Sugar regulation of gene expression in plants. *Curr. Opin. Plant Biol.* **1998**, *1*, 230–234. [[CrossRef](#)]
329. Gupta, A.; Singh, M.; Laxmi, A. The interaction between glucose and brassinosteroid signal transduction pathway in *Arabidopsis thaliana*. *Plant Physiol.* **2015**. [[CrossRef](#)]
330. Goetz, M.; Godt, D.E.; Roitsch, T. Tissue-specific induction of the mRNA for an extracellular invertase isoenzyme of tomato by brassinosteroids suggests a role for steroid hormones in assimilate partitioning. *Plant J.* **2000**, *22*, 515–522. [[CrossRef](#)] [[PubMed](#)]
331. Schlüter, U.; Köpke, D.; Altmann, T.; Müssig, C. Analysis of carbohydrate metabolism of CPD antisense plants and the brassinosteroid-deficient *ccb1* mutant. *Plant Cell Environ.* **2002**, *25*, 783–791. [[CrossRef](#)]
332. Lisso, J.; Altmann, T.; Müssig, C. Metabolic changes in fruits of the tomato *dx* mutant. *Phytochemistry* **2006**, *67*, 2232–2238. [[CrossRef](#)] [[PubMed](#)]
333. Wu, C.Y.; Trieu, A.; Radhakrishnan, P.; Kwok, S.F.; Harris, S.; Zhang, K.; Wang, J.; Wan, J.; Zhai, H.; Takatsuto, S.; et al. Brassinosteroids regulate grain filling in rice. *Plant Cell* **2008**, *20*, 2130–2145. [[CrossRef](#)] [[PubMed](#)]
334. Vicentini, R.; de Maria Felix, J.; Dornelas, M.C.; Menossi, M. Characterization of a sugarcane (*Saccharum* spp.) gene homolog to the brassinosteroid insensitive1-associated receptor kinase 1 that is associated to sugar content. *Plant Cell Rep.* **2009**, *28*, 481–491. [[CrossRef](#)] [[PubMed](#)]
335. Jiang, Y.P.; Cheng, F.; Zhou, Y.H.; Xia, X.J.; Mao, W.H.; Shi, K.; Chen, Z.; Yu, J.Q. Cellular glutathione redox homeostasis plays an important role in the brassinosteroid-induced increase in CO<sub>2</sub> assimilation in *Cucumis sativus*. *New Phytol.* **2012**, *194*, 932–943. [[CrossRef](#)] [[PubMed](#)]
336. Bitterlich, M.; Krügel, U.; Boldt-Burisch, K.; Franken, P.; Kühn, C. The sucrose transporter SI SUT 2 from tomato interacts with brassinosteroid functioning and affects arbuscular mycorrhiza formation. *Plant J.* **2014**, *78*, 877–889. [[CrossRef](#)] [[PubMed](#)]
337. Schröder, F.; Lisso, J.; Obata, T.; Erban, A.; Maximova, E.; Giavalisco, P.; Kopka, J.; Fernie, A.R.; Willmitzer, L.; Müssig, C. Consequences of induced brassinosteroid deficiency in *Arabidopsis* leaves. *BMC Plant Biol.* **2014**, *14*, 309. [[CrossRef](#)] [[PubMed](#)]
338. Xu, W.; Dubos, C.; Lepiniec, L. Transcriptional control of flavonoid biosynthesis by MYB–bHLH–WDR complexes. *Trends Plant Sci.* **2015**, *20*, 176–185. [[CrossRef](#)] [[PubMed](#)]
339. Nie, S.; Huang, S.; Wang, S.; Cheng, D.; Liu, J.; Lv, S.; Li, Q.; Wang, X. Enhancing brassinosteroid signaling via overexpression of tomato (*Solanum lycopersicum*) SIBR11 improves major agronomic traits. *Front. Plant Sci.* **2017**, *8*, 1386. [[CrossRef](#)] [[PubMed](#)]
340. Zhang, Y.; Liu, Z.; Wang, J.; Chen, Y.; Bi, Y.; He, J. Brassinosteroid is required for sugar promotion of hypocotyl elongation in *Arabidopsis* in darkness. *Planta* **2015**, *242*, 881–893. [[CrossRef](#)] [[PubMed](#)]

341. Zhang, Y.; He, J. Sugar-induced plant growth is dependent on brassinosteroids. *Plant Signal. Behav.* **2015**, *10*, e1082700. [[CrossRef](#)] [[PubMed](#)]
342. Gupta, A.; Singh, M.; Laxmi, A. Interaction between glucose and brassinosteroid during regulation of lateral root development in *Arabidopsis thaliana*. *Plant Physiol.* **2015**. [[CrossRef](#)] [[PubMed](#)]
343. Zhang, G.; Song, X.; Guo, H.; Wu, Y.; Chen, X.; Fang, R. A small G protein as a novel component of the rice brassinosteroid signal transduction. *Mol. Plant* **2016**, *9*, 1260–1271. [[CrossRef](#)] [[PubMed](#)]
344. Laxmi, A.; Paul, L.K.; Peters, J.L.; Khurana, J.P. *Arabidopsis* constitutive photomorphogenic mutant, *bls1*, displays altered brassinosteroid response and sugar sensitivity. *Plant Mol. Biol.* **2004**, *56*, 185–201. [[CrossRef](#)] [[PubMed](#)]
345. Stitt, M.; Krapp, A. The interaction between elevated carbon dioxide and nitrogen nutrition: The physiological and molecular background. *Plant Cell Environ.* **1999**, *22*, 583–621. [[CrossRef](#)]
346. Coruzzi, G.M.; Zhou, L. Carbon and nitrogen sensing and signaling in plants: Emerging ‘matrix effects’. *Curr. Opin. Plant Biol.* **2001**, *4*, 247–253. [[CrossRef](#)]
347. Miller, A.J.; Fan, X.; Shen, Q.; Smith, S.J. Amino acids and nitrate as signals for the regulation of nitrogen acquisition. *J. Exp. Bot.* **2007**, *59*, 111–119. [[CrossRef](#)] [[PubMed](#)]
348. Nunes-Nesi, A.; Fernie, A.R.; Stitt, M. Metabolic and signaling aspects underpinning the regulation of plant carbon nitrogen interactions. *Mol. Plant* **2010**, *3*, 973–996. [[CrossRef](#)] [[PubMed](#)]
349. Guo, Q.; Turnbull, M.H.; Song, J.; Roche, J.; Novak, O.; Späth, J.; Jameson, P.E.; Love, J. Depletion of carbohydrate reserves limits nitrate uptake during early regrowth in *Lolium perenne* L. *J. Exp. Bot.* **2017**, *68*, 1569–1583. [[CrossRef](#)] [[PubMed](#)]
350. Muller, B.; Touraine, B. Inhibition of  $\text{NO}_3^-$  uptake by various phloem translocated amino acids in soybean seedlings. *J. Exp. Bot.* **1992**, *43*, 617–623. [[CrossRef](#)]
351. Crawford, N.M. Nitrate: Nutrient and signal for plant growth. *Plant Cell* **1995**, *7*, 859–868. [[CrossRef](#)] [[PubMed](#)]
352. Forde, B.G.; Clarkson, D.T. Nitrate and ammonium nutrition of plants: Physiological and molecular perspectives. In *Advances in Botanical Research*; Academic Press: London, UK, 1999; Volume 30, pp. 1–90.
353. Coruzzi, G.; Bush, D.R. Nitrogen and carbon nutrient and metabolite signaling in plants. *Plant Physiol.* **2001**, *125*, 61–64. [[CrossRef](#)] [[PubMed](#)]
354. Stitt, M.; Müller, C.; Matt, P.; Gibon, Y.; Carillo, P.; Morcuende, R.; Scheible, W.; Krapp, A. Steps towards an integrated view of nitrogen metabolism. *J. Exp. Bot.* **2002**, *53*, 959–970. [[CrossRef](#)] [[PubMed](#)]
355. Coruzzi, G.M. Primary N-assimilation into amino acids in *Arabidopsis*. *Arabidopsis Book* **2003**, *2*, e0010. [[CrossRef](#)] [[PubMed](#)]
356. Geßler, A.; Kopriva, S.; Rennenberg, H. Regulation of nitrate uptake at the whole-tree level: Interaction between nitrogen compounds, cytokinins and carbon metabolism. *Tree Physiol.* **2004**, *24*, 1313–1321. [[CrossRef](#)]
357. Foyer, C.H.; Parry, M.; Noctor, G. Markers and signals associated with nitrogen assimilation in higher plants. *J. Exp. Bot.* **2003**, *54*, 585–593. [[CrossRef](#)] [[PubMed](#)]
358. Stitt, M. Nitrate regulation of metabolism and growth. *Curr. Opin. Plant Biol.* **1999**, *2*, 178–186. [[CrossRef](#)]
359. Pace, G.M.; Volk, R.J.; Jackson, W.A. Nitrate reduction in response to  $\text{CO}_2$ -limited photosynthesis: Relationship to carbohydrate supply and nitrate reductase activity in maize seedlings. *Plant Physiol.* **1990**, *92*, 286–292. [[CrossRef](#)] [[PubMed](#)]
360. Rufty, T.W.; MacKown, C.T.; Volk, R.J. Effects of altered carbohydrate availability on whole-plant assimilation of  $^{15}\text{NO}_3^-$ . *Plant Physiol.* **1989**, *89*, 457–463. [[CrossRef](#)] [[PubMed](#)]
361. Delhon, P.; Gojon, A.; Tillard, P.; Passama, L. Diurnal regulation of  $\text{NO}_3^-$  uptake in soybean plants. IV. Dependence on current photosynthesis and sugar availability to the roots. *J. Exp. Bot.* **1996**, *47*, 893–900. [[CrossRef](#)]
362. Constable, J.V.; Bassirirad, H.; Lussenhop, J.; Zerihun, A. Influence of elevated  $\text{CO}_2$  and mycorrhizae on nitrogen acquisition: Contrasting responses in *Pinus taeda* and *Liquidambar styraciflua*. *Tree Physiol.* **2001**, *21*, 83–91. [[CrossRef](#)] [[PubMed](#)]
363. Masclaux-Daubresse, C.; Daniel-Vedele, F.; Dechorgnat, J.; Chardon, F.; Gaufichon, L.; Suzuki, A. Nitrogen uptake, assimilation and remobilization in plants: Challenges for sustainable and productive agriculture. *Ann. Bot.* **2010**, *105*, 1141–1157. [[CrossRef](#)] [[PubMed](#)]

364. Lejay, L.; Tillard, P.; Lepetit, M.; Olive, F.D.; Filleur, S.; Daniel-Vedele, F.; Gojon, A. Molecular and functional regulation of two  $\text{NO}_3^-$  uptake systems by N- and C-status of *Arabidopsis* plants. *Plant J.* **1999**, *18*, 509–519. [[CrossRef](#)] [[PubMed](#)]
365. Lejay, L.; Gansel, X.; Cerezo, M.; Tillard, P.; Müller, C.; Krapp, A.; Wirén, N.; Daniel-Vedele, F.; Gojon, A. Regulation of root ion transporters by photosynthesis: Functional importance and relation with hexokinase. *Plant Cell* **2003**, *15*, 2218–2232. [[CrossRef](#)] [[PubMed](#)]
366. Chow, F.; Capociama, F.V.; Faria, R.; Oliveira, M.C.D. Characterization of nitrate reductase activity in vitro in *Gracilaria caudata* J. Agardh (Rhodophyta, Gracilariales). *Braz. J. Bot.* **2007**, *30*, 123–129. [[CrossRef](#)]
367. Balotf, S.; Kavooosi, G.; Kholdebarin, B. Nitrate reductase, nitrite reductase, glutamine synthetase, and glutamate synthase expression and activity in response to different nitrogen sources in nitrogen-starved wheat seedlings. *Biotechnol. Appl. Biochem.* **2016**, *63*, 220–229. [[CrossRef](#)] [[PubMed](#)]
368. Goel, P.; Bhuria, M.; Kaushal, M.; Singh, A.K. Carbon: Nitrogen interaction regulates expression of genes involved in n-uptake and assimilation in *Brassica juncea* L. *PLoS ONE* **2016**, *11*, e0163061. [[CrossRef](#)] [[PubMed](#)]
369. Gangappa, S.N.; Botto, J.F. The multifaceted roles of HY5 in plant growth and development. *Mol. Plant* **2016**, *9*, 1353–1365. [[CrossRef](#)] [[PubMed](#)]
370. Toledo-Ortiz, G.; Johansson, H.; Lee, K.P.; Bou-Torrent, J.; Stewart, K.; Steel, G.; Rodríguez-Concepción, M.; Halliday, K.J. The HY5-PIF regulatory module coordinates light and temperature control of photosynthetic gene transcription. *PLoS Genet.* **2014**, *10*, e100441. [[CrossRef](#)] [[PubMed](#)]
371. Chen, X.; Yao, Q.; Gao, X.; Jiang, C.; Harberd, N.P.; Fu, X. Shoot-to-root mobile transcription factor HY5 coordinates plant carbon and nitrogen acquisition. *Curr. Biol.* **2016**, *26*, 640–646. [[CrossRef](#)] [[PubMed](#)]
372. Palme, K.; Teale, W.; Dovzhenko, A. Plant signaling: HY5 synchronizes resource supply. *Curr. Biol.* **2016**, *26*, R328–R329. [[CrossRef](#)] [[PubMed](#)]
373. Chen, L.Q.; Qu, X.Q.; Hou, B.H.; Sosso, D.; Osorio, S.; Fernie, A.R.; Frommer, W.B. Sucrose efflux mediated by SWEET proteins as a key step for phloem transport. *Science* **2012**, *335*, 207–211. [[CrossRef](#)] [[PubMed](#)]
374. Nukarinen, E.; Nägele, T.; Pedrotti, L.; Wurzinger, B.; Mair, A.; Landgraf, R.; Börnke, F.; Hanson, J.; Teige, M.; Baena-Gonzalez, E.; et al. Quantitative phosphoproteomics reveals the role of the AMPK plant ortholog SnRK1 as a metabolic master regulator under energy deprivation. *Sci. Rep.* **2016**, *6*, 31697. [[CrossRef](#)] [[PubMed](#)]
375. Emanuelle, S.; Doblin, M.S.; Stapleton, D.I.; Bacic, A.; Gooley, P.R. Molecular insights into the enigmatic metabolic regulator, SnRK1. *Trends Plant Sci.* **2016**, *21*, 341–353. [[CrossRef](#)] [[PubMed](#)]
376. Dröge-Laser, W.; Weiste, C. The C/S 1 bZIP network: A regulatory hub orchestrating plant energy homeostasis. *Trends Plant Sci.* **2018**, *23*, 422–433. [[CrossRef](#)] [[PubMed](#)]
377. Yanagisawa, S. Dof1 and Dof2 transcription factors are associated with expression of multiple genes involved in carbon metabolism in maize. *Plant J.* **2000**, *21*, 281–288. [[CrossRef](#)] [[PubMed](#)]
378. Yanagisawa, S.; Akiyama, A.; Kisaka, H.; Uchimiya, H.; Miwa, T. Metabolic engineering with Dof1 transcription factor in plants: Improved nitrogen assimilation and growth under low-nitrogen conditions. *Proc. Natl. Acad. Sci. USA* **2004**, *101*, 7833–7838. [[CrossRef](#)] [[PubMed](#)]
379. Peña, P.A.; Quach, T.; Sato, S.; Ge, Z.; Nersesian, N.; Changa, T.; Dweikat, I.; Soundararajan, M.; Clemente, T.E. Expression of the maize Dof1 transcription factor in wheat and sorghum. *Front. Plant Sci.* **2017**, *8*, 434. [[CrossRef](#)] [[PubMed](#)]
380. Schneidereit, A.; Imlau, A.; Sauer, N. Conserved cis-regulatory elements for DNA-binding-with-one-finger and homeo-domain-leucine-zipper transcription factors regulate companion cell-specific expression of the *Arabidopsis thaliana* SUCROSE TRANSPORTER 2 gene. *Planta* **2008**, *228*, 651. [[CrossRef](#)] [[PubMed](#)]
381. Skirycz, A.; Reichelt, M.; Burow, M.; Birkemeyer, C.; Rolcik, J.; Kopka, J.; Zanor, M.I.; Gershenzon, J.; Strnad, M.; Szopa, J.; et al. DOF transcription factor AtDof1.1 (OBP2) is part of a regulatory network controlling glucosinolate biosynthesis in *Arabidopsis*. *Plant J.* **2006**, *47*, 10–24. [[CrossRef](#)] [[PubMed](#)]
382. Wu, Y.; Lee, S.K.; Yoo, Y.; Wei, J.; Kwon, S.Y.; Lee, S.W.; Jeon, J.S.; An, G. Rice transcription factor OsDOF11 modulates sugar transport by promoting expression of sucrose transporter and SWEET genes. *Mol. Plant* **2018**, *11*, 833–845. [[CrossRef](#)] [[PubMed](#)]
383. Castaings, L.; Camargo, A.; Pocholle, D.; Gaudon, V.; Texier, Y.; Boutet-Mercey, S.; Taconnat, L.; Renou, J.P.; Daniel-Vedele, F.; Fernandez, E.; et al. The nodule inception-like protein 7 modulates nitrate sensing and metabolism in *Arabidopsis*. *Plant J.* **2009**, *57*, 426–435. [[CrossRef](#)] [[PubMed](#)]



384. Konishi, M.; Yanagisawa, S. *Arabidopsis* NIN-like transcription factors have a central role in nitrate signalling. *Nat. Commun.* **2013**, *4*, 1617. [[CrossRef](#)] [[PubMed](#)]
385. Marchive, C.; Roudier, F.; Castaigns, L.; Bréhaut, V.; Blondet, E.; Colot, V.; Meyer, C.; Krapp, A. Nuclear retention of the transcription factor NLP7 orchestrates the early response to nitrate in plants. *Nat. Commun.* **2013**, *4*, 1713. [[CrossRef](#)] [[PubMed](#)]
386. Medici, A.; Krouk, G. The primary nitrate response: A multifaceted signalling pathway. *J. Exp. Bot.* **2014**, *65*, 5567–5576. [[CrossRef](#)] [[PubMed](#)]
387. De Jong, F.; Thodey, K.; Lejay, L.V.; Bevan, M.W. Glucose elevates NITRATE TRANSPORTER2. 1 protein levels and nitrate transport activity independently of its HEXOKINASE1-mediated stimulation of NITRATE TRANSPORTER2.1 expression. *Plant Physiol.* **2014**, *164*, 308–320. [[CrossRef](#)] [[PubMed](#)]
388. Ruffel, S.; Gojon, A.; Lejay, L. Signal interactions in the regulation of root nitrate uptake. *J. Exp. Bot.* **2014**, *65*, 5509–5517. [[CrossRef](#)] [[PubMed](#)]
389. Johannesson, H.; Wang, Y.; Engström, P. DNA-binding and dimerization preferences of *Arabidopsis* homeodomain-leucine zipper transcription factors in vitro. *Plant Mol. Biol.* **2001**, *45*, 63–73. [[CrossRef](#)] [[PubMed](#)]
390. Hanson, J.; Johannesson, H.; Engström, P. Sugar-dependent alterations in cotyledon and leaf development in transgenic plants expressing the HDZhdip gene *ATHB13*. *Plant Mol. Biol.* **2001**, *45*, 247–262. [[CrossRef](#)] [[PubMed](#)]
391. Ribone, P.A.; Capella, M.; Chan, R.L. Functional characterization of the homeodomain leucine zipper I transcription factor AtHB13 reveals a crucial role in *Arabidopsis* development. *J. Exp. Bot.* **2015**, *66*, 5929–5943. [[CrossRef](#)] [[PubMed](#)]
392. Mantioli, C.C.; Tomaz, J.P.; Duarte, G.T.; Prado, F.M.; Del Bem, L.E.V.; Silveira, A.B.; Gauer, L.; Corrêa, L.G.; Drumond, R.D.; Viana, A.J.C.; et al. The *Arabidopsis* bZIP gene *AtbZIP63* is a sensitive integrator of transient ABA and glucose signals. *Plant Physiol.* **2011**. [[CrossRef](#)] [[PubMed](#)]
393. Kunz, S.; Gardeström, P.; Pesquet, E.; Kleczkowski, L.A. Hexokinase 1 is required for glucose-induced repression of *bZIP63*, *At5g22920*, and *BT2* in *Arabidopsis*. *Front. Plant Sci.* **2015**, *6*, 525. [[CrossRef](#)] [[PubMed](#)]
394. Seok, H.Y.; Woo, D.H.; Nguyen, L.V.; Tran, H.T.; Tarte, V.N.; Mehdi, S.M.M.; Lee, S.Y.; Moon, Y.H. *Arabidopsis* AtNAP functions as a negative regulator via repression of AREB1 in salt stress response. *Planta* **2017**, *245*, 329–341. [[CrossRef](#)] [[PubMed](#)]
395. Sakuraba, Y.; Kim, Y.S.; Han, S.H.; Lee, B.D.; Paek, N.C. The *Arabidopsis* transcription factor NAC016 promotes drought stress responses by repressing AREB1 transcription through a trifurcate feed-forward regulatory loop involving NAP. *Plant Cell* **2015**. [[CrossRef](#)] [[PubMed](#)]
396. Des Marais, D.L.; Skillern, W.D.; Juenger, T.E. Deeply diverged alleles in the *Arabidopsis* AREB1 transcription factor drive genome-wide differences in transcriptional response to the environment. *Mol. Biol. Evol.* **2015**, *32*, 956–969. [[CrossRef](#)] [[PubMed](#)]
397. García, M.N.M.; Stritzler, M.; Capiati, D.A. Heterologous expression of *Arabidopsis* ABF4 gene in potato enhances tuberization through ABA-GA crosstalk regulation. *Planta* **2014**, *239*, 615–631. [[CrossRef](#)] [[PubMed](#)]
398. Jia, W.; Zhang, L.; Wu, D.; Liu, S.; Gong, X.; Cui, Z.; Cui, N.; Cao, H.; Rao, L.; Wang, C. Sucrose transporter AtSUC9 mediated by a low sucrose level is involved in *Arabidopsis* abiotic stress resistance by regulating sucrose distribution and ABA accumulation. *Plant Cell Physiol.* **2015**, *56*, 1574–1587. [[CrossRef](#)] [[PubMed](#)]
399. Shinozaki, K.; Yamaguchi-Shinozaki, K. Gene expression and signal transduction in water-stress response. *Plant Physiol.* **1997**, *115*, 327–334. [[CrossRef](#)] [[PubMed](#)]
400. Barczak-Brzyżek, A.; Kielkiewicz, M.; Górecka, M.; Kot, K.; Karpińska, B.; Filipecki, M. Abscisic Acid Insensitive 4 transcription factor is an important player in the response of *Arabidopsis thaliana* to two-spotted spider mite (*Tetranychus urticae*) feeding. *Exp. Appl. Acarol.* **2017**, *73*, 317–326. [[CrossRef](#)] [[PubMed](#)]
401. Liu, S.; Hao, H.; Lu, X.; Zhao, X.; Wang, Y.; Zhang, Y.; Xie, Z.; Wang, R. Transcriptome profiling of genes involved in induced systemic salt tolerance conferred by *Bacillus amyloliquefaciens* FZB42 in *Arabidopsis thaliana*. *Sci. Rep.* **2017**, *7*, 10795. [[CrossRef](#)] [[PubMed](#)]
402. Hsiao, Y.C.; Hsu, Y.F.; Chen, Y.C.; Chang, Y.L.; Wang, C.S. A WD40 protein, AtGHS40, negatively modulates abscisic acid degrading and signaling genes during seedling growth under high glucose conditions. *J. Plant Res.* **2016**, *129*, 1127–1140. [[CrossRef](#)] [[PubMed](#)]
403. Huang, X.; Zhang, X.; Gong, Z.; Yang, S.; Shi, Y. ABI4 represses the expression of type-A ARR2s to inhibit seed germination in *Arabidopsis*. *Plant J.* **2017**, *89*, 354–365. [[CrossRef](#)] [[PubMed](#)]



404. Ramon, M.; Rolland, F.; Thevelein, J.M.; Van Dijck, P.; Leyman, B. ABI4 mediates the effects of exogenous trehalose on *Arabidopsis* growth and starch breakdown. *Plant Mol. Biol.* **2007**, *63*, 195–206. [[CrossRef](#)] [[PubMed](#)]
405. Shkolnik-Inbar, D.; Adler, G.; Bar-Zvi, D. ABI4 downregulates expression of the sodium transporter HKT1; 1 in *Arabidopsis* roots and affects salt tolerance. *Plant J.* **2013**, *73*, 993–1005. [[CrossRef](#)] [[PubMed](#)]
406. Ezer, D.; Shepherd, S.J.; Brestovitsky, A.; Dickinson, P.; Cortijo, S.; Charoensawan, V.; Box, M.S.; Biswas, S.; Jaeger, K.; Wigge, P.A. The G-box transcriptional regulatory code in *Arabidopsis*. *Plant Physiol.* **2017**, *175*, 628–640. [[CrossRef](#)] [[PubMed](#)]
407. Pedrotti, L.; Weiste, C.; Nägele, T.; Wolf, E.; Lorenzin, F.; Dietrich, K.; Mair, A.; Weckwerth, W.; Teige, M.; Baena-González, E.; et al. Snf1-RELATED KINASE1-controlled C/S1-bZIP signaling activates alternative mitochondrial metabolic pathways to ensure plant survival in extended darkness. *Plant Cell* **2018**. [[CrossRef](#)] [[PubMed](#)]
408. Thalor, S.K.; Berberich, T.; Lee, S.S.; Yang, S.H.; Zhu, X.; Imai, R.; Takahashi, Y.; Kusano, T. Deregulation of sucrose-controlled translation of a bZIP-type transcription factor results in sucrose accumulation in leaves. *PLoS ONE* **2012**, *7*, e33111. [[CrossRef](#)] [[PubMed](#)]
409. Guo, H.; Ecker, J.R. Plant responses to ethylene gas are mediated by SCFEBF1/EBF2-dependent proteolysis of EIN3 transcription factor. *Cell* **2003**, *115*, 667–677. [[CrossRef](#)]
410. Nie, H.; Zhao, C.; Wu, G.; Wu, Y.; Chen, Y.; Tang, D. SR1, a calmodulin-binding transcription factor, modulates plant defense and ethylene-induced senescence by directly regulating NDR1 and EIN3. *Plant Physiol.* **2012**, *158*, 1847–1859. [[CrossRef](#)] [[PubMed](#)]
411. Solano, R.; Stepanova, A.; Chao, Q.; Ecker, J.R. Nuclear events in ethylene signaling: A transcriptional cascade mediated by *ETHYLENE-INSENSITIVE3* and *ETHYLENE-RESPONSE-FACTOR1*. *Genes Dev.* **1998**, *12*, 3703–3714. [[CrossRef](#)] [[PubMed](#)]
412. Wojcikowska, B.; Gaj, M.D. High activity of auxin response factors (ARF5, ARF6, ARF10 and ARF16) in somatic embryogenesis of *Arabidopsis*. *BioTechnol. J. Biotechnol. Comput. Biol. Bionanotechnol.* **2013**, *94*, 336–352.
413. Liu, X.; Zhang, H.; Zhao, Y.; Feng, Z.; Li, Q.; Yang, H.Q.; Luan, S.; Li, J.; He, Z.H. Auxin controls seed dormancy through stimulation of abscisic acid signaling by inducing ARF-mediated ABI3 activation in *Arabidopsis*. *Proc. Natl. Acad. Sci. USA* **2013**, *110*, 15485–15490. [[CrossRef](#)] [[PubMed](#)]
414. Ding, Z.; Friml, J. Auxin regulates distal stem cell differentiation in *Arabidopsis* roots. *Proc. Natl. Acad. Sci. USA* **2010**, *107*, 12046–12051. [[CrossRef](#)] [[PubMed](#)]
415. Liu, P.P.; Montgomery, T.A.; Fahlgren, N.; Kasschau, K.D.; Nonogaki, H.; Carrington, J.C. Repression of *AUXIN RESPONSE FACTOR10* by microRNA160 is critical for seed germination and post-germination stages. *Plant J.* **2007**, *52*, 133–146. [[CrossRef](#)] [[PubMed](#)]
416. Wang, J.W.; Wang, L.J.; Mao, Y.B.; Cai, W.J.; Xue, H.W.; Chen, X.Y. Control of root cap formation by microRNA-targeted auxin response factors in *Arabidopsis*. *Plant Cell* **2005**, *17*, 2204–2216. [[CrossRef](#)] [[PubMed](#)]
417. Wójcikowska, B.; Gaj, M.D. Expression profiling of *AUXIN RESPONSE FACTOR* genes during somatic embryogenesis induction in *Arabidopsis*. *Plant Cell Rep.* **2017**, *36*, 843–858. [[CrossRef](#)] [[PubMed](#)]
418. Mei, L.; Yuan, Y.; Wu, M.; Gong, Z.; Zhang, Q.; Yang, F.; Zhang, Q.; Luo, Y.; Xu, X.; Zhang, W.; et al. SLARF10, an auxin response factor, is required for chlorophyll and sugar accumulation during tomato fruit development. *bioRxiv* **2018**. [[CrossRef](#)]
419. Liang, J.; He, J. Protective role of anthocyanins in plants under low nitrogen stress. *Biochem. Biophys. Res. Commun.* **2018**, *498*, 946–953. [[CrossRef](#)] [[PubMed](#)]
420. Broeckling, B.E.; Watson, R.A.; Steinwand, B.; Bush, D.R. Intronic sequence regulates sugar-dependent expression of *Arabidopsis thaliana* production of anthocyanin pigment-1/MYB75. *PLoS ONE* **2016**, *11*, e0156673. [[CrossRef](#)] [[PubMed](#)]
421. Jeong, S.W.; Das, P.K.; Jeoung, S.C.; Song, J.Y.; Lee, H.K.; Kim, Y.K.; Kim, W.J.; Park, Y.I.; Yoo, S.D.; Choi, S.B.; et al. Ethylene suppression of sugar-induced anthocyanin pigmentation in *Arabidopsis*. *Plant Physiol.* **2010**, *154*, 1514–1531. [[CrossRef](#)] [[PubMed](#)]
422. Kwon, Y.; Oh, J.E.; Noh, H.; Hong, S.W.; Bhoo, S.H.; Lee, H. The ethylene signaling pathway has a negative impact on sucrose-induced anthocyanin accumulation in *Arabidopsis*. *J. Plant Res.* **2011**, *124*, 193–200. [[CrossRef](#)] [[PubMed](#)]

423. Bhargava, A.; Mansfield, S.D.; Hall, H.C.; Douglas, C.J.; Ellis, B.E. MYB75 functions in regulation of secondary cell wall formation in the *Arabidopsis* inflorescence stem. *Plant Physiol.* **2010**, *154*, 1428–1438. [[CrossRef](#)] [[PubMed](#)]
424. Xu, Z.; Mahmood, K.; Rothstein, S.J. ROS Induces Anthocyanin Production via Late Biosynthetic Genes and Anthocyanin Deficiency Confers the Hypersensitivity to ROS-Generating Stresses in *Arabidopsis*. *Plant Cell Physiol.* **2017**, *58*, 1364–1377. [[CrossRef](#)] [[PubMed](#)]
425. Lewis, D.R.; Ramirez, M.V.; Miller, N.D.; Vallabhaneni, P.; Ray, W.K.; Helm, R.F.; Winkel, B.S.; Muday, G.K. Auxin and ethylene induce flavonol accumulation through distinct transcriptional networks. *Plant Physiol.* **2011**, *156*, 144–164. [[CrossRef](#)] [[PubMed](#)]
426. Piskurewicz, U.; Jikumaru, Y.; Kinoshita, N.; Nambara, E.; Kamiya, Y.; Lopez-Molina, L. The gibberellic acid signaling repressor RGL2 inhibits *Arabidopsis* seed germination by stimulating abscisic acid synthesis and ABI5 activity. *Plant Cell* **2008**, *20*, 2729–2745. [[CrossRef](#)] [[PubMed](#)]
427. Finkelstein, R.R.; Lynch, T.J. The *Arabidopsis* abscisic acid response gene ABI5 encodes a basic leucine zipper transcription factor. *Plant Cell* **2000**, *12*, 599–609. [[CrossRef](#)] [[PubMed](#)]
428. Yu, L.H.; Wu, J.; Zhang, Z.S.; Miao, Z.Q.; Zhao, P.X.; Wang, Z.; Xiang, C.B. *Arabidopsis* MADS-box transcription factor AGL21 acts as environmental surveillance of seed germination by regulating ABI5 expression. *Mol. Plant* **2017**, *10*, 834–845. [[CrossRef](#)] [[PubMed](#)]
429. Chang, G.; Wang, C.; Kong, X.; Chen, Q.; Yang, Y.; Hu, X. AFP2 as the novel regulator breaks high-temperature-induced seeds secondary dormancy through ABI5 and SOM in *Arabidopsis thaliana*. *Biochem. Biophys. Res. Commun.* **2018**, *501*, 232–238. [[CrossRef](#)] [[PubMed](#)]
430. Dekkers, B.J.; Schuurmans, J.A.; Smeekens, S.C. Interaction between sugar and abscisic acid signalling during early seedling development in *Arabidopsis*. *Plant Mol. Biol.* **2008**, *67*, 151–167. [[CrossRef](#)] [[PubMed](#)]
431. Reeves, W.M.; Lynch, T.J.; Mobin, R.; Finkelstein, R.R. Direct targets of the transcription factors ABA-Insensitive (ABI) 4 and ABI5 reveal synergistic action by ABI4 and several bZIP ABA response factors. *Plant Mol. Biol.* **2011**, *75*, 347–363. [[CrossRef](#)] [[PubMed](#)]
432. Suzuki, M.; Wang, H.H.Y.; McCarty, D.R. Repression of the LEAFY COTYLEDON 1/B3 regulatory network in plant embryo development by VP1/ABSCISIC ACID INSENSITIVE 3-LIKE B3 genes. *Plant Physiol.* **2007**, *143*, 902–911. [[CrossRef](#)] [[PubMed](#)]
433. Qüesta, J.I.; Song, J.; Geraldo, N.; An, H.; Dean, C. *Arabidopsis* transcriptional repressor VAL1 triggers Polycomb silencing at FLC during vernalization. *Science* **2016**, *353*, 485–488. [[CrossRef](#)] [[PubMed](#)]
434. Chen, N.; Veerappan, V.; Abdelmageed, H.; Kang, M.; Allen, R.D. HSI2/VAL1 silences AGL15 to regulate the developmental transition from seed maturation to vegetative growth in *Arabidopsis*. *Plant Cell* **2018**, *30*, 600–619. [[CrossRef](#)] [[PubMed](#)]
435. Schneider, A.; Aghamirzaie, D.; Elmarakeby, H.; Poudel, A.N.; Koo, A.J.; Heath, L.S.; Grene, R.; Collakova, E. Potential targets of VIVIPAROUS1/ABI3-LIKE1 (VAL1) repression in developing *Arabidopsis thaliana* embryos. *Plant J.* **2016**, *85*, 305–319. [[CrossRef](#)] [[PubMed](#)]
436. Tsukagoshi, H.; Morikami, A.; Nakamura, K. Two B3 domain transcriptional repressors prevent sugar-inducible expression of seed maturation genes in *Arabidopsis* seedlings. *Proc. Natl. Acad. Sci. USA* **2007**, *104*, 2543–2547. [[CrossRef](#)] [[PubMed](#)]
437. Jia, H.; Suzuki, M.; McCarty, D.R. Regulation of the seed to seedling developmental phase transition by the LAFL and VAL transcription factor networks. *Wiley Interdiscip. Rev. Dev. Biol.* **2014**, *3*, 135–145. [[CrossRef](#)] [[PubMed](#)]
438. Sun, X.; Li, Y.; Cai, H.; Bai, X.; Ji, W.; Ding, X.; Zhu, Y. The *Arabidopsis* AtbZIP1 transcription factor is a positive regulator of plant tolerance to salt, osmotic and drought stresses. *J. Plant Res.* **2012**, *125*, 429–438. [[CrossRef](#)] [[PubMed](#)]
439. Liang, M.; Li, H.; Zhou, F.; Li, H.; Liu, J.; Hao, Y.; Wang, Y.; Han, S. Subcellular distribution of NTL transcription factors in *Arabidopsis thaliana*. *Traffic* **2015**, *16*, 1062–1074. [[CrossRef](#)] [[PubMed](#)]
440. Chung, M.S.; Lee, S.; Min, J.H.; Huang, P.; Ju, H.W.; Kim, C.S. Regulation of *Arabidopsis thaliana* plasma membrane glucose-responsive regulator (AtPGR) expression by *A. thaliana* storekeeper-like transcription factor, AtSTKL, modulates glucose response in *Arabidopsis*. *Plant Physiol. Biochem.* **2016**, *104*, 155–164. [[PubMed](#)]
441. Aghdasi, M.; Smeekens, S.; Schlueman, H. Microarray analysis of gene expression patterns in *Arabidopsis* seedlings under trehalose, sucrose and sorbitol treatment. *Int. J. Plant Prod.* **2008**, *2*, 309–320.

442. Peng, H.; Zhao, J.; Neff, M.M. ATAF2 integrates *Arabidopsis* brassinosteroid inactivation and seedling photomorphogenesis. *Development* **2015**, *142*, 4129–4138. [[CrossRef](#)] [[PubMed](#)]
443. Huh, S.U.; Lee, S.B.; Kim, H.H.; Paek, K.H. ATAF2, a NAC transcription factor, binds to the promoter and regulates *NIT2* gene expression involved in auxin biosynthesis. *Mol. Cells* **2012**, *34*, 305–313. [[CrossRef](#)] [[PubMed](#)]
444. Takasaki, H.; Maruyama, K.; Takahashi, F.; Fujita, M.; Yoshida, T.; Nakashima, K.; Myouga, K.; Toyooka, K.; Yamaguchi-Shinozaki, K.; Shinozaki, K. SNAC-As, stress-responsive NAC transcription factors, mediate ABA-inducible leaf senescence. *Plant J.* **2015**, *84*, 1114–1123. [[CrossRef](#)] [[PubMed](#)]
445. Nakano, T.; Suzuki, K.; Ohtsuki, N.; Tsujimoto, Y.; Fujimura, T.; Shinshi, H. Identification of genes of the plant-specific transcription-factor families cooperatively regulated by ethylene and jasmonate in *Arabidopsis thaliana*. *J. Plant res.* **2006**, *119*, 407–413. [[CrossRef](#)] [[PubMed](#)]
446. Delessert, C.; Kazan, K.; Wilson, I.W.; Straeten, D.V.D.; Manners, J.; Dennis, E.S.; Dolferus, R. The transcription factor ATAF2 represses the expression of pathogenesis-related genes in *Arabidopsis*. *Plant J.* **2005**, *43*, 745–757. [[CrossRef](#)] [[PubMed](#)]
447. Bi, Y.M.; Zhang, Y.; Signorelli, T.; Zhao, R.; Zhu, T.; Rothstein, S. Genetic analysis of *Arabidopsis* GATA transcription factor gene family reveals a nitrate-inducible member important for chlorophyll synthesis and glucose sensitivity. *Plant J.* **2005**, *44*, 680–692. [[CrossRef](#)] [[PubMed](#)]
448. Richter, R.; Behringer, C.; Müller, I.K.; Schwechheimer, C. The GATA-type transcription factors GNC and GNL/CGA1 repress gibberellin signaling downstream from DELLA proteins and PHYTOCHROME-INTERACTING FACTORS. *Genes Dev.* **2010**, *24*, 2093–2104. [[CrossRef](#)] [[PubMed](#)]
449. Mara, C.D.; Irish, V.F. Two GATA transcription factors are downstream effectors of floral homeotic gene action in *Arabidopsis*. *Plant Physiol.* **2008**, *147*, 707–718. [[CrossRef](#)] [[PubMed](#)]
450. Richter, R.; Behringer, C.; Zourelidou, M.; Schwechheimer, C. Convergence of auxin and gibberellin signaling on the regulation of the GATA transcription factors GNC and GNL in *Arabidopsis thaliana*. *Proc. Natl. Acad. Sci. USA* **2013**, *110*, 13192–13197. [[CrossRef](#)] [[PubMed](#)]
451. Chiang, Y.H.; Zubo, Y.O.; Tapken, W.; Kim, H.J.; Lavanway, A.M.; Howard, L.; Pilon, M.; Kieber, J.J.; Schaller, G.E. Functional characterization of the GATA transcription factors GNC and CGA1 reveals their key role in chloroplast development, growth, and division in *Arabidopsis*. *Plant Physiol.* **2012**, *160*, 332–348. [[CrossRef](#)] [[PubMed](#)]
452. Gangappa, S.N.; Chattopadhyay, S. MYC2 differentially regulates GATA-box containing promoters during seedling development in *Arabidopsis*. *Plant Signal. Behav.* **2013**, *8*, e25679. [[CrossRef](#)]
453. An, D.; Kim, H.; Ju, S.; Go, Y.S.; Kim, H.U.; Suh, M.C. Expression of *Camelina* WRINKLED1 isoforms rescue the seed phenotype of the *Arabidopsis wri1* mutant and increase the triacylglycerol content in tobacco leaves. *Front. Plant Sci.* **2017**, *8*, 34. [[CrossRef](#)] [[PubMed](#)]
454. Lee, H.G.; Kim, H.; Suh, M.C.; Kim, H.U.; Seo, P.J. The MYB96 transcription factor regulates triacylglycerol accumulation by activating *DGAT1* and *PDAT1* expression in *Arabidopsis* seeds. *Plant Cell Physiol.* **2018**, *59*, 1432–1442. [[CrossRef](#)] [[PubMed](#)]
455. Kang, N.K.; Kim, E.K.; Kim, Y.U.; Lee, B.; Jeong, W.J.; Jeong, B.R.; Chang, Y.K. Increased lipid production by heterologous expression of AtWRI1 transcription factor in *Nannochloropsis salina*. *Biotechnol. Biofuels* **2017**, *10*, 231. [[CrossRef](#)] [[PubMed](#)]
456. Zhai, Z.; Liu, H.; Shanklin, J. Phosphorylation of WRINKLED1 by KIN10 results in its proteasomal degradation, providing a link between energy homeostasis and lipid biosynthesis. *Plant Cell* **2017**, *29*, 871–889. [[CrossRef](#)] [[PubMed](#)]
457. Durrett, T.P.; Weise, S.E.; Benning, C. Increasing the energy density of vegetative tissues by diverting carbon from starch to oil biosynthesis in transgenic *Arabidopsis*. *Plant Biotechnol. J.* **2011**, *9*, 874–883.
458. Baud, S.; Wuillème, S.; To, A.; Rochat, C.; Lepiniec, L. Role of WRINKLED1 in the transcriptional regulation of glycolytic and fatty acid biosynthetic genes in *Arabidopsis*. *Plant J.* **2009**, *60*, 933–947. [[CrossRef](#)] [[PubMed](#)]
459. Santos-Mendoza, M.; Dubreucq, B.; Baud, S.; Parcy, F.; Caboche, M.; Lepiniec, L. Deciphering gene regulatory networks that control seed development and maturation in *Arabidopsis*. *Plant J.* **2008**, *54*, 608–620. [[CrossRef](#)] [[PubMed](#)]
460. Min, J.H.; Ju, H.W.; Yoon, D.; Lee, K.H.; Lee, S.; Kim, C.S. *Arabidopsis* basic Helix-Loop-Helix 34 (bHLH34) is involved in glucose signaling through binding to a GAGA cis-element. *Front. Plant Sci.* **2017**, *8*, 2100. [[CrossRef](#)] [[PubMed](#)]

461. Wang, C.; Yao, X.; Yu, D.; Liang, G. Fe-deficiency-induced expression of *bHLH104* enhances Fe-deficiency tolerance of *Arabidopsis thaliana*. *Planta* **2017**, *246*, 421–431. [[CrossRef](#)] [[PubMed](#)]
462. Li, X.; Zhang, H.; Ai, Q.; Liang, G.; Yu, D. Two bHLH transcription factors, bHLH34 and bHLH104, regulate iron homeostasis in *Arabidopsis thaliana*. *Plant Physiol.* **2016**, *170*, 2478–2493. [[CrossRef](#)] [[PubMed](#)]
463. Tripathi, P.; Rabara, R.C.; Reese, R.N.; Miller, M.A.; Rohila, J.S.; Subramanian, S.; Shen, Q.J.; Morandi, D.; Bücking, H.; Shulaev, V.; et al. A toolbox of genes, proteins, metabolites and promoters for improving drought tolerance in soybean includes the metabolite coumestrol and stomatal development genes. *BMC Genom.* **2016**, *17*, 102. [[CrossRef](#)] [[PubMed](#)]
464. Pandey, G.K.; Grant, J.J.; Cheong, Y.H.; Kim, B.G.; Li, L.; Luan, S. ABR1, an APETALA2-domain transcription factor that functions as a repressor of ABA response in *Arabidopsis*. *Plant Physiol.* **2005**, *139*, 1185–1193. [[CrossRef](#)] [[PubMed](#)]
465. Serra, T.S.; Figueiredo, D.D.; Cordeiro, A.M.; Almeida, D.M.; Lourenço, T.; Abreu, I.A.; Sebastián, A.; Fernandes, L.; Contreras-Moreira, B.; Oliveira, M.M.; et al. OsRMC, a negative regulator of salt stress response in rice, is regulated by two AP2/ERF transcription factors. *Plant Mol. Biol.* **2013**, *82*, 439–455. [[CrossRef](#)] [[PubMed](#)]
466. Chow, C.N.; Zheng, H.Q.; Wu, N.Y.; Chien, C.H.; Huang, H.D.; Lee, T.Y.; Chiang-Hsieh, Y.F.; Hou, P.F.; Yang, T.Y.; Chang, W.C. PlantPAN 2.0: An update of plant promoter analysis navigator for reconstructing transcriptional regulatory networks in plants. *Nucleic Acids Res.* **2015**, *44*, D1154–D1160. [[CrossRef](#)] [[PubMed](#)]



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