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Sugar Signaling and Post-transcriptional Regulation in Plants: An Overlooked or an Emerging Topic?

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Plants are autotrophic organisms that self-produce sugars through photosynthesis. These sugars serve as an energy source, carbon skeletons, and signaling entities throughout plants' life. Post-transcriptional regulation of gene expression plays an important role in various sugar-related processes. In cells, it is regulated by many factors, such as RNA-binding proteins (RBPs), microRNAs, the spliceosome, etc. To date, most of the investigations into sugar-related gene expression have been focused on the transcriptional level in plants, while only a few studies have been conducted on post-transcriptional mechanisms. The present review provides an overview of the relationships between sugar and post-transcriptional regulation in plants. It addresses the relationships between sugar signaling and RBPs, microRNAs, and mRNA stability. These new items insights will help to reach a comprehensive understanding of the diversity of sugar signaling regulatory networks, and open onto new investigations into the relevance of these regulations for plant growth and development.

Keywords: sugar, RNA-binding protein, post-transcriptional regulation, microRNA, mRNA stability

INTRODUCTION

As living organisms, plants need various compounds to meet the requirements of their global metabolism and to finely adapt to different external stimuli. In this process, one of the most essential compounds is sugar, which has both trophic and signaling activities during plant development – a high-energy-demanding and well-controlled process. Plants synthesize sugar from carbon dioxide and water through photosynthesis and finely tune their sugar status to avoid sugar starvation (Stitt and Zeeman, 2012; Kanwar and Jha, 2019; Signorelli et al., 2019). They have evolved a sophisticated machinery to sense different forms of sugars, including hexoses, sucrose, and various sugar phosphates (e.g., trehalose-6-phosphate), and elicit the appropriate responses. Some responses are sugar-type-specific (Granot et al., 2014; Figueroa and Lunn, 2016; Li and Sheen, 2016; Janse van Rensburg and Van den Ende, 2018; Wingler, 2018). As a signaling entity, sugar can influence a diversity of physiological processes of the plant life cycle and operates on transcriptional, post-transcriptional, translational, and post-translational regulation. Most of the currently available knowledge is focused on sugar-dependent transcriptional

regulation (Lastdrager et al., 2014; Li and Sheen, 2016; Sakr et al., 2018; Wingler, 2018; Jiao et al., 2019; Rodriguez et al., 2019; Sami et al., 2019). Post-transcriptional regulation of gene expression is a pivotal mechanism whereby plants rapidly reprogram their transcriptome and proteome in response to endogenous and environmental cues and involves many factors such as proteins [RNA-binding proteins (RBPs)], microRNAs (miRNAs), and the spliceosome (Guerra et al., 2015; Romanowski and Yanovsky, 2015; Zhang, 2015; Kawa and Testerink, 2017; Samad et al., 2017; Marondedze et al., 2019; Rigo et al., 2019). RBPs are mainly cytosolic and nuclear proteins that govern the processing, cellular localization, and decay of cellular RNA. They contain RNA recognition motifs (RRMs) that allow their binding to a specific sequence in the target transcripts (Chou et al., 2017; Tian et al., 2018a; Lu et al., 2019; Mahalingam and Walling, 2020). miRNAs are small non-coding RNA molecules that function in RNA silencing *via* base-pairing with complementary sequences within mRNA molecules (Bartel, 2004, 2018), leading to mRNA cleavage; they shorten the poly(A) tail of mRNAs, or influence mRNA translation, altogether downregulating gene expression through the target transcript (Zhang, 2015; Meyers and Axtell, 2019). Alternative splicing – also termed alternative RNA splicing – is mediated by the spliceosome, a complex and large molecular machinery mainly located within the nucleus of eukaryotic cells (Wilkinson et al., 2020). Splicing can also have other functions, like the generation of premature stop codons that recruit the nonsense-mediated decay (NMD) machinery (Kesarwani et al., 2019; Wilkinson et al., 2020). Consequently, the proteins translated from alternatively spliced mRNAs are expected to have different amino acid sequences, different protein structures, and even different biological functions.

Sugar signaling-dependent regulation represents an intricate regulatory network that relies on highly diverse mechanisms that coordinate the appropriate use of available energy and sugar to sustain plant development and growth under the ever-changing environment. Sugar-dependent post-transcriptional regulation could be one important mechanistic aspect of this network. Current knowledge in this topic is still fragmented and makes it very difficult to draw a comprehensive scheme and bring out new research questions. The present review addresses the relationship between sugar and post-transcriptional gene regulation in plants and provides first insights into the role of various important mechanisms of post-transcriptional regulation, i.e., RBPs, miRNAs, and mRNA decay/stability in sugar-related pathways. It underlines the physiological relevance of such regulation mechanisms in different biological contexts and raises questions for upcoming studies.

SUGAR AND RNA-BINDING PROTEINS

RNA-binding proteins control nearly all aspects of eukaryotic post-transcriptional gene regulation and consequently determine the fate and expression of the plant transcriptome. Hundreds of RBPs have been identified in *Arabidopsis*. Most of them are plant specific, and could carry out specific functions in plant physiology (Lorković, 2009, Reichel et al., 2016). They share one or more canonical RNA-binding domains including the RRM, the K-homology (KH) domain, the Pumilio/FBF (PUF) domain, the RRM and KH domains, DEAD/DEAH boxes, zinc-finger structures, the Piwi/Argonaute/Zwille (PAZ) domain, double-stranded RNA-binding domains (DS-RBD), pentatricopeptide-repeat (PPR) domains, etc. (Silverman et al., 2013; Lee and Kang, 2016; Wang et al., 2018a). The link between glucose signaling and RBP-mediated post-transcriptional regulation has been explored in the model plant *Arabidopsis thaliana*. Transgenic *Arabidopsis* plants overexpressing *atRZ-1a*, which encodes a zinc-finger-containing glycine-rich RNA-binding protein (GRP), exhibited delayed germination and seedling growth under abiotic stresses (dehydration or salt stress), and hypersensitivity to glucose and ABA, relatively to the wild type (Kim and Kang, 2006; Kim et al., 2007b). Yet, the molecular function of *atRZ1* in glucose-dependent post-transcriptional regulation of seedling establishment is still unknown. The RBP FLOWERING CONTROL LOCUS A (FCA) contains two RRM domains and one WW domain (Jang et al., 2009; **Table 1**) and operates as an inhibitor of FLOWERING LOCUS C (FLC; Macknight et al., 1997, Liu et al., 2007), one of the repressor integrators, tightly controls flowering signals (Michaels and Amasino, 1999). FLC is positively and transcriptionally regulated by the ABI5 transcription factor (ABA-insensitive 5, **Figure 1**), which is involved in ABA-mediated floral transition (Wang et al., 2013) and in integrating glucose

TABLE 1 | The type and function of sugar related RBPs.

Gene	RNA-binding protein type	Function
AtRZ-1a	Zinc finger-containing glycine-rich RNA-binding protein	Involve in freezing tolerance and cold stress
GLYCINE RICH PROTEIN 2	RRM protein	Response to cold, osmotic stress, water deprivation, and seed germination
FLOWERING CONTROL LOCUS A	RRM protein and contain WW domain	Involved in the promotion of the transition of the vegetative meristem to reproductive development
HYPONASTIC LEAVES 1	No reports	Flowering, leaf, and root development
APUM2, APUM3, and APUM4	Pumilio/FBF protein	No reports
ALDH7B4	No reports	Aldehyde dehydrogenase
RAFFINOSE SYNTHASE 6	No reports	Biosynthesis of the raffinose; response to cold, karrikin, and oxidative stress
SOAR1	PPR protein	ABA responses, probably located upstream of an ABA-responsive transcription factor ABI5
RhPUF4	Pumilio/FBF protein	Involved in bud outgrowth probably

The function of Arabidopsis protein is from the annotation of TAIR database (www.arabidopsis.org; Swarbreck et al., 2007; Berardini et al., 2015).

and ABA-signaling during early seedling development of *Arabidopsis* (Arroyo et al., 2003; Dekkers et al., 2008). AtSOAR1 (SUPPRESSOR OF THE ABAR OVEREXPRESSOR 1) encodes a dual-localized (cytoplasm-nucleus) pentatricopeptide repeat (PPR) protein repeat (Mei et al., 2014; Jiang et al., 2015). By binding to the mRNA of *ABI5*, it represses ABI5 translation in the regulatory cascade downstream of a putative ABA receptor (ABAR; Bi et al., 2019). At the transcriptional level, the transcription factor RAV1, a member of the RAV (Related to ABI3/VP1) subfamily (Riechmann et al., 2000; Feng et al., 2005), binds directly to the *ABI5* promoter and represses its expression, which is alleviated when RAV1 is phosphorylated by ABA-activated sucrose-non-fermenting-1-related protein kinase-2s (SnRK2s; Feng et al., 2014). SnRK2s is a central node that integrates plant growth and development with ABA signaling and environmental stresses (Zheng et al., 2010; Zhang et al., 2011; Shinozawa et al., 2019), partially through dissociation and inhibition of the target of rapamycin (TOR) kinase complex (Wang et al., 2018b; **Figure 1**). TOR kinase is, itself, an evolutionary conserved master regulator that integrates nutrients, hormones, and energy to promote cell proliferation (Dobrenel et al., 2016; Rosenberger and Chen, 2018; Shi et al., 2018). Interestingly, TOR kinase can directly phosphorylate APUM2, APUM3, and APUM4, three PUF proteins in *Arabidopsis* (**Figure 1**), providing a direct link between the nutrient status and the activity of RBPs (**Table 1**; Van Leene et al., 2019). Although their genuine activity is still unclear, APUM-1 to APUM-6 might act as regulators of stem cell maintenance in the shoot meristem (Francischini and Quaggio, 2009), where TOR kinase signaling is required for integrating sugar, hormone, and environmental signals (Li et al., 2017). The expression of *Rosa hybrida PUF4* (*RhPUF4*, an ortholog of *APUM2*) is upregulated by sucrose before the onset of bud outgrowth and may contribute to the promotion of sugar-mediated shoot branching by binding to the 3'UTR of *RhBRC1* (Wang et al., 2019a), a main repressor hub of shoot branching (Wang et al., 2019b). Furthermore, pharmacological disruption of the oxidative pentose phosphate pathway (OPPP) alters sucrose-related *RhPUF4* upregulation and *RhBRC1* downregulation, suggesting a major role of the OPPP in this process (Wang et al., 2019a). The fact that TOR kinase could mediate the upregulation of glucose-6-phosphate dehydrogenase (G6PD, one of key enzymes of the OPPP) and the activity of TOR kinase is probably under the positive regulation of NADPH, a product of the OPPP (Corradetti and Guan, 2006; Liu and Bassham, 2010), it would be noteworthy to investigate the crosstalk between these two pathways in this post-transcriptional process. In addition, although these findings suggest a plausible role of TOR kinase and the OPPP in sugar-mediated RBP-dependent post-transcriptional regulation, questions about whether additional sugar signaling could contribute to this regulation and the nature of the underlying molecular mechanisms are still open.

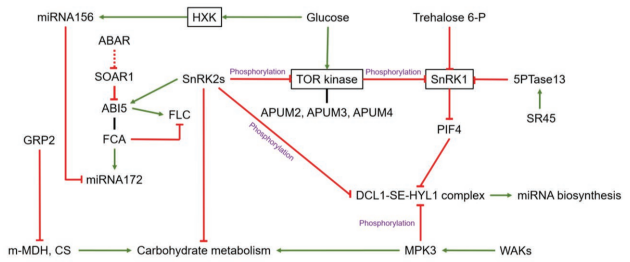

FIGURE 1 | The relationship between sugar and RNA-binding proteins (RBPs), the crosstalk between miRNA and sugar related RNA binding proteins, and alternative splicing in *Arabidopsis*. The green arrow means stimulation or positive effect, the red line means inhibitory effect, and the black line means protein interaction. GRP2, GLYCINE RICH PROTEIN 2; m-MDH, mitochondrial malate dehydrogenase; CS, citrate synthase; FCA, FLOWERING CONTROL LOCUS A; FLC, FLOWERING LOCUS C; ABI5, ABA-insensitive 5; SOAR1, SUPPRESSOR OF THE ABAR OVEREXPRESSOR 1; DRM2, DORMANCY-ASSOCIATED GENE2; SEN1, SENESCENCE-ASSOCIATED GENE1; ASN1, GLUTAMINE-DEPENDENT ASPARAGINE SYNTHETASE1; 5PTase13, 5-phosphatase 13; SR45, serine/arginine-rich 45; PIF4, phytochrome-interacting factor 4; MPK3, MITOGEN-ACTIVATED PROTEIN KINASE 3; WAKs, WALL-ASSOCIATED KINASES.

RNA-binding-proteins can also directly regulate the sugar metabolism by triggering sugar metabolism-related enzymes. GLYCINE RICH PROTEIN 2 (GRP2), a cold-induced zinc-finger-containing GRP (Fusaro et al., 2007), negatively affects germination, in interaction with ABA and glucose (Kim et al., 2007a). GRP2 can interact with mitochondrial malate dehydrogenase (m-MDH) and citrate synthase (CS), two enzymes of the tricarboxylic acid cycle (TCA), probably leading to an adjustment of the sugar metabolism (Kim et al., 2007a; **Figure 1**). The response of GRP2 to other environmental cues and to endogenous factors, including sugars, deserves to be investigated to evaluate the physiological relevance of this regulation. Interestingly, sugar metabolism-related enzymes could both include RBPs and display metabolic activities. Based on an interactome capture technique in *Arabidopsis* cell cultures and leaves, Marondedze et al. (2016) identified 18 RBPs involved in glycolysis, and 15 involved in the glyoxylate and dicarboxylate metabolism, while their respective target mRNAs are still unknown. A similar plausible dual function was also reported for RAFFINOSE SYNTHASE 6 (RS6), a metabolic enzyme, involved in the biosynthesis of the raffinose family oligosaccharides and ALDEHYDE DEHYDROGENASE 7B4 (ALDH7B4; Fujiki et al., 2000; Hou and Bartels, 2015; Reichel et al., 2016; Gilmonreal et al., 2017; Marondedze et al., 2019) in different biological contexts (**Table 1**). ALDH7B4 protein accumulates abundantly in response to abiotic stress and function as aldehyde-detoxifiying enzymes and ROS scavengers enzymes (Kirch et al., 2005; Zhao et al., 2017). Zhao et al. (2018) demonstrated that *ALDH7B4* is a direct target of the NO APICAL MERISTEM/ARABIDOPSIS TRANSCRIPTION ACTIVATION FACTOR/CUP-SHAPED COTYLEDON (NAC) transcription factor ARABIDOPSIS TRANSCRIPTION ACTIVATION FACTOR1 (ATAF1) that integrate carbon starvation responses and trehalose metabolism (Garapati et al., 2015). These findings open onto new investigations on the functional role of their respective target mRNAs and their role in sugar signaling-dependent post-transcriptional regulation.

SUGARS AND MICRORNAs

miRNAs are small non-coding RNA molecules that participate in RNA silencing and post-transcriptional regulation of gene expression (Song et al., 2019). *miRNA* genes are transcribed by RNA polymerase II in the nucleus. This generates long primary transcripts of miRNA (primary miRNAs, pri-miRNA in short), which are converted into a precursor miRNA (pre-miRNA) by endonuclease DICER-like1 (DCL1). After a complex processing involving the C2H2-zinc finger protein SERRATE (SE), DCL1 and the double-stranded RBP HYPONASTIC LEAVES1 (HYL1), the miRNA is loaded onto ARGONAUTE1 (AGO1) to integrate the RNA-induced silencing complex (RISC; Voinnet, 2009; Rogers and Chen, 2013). Several studies support a direct link between sugar signaling and miRNAs in a variety of physiological processes in plants. Duarte et al. (2013) shown that *Arabidopsis* mutants disrupted in miRNA biosynthesis (*hyl1-2* and *dcl1-11*) and miRNA activity (*ago1-25*) exhibited a glucose-hyposensitive phenotype at the early seedling stage, and the expression of several miRNA target genes was deregulated, mainly *via* hexokinase-independent pathway. miRNA156 is one of the best characterized miRNAs in terms of sugar-dependent regulation. It is conserved in land plants and contributes to diverse physiological processes such as leaf development, heat stress memory, developmental transition, apical dominance, and flowering (Kim et al., 2012; Bhogale et al., 2014; Yu et al., 2015; Zhang, 2015; Gao et al., 2018; Kumar et al., 2020). The biological function of miRNA156 implies the repression of SQUAMOSA-PROMOTER BINDING PROTEIN-LIKEs (SPLs; Wang et al., 2009; Wahl et al., 2013; Xu et al., 2016; Wei et al., 2017; Zheng et al., 2019a,b; Hu et al., 2020, Jiao et al., 2020; Ponnu et al., 2020). A direct link between sugar and miRNA156 abundance is based on the ability of exogenous glucose or sucrose supply to cause the levels of mature miRNA156 to drop and thereby accelerate the vegetative-reproductive phase transition, along with the juvenile-to-adult phase transition. Conversely, defoliation and a reduced photosynthetic rate delay plant developmental transitions (Yang et al., 2013; Yu et al., 2013). The glucose-induced repression of miRNA156 is dependent on the hexokinase 1-signaling pathway (Yang et al., 2013), while trehalose-6-phosphaste regulates developmental transition through a distinct mechanism (Wahl et al., 2013; Ponnu et al., 2020). miRNA156 also targets a variety of mRNAs that encode regulatory proteins involved in various physiological processes in plants (Wang and Wang, 2015). Like miRNA156, miRNA399 was determined to be sucrose-responsive through a microRNA array assay and high levels of sucrose inhibited the accumulation of microRNA399 family under phosphate starvation conditions in *Arabidopsis* (Tian et al., 2018b). miRNA398, that is associated with the adaptive plant response to biotic, abiotic, and nutrient stresses and could be involved in sugar-signaling pathway (Sunkar et al., 2006; Dugas and Bartel, 2008; Jia et al., 2009; Feng et al., 2015). *miRNA398* accumulation is repressed by carbon depletion (Pant et al., 2009), while sucrose supply induces its accumulation through the SPL7 transcription factor that directly recognizes the GTAC boxes located in the *miRNA398* promoter (Yamasaki et al., 2009). In line with this, *spl7* knockdown mutants consistently accumulate lower levels of miRNA398 under normal conditions (Ren and Tang, 2012). Targets of miR398a include two ROS-scavenging enzymes (COPPER/ZINC SUPEROXIDE DISMUTASE, CSD1 and CSD2) necessary for detoxification of stress-dependent reactive oxygen species stimulation (Farooq et al., 2019) and this sugar-mediated regulation of *miRNA398* would be an appropriate response to nutrient stress. The *miRNA398* binding site of *CSD1* can be eliminated by alternative splicing in peanut and *Arabidopsis*, resulting in different tolerance levels to abiotic stress (Park and Grabau, 2017), indicating how alternative splicing processes influence plant response through interactions with miRNAs. Microarray analyses have also shown responsiveness to sucrose from other mature miRNAs in *Arabidopsis* (**Figure 2**), including miRNA408 (involved in the response to iron deficiency and in photosynthesis; Pan et al., 2018; Carrió-Seguí et al., 2019), miRNA319 (involved in leaf development; Koyama et al., 2017), and miRNA160 (involved in heat tolerance; Lin et al., 2018). The levels of miRNA319 and miRNA408 are enhanced by sucrose supply, while the levels of miRNA160 are reduced. Moreover, the induction of miRNA408 by sucrose is associated once again with SPL7 (Ren and Tang, 2012), which may play a prominent role in sugar-mediated regulation of miRNA biosynthesis (**Figure 2**). In sweet sorghum (*Sorghum bicolor*), the expression levels of nine known mature miRNAs and 12 novel mature miRNAs have been found influenced by sugar abundance in the stem (Yu et al., 2015). Although the targets of these mature miRNAs exhibit functions related to shoot apical meristem specification, polar specification of the adaxial/abaxial axis, bilateral symmetry determination, and transcriptional regulation (Yu et al., 2015), the genuine participation of sugar sensing and signaling in this regulatory network remains to be elucidated.

A link between sucrose transporters (SUTs, H^+/Suc symporters) and miRNAs exists in plants. SUTs are key players in sucrose phloem loading and sugar allocation within plants

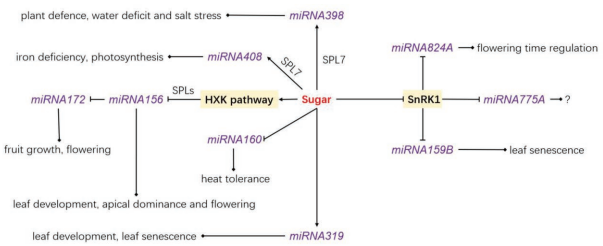

FIGURE 2 | The relationship between sugar and reported *miRNA*, and the function of the related *miRNA*. Sugar stimulates the transcription of *miRNA398*, *miRNA408*, and *miRNA319* but inhibits that of *miRNA160* and *miRNA156*. SnRK1 inhibits the transcription of *miRNA824A*, *miRNA775A*, and *miRNA159B*. HKX1, *hexokinase 1*; SPL, *SQUAMOSA-PROMOTER BINDING PROTEIN-LIKE*.

(Braun et al., 2014; Milne et al., 2017; Doidy et al., 2019). The half-life of SUT mRNAs ranges between 60 and 130 min and is tightly related to miRNA regulation (He et al., 2008; Liesche et al., 2011). Interestingly, the relationship between miRNA biosynthesis and the cellular energy status is also supported by the fact that the transient overexpression of the energy-sensing SnRK1 in protoplasts leads to the repression of a variety of miRNAs (Confraria et al., 2013). These include miRNA159B (involved in leaf senescence, Huo et al., 2015), miRNA161 (induces the expression of PPR genes, Cai et al., 2018), miRNA775A (no function reported to date), and miRNA824A (involved in flowering time regulation, Hu et al., 2014) and might be involved in SnRK1-dependent energy signaling. However, the molecular regulatory network involved in this SnRK1-dependent miRNA biosynthesis remains an open question.

CROSSTALK BETWEEN SUGAR-RELATED RNA-BINDING PROTEINS AND MICRORNAs

Post-translational modifications have been reported as a key regulator of the miRNA-biogenesis machinery. In *Arabidopsis*, HYL1 activity is controlled by its phosphorylation state through complex mechanisms. The Protein Phosphatase 4 (PP4)/Suppressor of MEK 1 (SMEK1) complex and C-TERMINAL DOMAIN PHOSPHATASE-LIKE 1 and 2 (CPL1 and CPL2) dephosphorylate and activate HYL1, while Mitogen-activated Protein Kinase (MPK) phosphorylates and inactivates it (Manavella et al., 2012; Su et al., 2017; Meng et al., 2018, Wang et al., 2019c). MPK might bridge a gap between miRNA biosynthesis and sugar signaling, based on its transducing role the WALL-ASSOCIATED KINASE (WAK)-dependent regulation of vacuolar invertase, a driver of cell expansion and growth and a player of sugar signaling (Kohorn et al., 2006, 2009; **Figure 1**). SnRK2s can also affect the phosphorylation status of HYL and SE (Yan et al., 2017), and it will be very interesting to explore the sensitivity of these two proteins to the kinase activity of SnRK1 and, thereby, its relevance in SnRK1-dependent miRNA biosynthesis regulation (Confraria et al., 2013). Beyond this, the basic helix-loop-helix (bHLH) transcription factor phytochrome-interacting factor 4 (PIF4) interacts directly with DCL1 and HYL1 to promote their destabilization and regulate the processing of primary miRNAs during the dark-to-red-light transition (Sun et al., 2018). PIF4 is also controlled through the trehalose-6-phosphate pathway and SnRK1 to modulate *Arabidopsis* hypocotyl elongation in response to high temperature (Delatte et al., 2011; Hwang et al., 2019), so it might be seen as a hub integrating sugar signaling and environmental cues to modulate the regulation of miRNA biogenesis through the DCL1-SE-HYL complex.

Many previous studies indicate that various RBPs participate in miRNA homeostasis. For instance, the WD-40 protein PLEIOTROPIC REGULATORY LOCUS1 (PRL1) is required for miRNAs and small siRNAs to accumulate, by stabilizing pri-miRNAs through its RNA-binding activity and enhancing DCL1 activity (Zhang et al., 2014). Beyond this function, PRL1 acts as a global regulator of sugar, stress, and hormone responses, partly through SnRK1 repression (Flores-Pérez et al., 2010). However, additional investigations are required to elucidate the molecular connections between these different PRL1-dependent regulatory mechanisms. miRNA172 is a downstream component of the regulatory cascade involved in the regulation of flowering time by sugar-dependent miRNA156 repression (Wu et al., 2009; Martin et al., 2010), in which miRNA172 acts as an inducer of FLOWERING LOCUS T (FT) expression. FCA, an RBP, binds to the flanking sequences of the stem-loop within primary miRNA172 transcripts (pri-mRNA172) *via* the RRM, and promotes its accumulation in response to ambient temperature (**Figure 1**). FCA also binds to the primary transcripts of other temperature-responsive miRNAs, such as miRNA398 and miRNA399 (Jung et al., 2012). The RBP TOUGH (TGH) contributes to the pri-miRNA-HYL1 interaction (Ren et al., 2012), while MOS2 (MODIFIER OF SNC1, 2) is involved in pri-miRNA processing (Wu et al., 2013). Many other examples exist, including EMBRYO DEFECTIVE 2793 (EMB2793, THO2), MOS4-ASSOCIATED COMPLEX 7 (MAC7), and REGULATOR OF CBF GENE EXPRESSION 3 (RCF3) which participate in the regulation of miRNA biogenesis by interacting with HYL1 (Francisco-Mangilet et al., 2015; Karlsson et al., 2015; Jia et al., 2017). However, whether other core components of miRNA processing are dependent on RBPs and the way sugar signaling could contribute to this regulatory network still remains unclear.

SUGAR AND MRNA DECAY/STABILITY

In plants, mRNA decay/stability is an important control point in the regulation of gene expression and can discard potentially deleterious errors in mRNA synthesis (Nagarajan et al., 2019). The mRNA decay/stability of many sugar-metabolism-related enzymes is controlled through post-transcriptional regulation. This holds true for the maize cell wall invertase gene (*Incw1*) that displays two transcripts – *Incw1-S* (small) and *Incw1-L* (large) – according to the respective lengths of its 3'untranslated regions (UTR; Cheng et al., 1999). Since sucrose and D-glucose appear to be associated with the increased steady-state abundance of *Incw1-S* mRNA and cell wall invertase activity, these authors suggested that the 3'UTR of the *Incw1* gene was a regulatory sensor of carbon starvation and acted as a link between translation activity and the sink metabolism in plants. The 3'UTRs of *OsVIN1* and *AtvacINV2*, encoding vacuolar invertases in rice and *Arabidopsis*, respectively, are involved in this process. Downstream regulatory elements or a motif that participates in the rapid degradation of mRNAs, e.g., small auxin-up RNAs (SAUR; Feldbrügge et al., 2002; van Mourik et al., 2017), may be involved too (Huang et al., 2007). The expression of α-amylase, an endo-amylolytic enzyme that catalyzes starch degradation in plants, is induced by sucrose starvation and suppressed by sucrose availability in rice. Sugar repression of α-amylase 3 (*αAMY3*) expression in rice suspension cells involves controlling both its transcription rate and mRNA stability (Sheu et al., 1994;

Chan and Yu, 1998). An analysis of reporter mRNA half-lives indicated that two subdomains of the *αAMY3* 3'UTR contained the UAUAUAUGUA motif required for the sugar-dependent destabilization of *αAMY3* mRNA (Sheu et al., 1994; Chan and Yu, 1998). The same motif might also be involved in sugar-mediated post-transcriptional downregulation of *RhBRC1* in *R. hybrida* (Wang et al., 2019a), and could be conserved in angiosperms. Such sugar-dependent regulation of mRNA stability is required for the rapid adjustment of gene expression in response to the sugar status of the cell. In *Arabidopsis* cell cultures, the stability of 224 mRNAs was repressed by sucrose limitation, concomitantly with a drop in the cell metabolic activity (Nicolai et al., 2006). The mRNA half-lives of actin (*ACT*), alcohol dehydrogenase 2 (*ADH2*), glyceraldehyde 3-phosphate dehydrogenase (G3PD), and sucrose synthase P-2 (*SSP2*) were consistently 1.6- to 2.6-fold longer in sucrose-supplied rice cells (Ho et al., 2001). In line with this, the mRNA stability of the bZIP63 transcription factor, an important mediator of the adaptive response induced by SnRK1 during energy or sugar depletion (Baena-González et al., 2007) decreased following exogenous glucose supply in *Arabidopsis* seedlings (Matiolli et al., 2011). The involvement of bZIP63 as a hub integrating the sugar and energy statuses and mRNA stability deserves to be addressed. *Low-β-amylase1* (*lba1*) is a missense mutation of UP-FRAMESHIFT 1 (UPF1) RNA helicase, involved in nonsense-mediated mRNA decay (NMD). Its *Arabidopsis* mutant exhibited lower sugar induction of the *AtβAmy* transcript, which was restored by complementation of the *lba1* mutation with wild type UPF1, further supporting the link between sugar signaling and the fate of the mRNA (Yoine et al., 2006). All these findings clearly indicate a relationship between the sugar status and mRNA stability in a variety of biological contexts, opening the avenue for deciphering the sugar sensing and signaling mechanisms. In line with that, mRNA stability might also be important for the diurnal regulation of mRNA levels of sucrose transporters and in turn in sugar allocation at the whole plant level. For example, a sucrose transporter (SUT1) displayed a quick turnover rate in leaves of tomato (*Lycopersicon esculentum*), potato (*Solanum tuberosum*), and tobacco (*Nicotiana tabacum*; Kühn et al., 1997; Kühn and Grof, 2010). The mRNA levels of *StSUT2* and *StSUT4* may be regulated by putative RBPs (He et al., 2008). Two AUUUA motifs exist in the 3'UTR or CDS region of *StSUT2* and *StSUT4* mRNA (He et al., 2008); they have been characterized as the binding sites of proteins involved in mediating mRNA degradation (Chen and Shyu, 1995; He et al., 2008; Liesche et al., 2011). However, the nature of these proteins is still unknown.

SUGAR AND ALTERNATIVE SPLICING

Alternative splicing is a finely regulated process that takes place during gene expression and leads to a single gene coding for multiple proteins. Serine/arginine-rich 45 (SR45) is a serine/arginine-rich splicing factor that participates in 5' and 3' splicing site selection of introns and can bridge the 5' and 3' components of the spliceosome. The SR45 splicing factor regulates glucose signaling during early seedling development in *Arabidopsis* (Carvalho et al., 2010), more likely through the modulation of SnRK1-stability (Carvalho et al., 2016). The *sr45-1* knockout mutant indeed displays a high level of the energy-limitation-sensing SnRK1 protein under glucose supply, which is in agreement with the upregulation of SnRK1-activated genes such as *SENESCENCE-ASSOCIATED GENE1* (*SEN1*), *GLUTAMINE-DEPENDENT ASPARAGINE SYNTHETASE1* (*ASN1*), and *DORMANCY-ASSOCIATED GENE2* (*DRM2*). Moreover, the glucose hypersensitivity of the *sr45-1* mutant is alleviated when SnRK1 is disrupted (**Figure 1**). SR45 controls the alternative splicing of *5-phosphatase 13* (*5PTase13*) in *Arabidopsis*, which encodes an inositol polyphosphate 5-phosphatase involved in regulating SnRK1 stability negatively *in vitro* (Carvalho et al., 2016; **Figure 1**). This link between sugar signaling and RNA splicing has also been reported for the photomorphogenesis-related alternative splicing shifts primarily controlled by a metabolic photosynthesis-derived signal and exogenous sucrose supply, correlated with the expression of dark-induced genes under the control of SnRK1 (Hartmann et al., 2016). *AtTZF1/AtCTH/AtC3H23* (a tandem-arrayed CCCH-type zinc finger motif involved in stress- and hormone-mediated growth), was also identified as a sugar-sensitive gene in *Arabidopsis* (Qu et al., 2014). AtTZF1 can traffick between the nucleus and cytoplasmic foci and bind both DNA and RNA *in vitro*; it may be involved in RNA regulation and under the control of sugar signaling (Pomeranz et al., 2010). However, the basic molecular mechanisms behind this regulation have not been addressed to date.

CONCLUSION

Post-transcriptional regulation is an essential component of gene expression regulation in plants. Numerous findings have unveiled and characterized various factors involved in post-transcriptional regulation. The present review provides a first comprehensive picture of the relationship between sugar (metabolism and signaling) and post-transcriptional regulation factors in plants, including RBPs, miRNAs, and mRNA stability of sugar-related genes. More work needs to be carried out to figure out the functions and mechanisms related to the involvement of post-transcriptional regulation in sugar-related processes, e.g., whether regulatory mechanisms found in human cells or yeast are also conserved in plants. Considering the frequently observed connection between mRNA abundance and sugar, some recently developed technologies for RNA editing (CRISPR-Cas13), RNA binding (RNA interactome capture, photoactivatable ribonucleoside-enhanced crosslinking), and RNA folding (DMS-seq, SHAPE-seq) will support future studies. Besides, many aspects of RNA decay still need to be studied in depth, such as the spliceosome and the editosome (a large multi-protein complex that catalyzes RNA editing), which play a crucial role in post-transcriptional regulation. Although some reports about the interaction between sugar-related RBPs and miRNAs exist, further investigations are still required to gain a comprehensive understanding of the way sugar signaling operates through each of these post-transcriptional regulation

mechanisms and how they crosstalk to regulate plant growth and development. The hub role of hexokinase, SnRK1, and/or TOR kinase but also the relevance of the trehalose signaling pathway in the different post-transcriptional regulation networks could be two main future lines of research. This further knowledge will also pave the way for discovering a new and complex sugar regulatory network in plants.

AUTHOR CONTRIBUTIONS

All authors listed have made direct contribution to the work, and approved it for publication. MW, LZ, FJ, SS, and JC have written different part of the manuscript. M-DP-G, LO, and LH have contributed to the section sugar and RNA binding proteins and JL to the section of sugars and miRNA.

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