Polysomes, Stress Granules, and Processing Bodies: A Dynamic Triumvirate Controlling Cytoplasmic mRNA Fate and Function[1][OPEN]

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The export of an mRNA from the nucleus to the cytoplasm begins an odyssey of dynamic regulation that determines the location, longevity, and use of the transcript in the production of polypeptides by ribosomes in plant cells. Recent leveraging of mutants, imaging of fluorescent proteins, and omics of protein and ribosome association with mRNAs have significantly enriched our understanding of the intricate regulation of the fates of transcripts within the cytoplasm of plant cells. This Update explores the connections between translation, decay, and storage of mRNAs that involve three heterogenous mRNA-ribonucleoprotein (mRNP) complexes: polyribosomes (polysomes), processing bodies (PBs), and stress granules (SGs; Box 1; Eulalio et al., 2007; Horvathova et al., 2017; Hubstenberger et al., 2017; Hummel et al., 2015; Merchante et al., 2017; Moore et al., 2016; Roy and von Armin et al., 2013). We begin with a brief overview of cellular surveillance of mRNA integrity during the first (pioneer) round of translation. Next, we consider mRNA decay initiated on translating ribosomes, including cotranslational exonucleolytic decay and microRNA (miRNA)-targeted decay. Then, we detail the general decay process of mRNAs initiated by enzymatic deadenylation of the 3′ polyadenylated (poly[A]) tail and removal of the 5′ 7-methyl guanosine (^{7}mG)-cap. Finally, we discuss the selective sequestration of translationally repressed mRNAs in SGs under severe environmental stress. This dynamic interplay between mRNA translation, stabilization, and turnover fine-tunes the differential regulation of genes to enable developmental plasticity and effective environmental responses.

CONNECTIONS BETWEEN mRNA DECAY AND TRANSLATION

mRNA turnover occurs via multiple selective pathways that serve to modulate the abundance of transcripts and to eliminate those that are dysfunctional. Upon export from the nucleus to the cytoplasm, an mRNA may be bound at its 5′ terminus by the two-subunit nuclear cap-binding complex (CBC) composed of CAP BINDING PROTEIN20 (CBP20) and CBP80 (Fig. 1). It is not well understood how the CBC is exchanged for a cytoplasmic cap-binding complex, composed of either eIF4E and eIF4G or eIFiso4E and eIFiso4G. Both eIF4E and eIFiso4E bind directly to the ^{7}mG-cap structure at the 5′ terminus and are tethered to the scaffold proteins eIF4G and eIFiso4G, respectively, which interact directly with a PABP among those bound to the poly(A) tail at the 3′ terminus of the transcript (Browning and Bailey-Serres, 2015). This physical circularization of the polysome enhances primary initiation or subsequent ribosome-recycling events (Gallie, 2014; Browning and Bailey-Serres, 2015).

ADVANCES

- Advancements in imaging and RNA-protein-based "omic" technologies reveal complex dynamics of mRNA activities and fate.
- mRNAs are selectively modulated in cytoplasmic translation, sequestration, and turnover during development and in response to the environment.
- Multiple pathways of mRNA turnover are linked to translation.
- Processing bodies and stress granules are heterogeneous cytoplasmic sites of mRNA turnover and transient restriction from translation, respectively.
- mRNA sequestration and translation are rapidly and reversibly controlled by external and internal stimuli.

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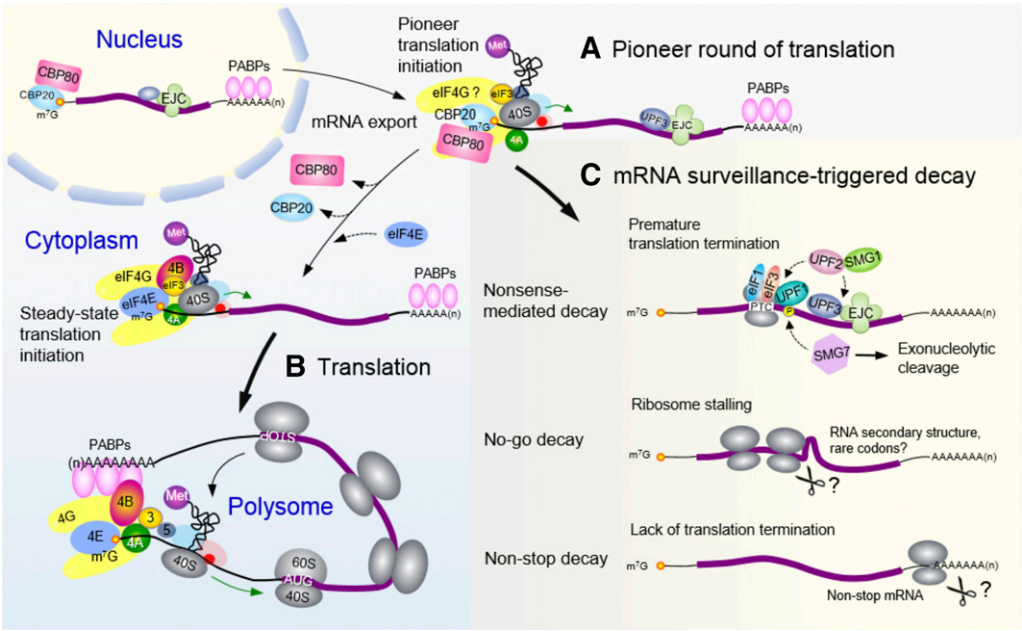

Figure 1. mRNA surveillance-triggered decay during the pioneer round of translation. A, An mRNA is exported from the nucleus to the cytoplasm as an mRNP with the nuclear CBP20/CBP80 cap-binding complex (CBC) bound to the 5′-cap and poly(A)-binding proteins (PABPs) bound to the 3′ poly(A) tail. Within minutes after export, the mRNA undergoes a pioneer round of translation as a quality-control mechanism. B, After the first round of translation and replacement of CBP20 by the eukaryotic translation initiation factor 4E (eIF4E), only mRNAs that pass the quality-control check can enter into active translation as templates for bulk protein synthesis. C, mRNAs with defects in translation are subjected to degradation via different pathways. mRNAs containing a sequence feature that causes premature translation termination (e.g. a premature termination codon [PTC] upstream of an exon junction complex [EJC]) are targeted for nonsense-mediated decay (NMD). mRNAs with stalled translating ribosomes in the coding region or lacking a termination codon may be targeted to the no-go decay and non-stop decay pathways, respectively. In contrast to NMD, which has been characterized, it is less clear if the no-go decay and non-stop decay pathways function in plants. AUG, Translation initiation codon; STOP, termination codon.

It also may safeguard the transcript termini from enzymatic end attacks that can commence its degradation.

mRNA Surveillance-Triggered Decay

mRNAs exported through the nuclear pore undergo a quality-control round of translation that routes transcripts with aberrant features to the NMD pathway (Fig. 1). Several mRNA qualities that compromise the integrity of translation termination trigger NMD, including a PTC marked by the presence of an exon junction complex 3′ of a stop codon (Reddy et al., 2013; Shaul, 2015). This is often a hallmark of incomplete or alternative splicing. Other mRNA features that trigger NMD include a more than 300-nucleotide-long 3′ untranslated region (UTR), an intron in the 3′ UTR that is 50 or more nucleotides downstream of the stop codon, an upstream open reading frame (ORF) that is out of frame with the start codon of the main (protein-coding) ORF (mORF), a truncated transcript due to premature 3′ polyadenylation, or an inefficient or absent stop codon (Reddy et al., 2013).

The early steps of PTC recognition and NMD complex formation in eukaryotes involve UP FRAMESHIFT1 (UPF1), UPF2, UPF3, and SUPPRESSOR WITH MORPHOLOGICAL EFFECT ON GENITALIAs (SMGs; for review, see Shaul, 2015; Dai et al., 2016). The late steps of NMD involve translational repression and the degradation of target mRNAs. In mammals, the degradation of NMD targets is initiated by SMG6-mediated endonucleolytic cleavage followed by exonucleolytic degradation of the 3′ and 5′ cleavage products by the 5′-3′ exoribonuclease EXORIBONUCLEASE1 (XRN1) and the exosome (see below), respectively (Shaul, 2015). In Arabidopsis (*Arabidopsis thaliana*), an ortholog of SMG6 has not been identified, but degradation of NMD substrates occurs in PBs and requires UPF1 and SMG7. It was proposed that AtSMG7 recruits the NMD complex to PBs for mRNA degradation through its interaction with phosphorylated AtUPF1. However, the mechanism by which NMD targets are fully degraded to nucleotides is unknown, since AtXRN4, the functional cytoplasmic ortholog of mammalian XRN1, is not required (Kerényi et al., 2013; Mérai et al., 2013).

In addition to restricting the synthesis of nonfunctional proteins from PTC-containing mRNAs, NMD conditionally regulates the abundance and translation of a number of functional transcripts. For example, NMD controls the developmental transition to flowering by down-regulating a functional *FLOWERING LOCUS M* transcript isoform under elevated temperatures in

Arabidopsis (Sureshkumar et al., 2016). It also tempers levels of defense-related transcripts under normal growth conditions (Jeong et al., 2011; Gloggnitzer et al., 2014; Shaul, 2015), contributes to the repression of *EIN3-BINDING F BOX PROTEIN2* mRNA translation in response to ethylene (Merchante et al., 2015), and promotes the acclimation response to salt stress in Arabidopsis (Vexler et al., 2016). A general dampening of NMD by stresses could be responsible for the increase in NMD-sensitive splicing variants in response to high salt (Drechsel et al., 2013) and prematurely polyadenylated transcripts under hypoxia (de Lorenzo et al., 2017).

XRN4-Mediated Cotranslational Decay

As polysomes and the decay machinery act antagonistically in controlling the function and fate of cytoplasmic mRNAs, it has been generally thought that turnover takes place on ribosome-free mRNPs following translational repression and removal of the 3′ poly(A) tail. Several new studies demonstrate that, in addition to a deadenylation-dependent mechanism (see below), cytoplasmic mRNA degradation can occur cotranslationally in the 5′ to 3′ direction in a deadenylation-independent manner (Fig. 2). By selective purification of polyadenylated mRNAs with a free 5′-monophosphate, studies of Arabidopsis, rice (*Oryza sativa*), and soybean (*Glycine max*) show a global pervasiveness of 5′ decay-intermediate termini that display a three-nucleotide periodicity throughout the mORF, in the same register as the codon periodicity generated by RNase digestion in ribosome footprinting analyses (Hou et al., 2016; Yu et al., 2016; Crisp et al., 2017). This in-frame periodicity in decay intermediates is dependent on XRN4 function, indicating that 5′-3′ mRNA degradation can accompany the codon-by-codon translocation of elongating ribosomes. This cotranslational XRN4 activity most likely follows an inhibition of translational initiation before or as a consequence of removal of the 5′-^{7}mG-cap. Interestingly, cotranslational mRNA degradation is associated with paused or stacked ribosomes on upstream ORFs, within and at the stop codon of certain mORFs, and near to noncleavable miRNA target sites (Hou et al., 2016; Yu et al., 2016). This suggests that cotranslational XRN4-dependent decay may be linked to the kinetics of ribosome translocation, destabilizing mRNAs with sites of rate-limiting translational elongation or termination.

Ribosome pausing and cotranslational decay also may serve as an efficient means for rapid transcriptome adjustment in response to environmental stimuli and transcriptome resetting during stress recovery. For example, cotranslational decay appears to control rapid down-regulation of excess-light-activated transcripts during stress recovery in Arabidopsis plants (Crisp et al., 2017). Moreover, within 15 min of pronounced heat stress (38°C), approximately 25% of the Arabidopsis seedling transcriptome is targeted for XRN4-dependent degradation, including both polysome-associated and polysome-released mRNAs (Merret et al., 2013). The heat-induced decay of polysomal mRNAs is dependent on LA RELATED PROTEIN 1A (LARP1A). High heat triggers the accumulation of XRN4 and the decapping proteins DECAPPING1 (DCP1) and DCP2 in polysomes (Merret et al., 2013) and seems to coincide with ribosome pausing in 5′ mRNA regions to elicit XRN4-dependent decay (Merret et al., 2015). It will be of interest to know how heat triggers the prerequisite mRNA decapping and whether the discrimination of mRNAs for heat-regulated turnover is integrated with the recently uncovered role of eIF5B1 in maintaining efficient translation of a subset of mRNAs, notably those that encode low-M_r nonstress proteins, during heat stress in Arabidopsis (Zhang et al., 2017a).

miRNA-Triggered Decay of Translating mRNAs

miRNA-mediated gene silencing regulates key biological processes in plants, including the plasticity of development in the context of the environment (for review, see Ferdous et al., 2015; Fouracre and Poethig, 2016; D'Ario et al., 2017). The fully processed 21- or 22-nucleotide miRNA and its effector ARGONAUTE1 (AGO1) form a core RNA-induced silencing complex (RISC) that controls the fate of specific mRNAs through a mechanism that involves endonucleolytic cleavage and/or translational repression (Rogers and Chen, 2013). Slicing of miRNA targets by AGO1 generates two truncated cleavage products, termed RISC 5′-and 3′-cleaved fragments, which are further degraded by the cellular RNA decay machinery. In Arabidopsis, the RISC 3′-cleaved fragment contains a free 5′-monophosphate, making it a substrate for XRN4 (Souret et al., 2004). RISC 5′-cleaved fragments undergo rapid turnover upon uridylation at their 3′ end by the miRNA nucleotidyl transferase HEN1 SUPPRESSOR1 (Ren et al., 2014). The pathways participating in RISC 5′-cleaved fragment demise could include 5′-3′ decay by XRN4 (Ren et al., 2014), although the mechanism of the prerequisite removal of the 5′ cap from these fragments is largely unknown. Alternatively, the uridylated fragments may be degraded in the 3′ to 5′ direction by the exosome (see below). This is supported by the observation of their increased abundance in genotypes of Arabidopsis deficient in exosome cofactor SUPERKILLER (SKI) proteins (Branscheid et al., 2015). Recently, Arabidopsis RISC-INTERACTING CLEARING 3′-5′ EXORIBONUCLEASE1 (RICE1) and RICE2 were identified as AGO1- and AGO10-binding proteins that degrade uridylated RISC 5′-cleaved fragments and facilitate RISC recycling (Zhang et al., 2017b).

The copurification of AGO1 and several miRNAs with Arabidopsis polysomes was reported some time ago (Lanet et al., 2009), but only recent coupling of mutant analyses, subcellular fractionation, and ribosome footprinting methods has clearly demonstrated their preferential association with membrane-bound polysomes (MBPs), including those at the

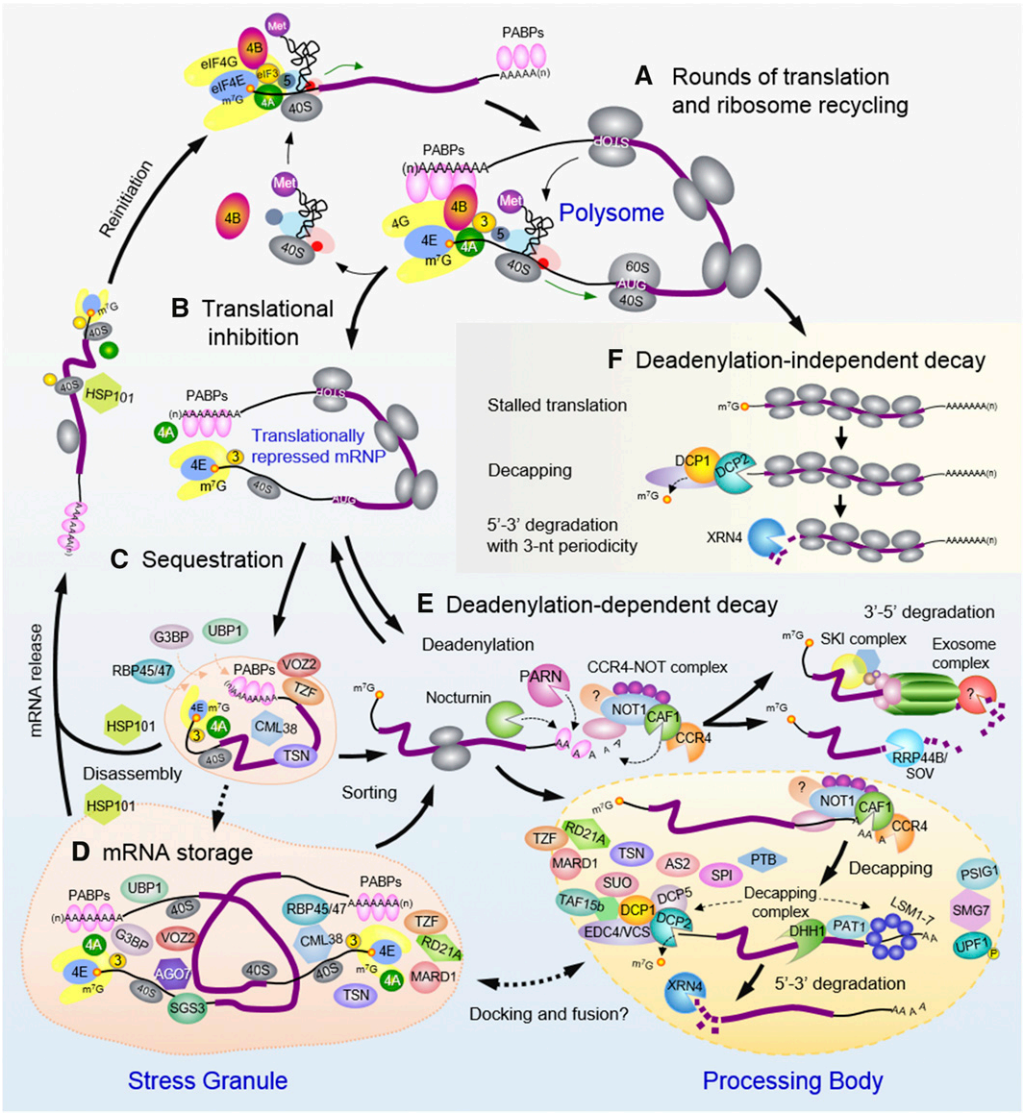

Figure 2. Overview of cytoplasmic mRNA translation, storage, and decay in plants. A, Cytoplasmic mRNAs undergoing active translation form polysomes and remain in a translationally active state until damaged or translationally repressed. B, Repression can result from multiple causes (i.e. altered abundance or phosphorylation of specific translation factors or RNA-binding proteins and ribosome stalling) that limit translational initiation or ribosome translocation, promoting transition into a translationally repressed mRNP, where the mRNA is either sequestered by RNA-binding proteins (e.g. UBP1, G3BP, and RBP45/47) or degraded via different pathways. C, mRNA sequestration is typically triggered by cellular stress, serving as a sorting nucleation point for mRNP assembly into SGs for storage or PBs for degradation. D, During a stress-recovery period, intact mRNAs stored in SGs can reenter translation via a process facilitated by a chaperone (e.g. HSP101 during heat stress recovery). Some mRNAs released from SGs may be targeted for degradation after stress. E, In general mRNA decay, the 3′ protective poly(A) tail is removed by different classes of deadenylases [Nocturnin, poly(A)-specific RNase (PARN), and the CCR-NOT complex], then degradation proceeds in the 3′ to 5′ direction by the multimeric SKI-exosome complex and/or the RRP44B/SOV exonuclease. After deadenylation, mRNA degradation also can occur from the 5′ to 3′ direction. mRNAs degraded via this mode could be localized in the cytosol and/or PBs, where the multiprotein mRNA-decapping complex removes the protective 5′-cap and, subsequently, the 5′-3′ XRN4 exoribonuclease catalyzes nucleotide hydrolysis. F, In addition to the deadenylation-dependent decay pathway, translationally repressed mRNAs can be degraded directly in the 5′ to 3′ direction while in association with elongating ribosomes via XRN4-mediated cotranslational decay. This mode of degradation bypasses deadenylation but may require mRNA decapping. The progressive 5′-3′ exonucleolytic destruction of the mRNA by XRN4 yields a codon-by-codon three-nucleotide signature that is thought to reflect the movement of the most 5′ ribosome along the transcript. AUG, Translation initiation codon; STOP, termination codon.

endoplasmic reticulum (Li et al., 2013, 2016). These studies show that both translational repression and cleavage of miRNA targets occur mainly in these subcellular domains. Notably, MBP association of AtAGO1 is required for miRNA-triggered production of phased secondary small interfering RNAs (phasiRNAs) from select RNAs (e.g. *TRANS-ACTING SIRNA* [*TAS*] transcripts; Li et al., 2016). This is corroborated by the presence of two proteins required for phasiRNA biogenesis, SUPPRESSOR OF GENE SILENCING3 (SGS3) and RNA-DEPENDENT RNA POLYMERASE6, in specific granules called siRNA bodies that reside on the cytoplasmic side of membrane compartments (Jouannet et al., 2012). The position of ribosome footprints generated from MBPs suggests that ribosome occupancy contributes to defining the site of phasiRNA biogenesis on these transcripts (Li et al., 2016). Indeed, functional translation of a positionally conserved short ORF of the AtTAS3 transcript is critical to efficient tasiRNA production (Bazin et al., 2017).

The complex interactions between miRNA-targeted mRNAs and the translational and degradation apparatus raise new questions about the subcompartments of the cytoplasm where these processes take place. Although miRNA-mediated translational repression involves MBPs, prior protein colocalization studies suggest that these processes occur in PBs (Brodersen et al., 2008; Yang et al., 2012). The location of XRN4-mediated decay of the RISC 5′- and 3′-cleaved fragments could be in PBs or freely in the cytosol, since XRN4 is present in both locations (Weber et al., 2008).

GENERAL CYTOPLASMIC mRNA DEGRADATION

General cytoplasmic mRNA degradation in eukaryotic cells is initiated by the removal of the 3′ poly(A) tail, a reversible step known as deadenylation, followed by 5′-cap hydrolysis (decapping) and subsequent 5′ to 3′ mRNA decay by XRN1/4 (Siwaszek et al., 2014). Both processes may occur in but are not confined to PBs. Alternatively, deadenylated mRNAs can be degraded in the 3′ to 5′ direction by the exosome. This section summarizes our current understanding of deadenylation-dependent mRNA turnover machinery and mechanisms as well as the significance of their regulation in plants (Fig. 2; Table I).

Deadenylation

Progressive cytoplasmic mRNA poly(A) tail shortening displaces PABPs from the mRNA 3′ end, likely disrupting the 5′-cap to 3′-tail (eIF4G-PABP) interaction that promotes translational reinitiation (Gallie, 2014), shifting mRNAs toward a translationally silent state and exposing the 3′ terminus to exonucleases (Łabno et al., 2016). This first, rate-limiting step of mRNA decay is catalyzed by Mg^{2+}-dependent 3′-5′ exoribonucleases called deadenylases that are classified into two superfamilies: EEP (exonuclease-endonuclease-phosphatase) and DEDD (Asp-Glu-Asp-Asp) nucleases (Siwaszek et al., 2014).

In yeast and metazoa, shortening and removal of the mRNA 3′ poly(A) tail is performed by two major deadenylase complexes: poly(A)-nuclease PAN2-PAN3 and CARBON CATABOLITE REPRESSOR4-NEGATIVE ON TATA (CCR4-NOT; Wahle and Winkler, 2013). The PAN2-PAN3 complex is a heterotrimer of the DEDD-type PAN2 deadenylase interacting with a PAN3 homodimer (Siwaszek et al., 2014). Interestingly, the PAN2-PAN3 complex is present across higher eukaryotes, including the green alga *Chlamydomonas reinhardtii*, but has not been recognized to date in flowering plants. The CCR4-NOT complex contains two catalytic subunits (i.e. CCR4 and CAF1) and at least seven additional proteins (NOT1–NOT5, CAF40, and CAF130), with NOT1 serving as a scaffold (Miller and Reese, 2012). Of these, CCR4, CAF1, and NOT1 orthologs have been identified in plants (Table I). Arabidopsis encodes two *CCR4* paralogs, *AtCCR4a* and *AtCCR4b*, both of which produce gene products that interact with the decapping complex proteins AtDCP1 and AtDCP2 within and outside of PBs (Suzuki et al., 2015). Mutant analyses have identified some important functions of these functionally redundant EEP deadenylases. For example, they appear to influence Suc and starch metabolism by controlling the poly(A) tail length and steady-state level of *GRANULE-BOUND STARCH SYNTHASE1* mRNA (Suzuki et al., 2015). The expansive Arabidopsis *CAF1* family includes 11 members. The products of two of these, CAF1a and CAF1b, exhibit 3′-5′ exonucleolytic activity in vitro via their conserved DEDD domain, contribute to effective defense response (Liang et al., 2009), and regulate the poly(A) length of a defined set of stress-related transcripts rather than acting as general deadenylases (Liang et al., 2009; Walley et al., 2010).

The study of rice deadenylases has provided further insight. OsCCR4a and OsCCR4b are located predominantly in visible foci, presumably PBs, that include XRN4. The EEP domain of OsCCR4s is sufficient for in vitro 3′-5′ exonuclease activity on poly(A), poly(U), and poly(C) substrates (Chou et al., 2017). Similarly, recombinant OsCAF1A, OsCAF1B, OsCAF1G, and OsCAF1H are 3′-5′ exonucleases, with at least OsCAF1B associating with XRN4 in PB-like foci (Chou et al., 2014). In yeast and mammals, CAF1 serves as a bridge between CCR4 and NOT1 via interactions between the N-terminal Leu-rich repeat of CCR4 and the MIF4G domain of NOT1. The rice CCR4-NOT complex appears to share this topology, although the N-terminal Leu-rich repeat domain of CCR4s is absent and the interaction with CAF1 is apparently replaced by an N-terminal zf-MYND-like domain of CCR4 (Chou et al., 2017).

Two other conserved deadenylases control the turnover of specific transcripts. The first is the EEP-type deadenylase Nocturnin that is distinguished by its circadian clock-regulated transcript abundance in multicellular eukaryotes (Godwin et al., 2013). Arabidopsis *HESPERIN* (*AtHESP*) is closely related to mammalian *Nocturnin*, with maximal mRNA levels in the evening. Intriguingly, altered *AtHESP* expression

Table I. *Proteins involved in the regulation of bulk cytoplasmic mRNA degradation in plants*

AtRRP44A, AtRRP6L1, and AtRRP6L2 are components of the exosome complex, but they are not included here because subcellular localization data suggest that they are nuclear proteins and, hence, components of the nuclear exosome (Lange et al., 2008; Zhang et al., 2010). At, *Arabidopsis thaliana*; Ca, *Capsicum annuum*; Nb, *Nicotiana benthamiana*; Os, *Oryza sativa*; Ta, *Triticum aestivum*.

Protein	Molecular Function	Gene Symbol	Gene Identifier	Biological Functions	References
Deadenylation					
CCR4-NOT complex					
Carbon catabolite repressor4	3′-5′ exoribonuclease, EEP superfamily	*AtCCR4a*	AT3G58560	Suc and starch metabolism	Suzuki et al. (2015)
		AtCCR4b	AT3G58580		
		OsCCR4a	Os10g27230	Unknown	Chou et al. (2017)
		OsCCR4b	Os03g07080		
CCR4-associated factor1	3′-5′ exoribonuclease, DEDD superfamily	*AtCAF1a*	AT3G44260	Defense response to bacterial pathogens; abiotic stress response	Liang et al. (2009); Walley et al. (2010)
		AtCAF1b	AT5G22250		
		OsCAF1A	Os08g34170	Unknown	Chou et al. (2014, 2017)
		OsCAF1B	Os04g58810		
		OsCAF1G	Os09g24990		
		OsCAF1H	Os02g55300		
		CaCAF1		Development and defense response	Sarowar et al. (2007)
Negative on TATA1	CCR4-NOT complex scaffold	*OsNOT1*	Os10g40780	Unknown	Chou et al. (2017)
Nocturnin	Poly(A)-specific 3′-5′ exoribonuclease, EEP superfamily	*AtHESP*	AT1G31500	Circadian clock regulation	Delis et al. (2016)
Poly(A) RNase	Poly(A)-specific 3′-5′ exoribonuclease, DEDD superfamily	*AtPARN/AHG2*	AT1G55870	Embryogenesis; ABA sensitivity; abiotic stress response	Reverdatto et al. (2004); Nishimura et al. (2005)
5′-3′ mRNA decay					
Decapping complex					
Decapping1	Decapping cofactor	*AtDCP1*	AT1G08370	Postembryonic development; dehydration and heat stress response	Xu et al. (2006); Xu and Chua (2012); Motomura et al. (2015)
Decapping2	Decapping enzyme	*AtDCP2/TDT*	AT5G13570	Postembryonic development; heat stress response	Xu et al. (2006); Motomura et al. (2015)
Decapping5	Decapping enhancer	*AtDCP5*	AT1G26110	Postembryonic development; osmotic stress response	Xu and Chua (2009, 2012)
Enhancer of mRNA decapping4	Core decapping complex scaffold	*AtEDC4/VCS*	AT3G13300	Postembryonic development; osmotic stress response; seed dormancy and germination	Xu et al. (2006); Goeres et al. (2007); Soma et al. (2017)
		TaEDC4	Traes_6DL_3FBA5B70E	Plant-fungal pathogen interaction	Petre et al. (2016)
LSM1-7 complex	Decapping enhancer	*AtLSM1a*	AT1G19120	Postembryonic development; heat stress tolerance; ABA-mediated response to cold, drought, and salt tolerance	Perea-Resa et al. (2012, 2016); Golisz et al. (2013); Okamoto et al. (2016)
		AtLSM1b	AT3G14080		
		AtLSM2	AT1G03330		
		AtLSM3a	AT1G21190		
		AtLSM3b	AT1G76860		
		AtLSM4	AT5G27720		
		AtLSM5	AT5G48870		
		AtLSM6a	AT2G43810		
		AtLSM6b	AT3G59810		
		AtLSM7	AT2G03870		
Protein-associated with topoisomerase1	Decapping enhancer, translation repressor?	*AtPAT1*	AT1G79090	Immune response	Roux et al. (2015)

(*Table continues on following page.*)

Table I. (*Continued from previous page.*)

Protein	Molecular Function	Gene Symbol	Gene Identifier	Biological Functions	References
DEAD-box RNA helicase		*AtDHH1*	AT3G61240	Unknown	Xu et al. (2006); Bhullar et al. (2017)
Asymmetric leaf2	Decapping activator	*AtAS2*	AT1G65620	Plant-virus interaction	Ye et al. (2015)
5′-3′ mRNA decay					
Exoribonuclease4	5′-3′ exoribonuclease	*AtXRN4/EIN5*	AT1G54490	Ethylene response/ signaling; heat stress response	Potuschak et al. (2006); Merret et al. (2013)
		NbXRN4	gi|242037819	Defense response to viral pathogen	Peng et al. (2011); Lee et al. (2016)
LA-related protein1A	Heat-specific cofactor of AtXRN4	*AtLARP1A*	AT5G21160	Heat stress response	Merret et al. (2013)
3′-5′ mRNA decay					
Cytoplasmic exosome rRNA processing proteins	RNase PH domain-containing proteins; hexameric core ring subunits of exosome	*AtRRP41*	AT3G61620	Female gametogenesis	Chekanova et al. (2007)
		AtRRP42	AT3G07750	Unknown	Chekanova et al. (2007)
		AtRRP43	AT1G60080	Unknown	Chekanova et al. (2007)
		AtRRP45A	AT3G12990	Essential for viability; cuticular wax biosynthesis	Hooker et al. (2007)
		AtRRP45B/CER7	AT3G60500		
		AtRRP46	AT3G46210	Unknown	Chekanova et al. (2007)
		AtRRP41L/MTR3	AT4G27490	Germination and seedling development	Yang et al. (2013)
	S1/KH domain-containing proteins; cap structure subunits of core exosome	*AtRRP4*	AT1G03360	Postzygotic development	Chekanova et al. (2007)
		AtRRP40A	AT2G25355	Unknown	Chekanova et al. (2007)
		AtRRP40B	AT4G32175	Unknown	Chekanova et al. (2007)
		AtCSL4	AT5G38885	Unknown	Chekanova et al. (2007)
	RNase II-type 3′-5′ exoribonuclease	*AtRRP44B/SOV*	AT1G77680	Compensation of VCS function in postembryonic development	Zhang et al. (2010); Kumakura et al. (2013)
	RNase D-type 3′-5′ exoribonuclease, DEDD superfamily	*AtRRP6L3*	AT2G32415	Unknown	Lange et al. (2008)
Superkiller (SKI) complex					
Superkiller proteins	Auxiliary factors of the exosome	*AtSKI2*	AT3G46960	Cuticular wax biosynthesis	Zhao and Kunst (2016)
		AtSKI3	AT1G76630		
		AtSKI8/VIP3	AT4G29830		

affects the rhythmicity of the core clock oscillator mRNAs *TIMING OF CAB EXPRESSION1* and *CIRCADIAN CLOCK ASSOCIATED1* (Delis et al., 2016). The second is the homodimeric DEDD-class PARNs found in plants and humans but apparently absent from budding yeast (*Saccharomyces cerevisiae*) and fruit flies (*Drosophila melanogaster*; Godwin et al., 2013). Arabidopsis PARN (AtPARN)/ABA HYPERSENSITIVE GERMINATION2 (AHG2) is required for the poly(A) tail shortening of select embryonic transcripts, affecting embryonic development and some stress responses (Chiba et al., 2004; Reverdatto et al., 2004; Nishimura et al., 2005). Altogether, the diversity of factors involved in deadenylation indicates significant control of deadenylation, the first step of general mRNA turnover.

Decapping

Removal of the mRNA 5′-^{7}mG-cap inhibits translation initiation and commits a deadenylated mRNA to complete degradation. mRNA decapping is carried out by DCP2, a conserved bilobed Nudix family enzyme that hydrolyzes the 5′-cap structure in a divalent cation (Mn^{2+}/Mg^{2+})-dependent manner, releasing ^{7}mGDP and a 5′-monophosphorylated mRNA (Arribas-Layton et al., 2013). DCP2 functions in a multisubunit decapping complex, which includes cofactors that mediate its activity and regulators that coordinate decapping with translational repression, deadenylation, and hydrolysis of the mRNA body (Table I). In Arabidopsis, DCP1 and VARICOSE (VCS)/ENHANCER OF mRNA DECAPPING4 (EDC4)

directly modulate DCP2 activity (Xu et al., 2006). All three proteins are considered core decapping complex factors, indispensable for mRNA decapping and essential for postembryonic development (Xu and Chua, 2011). Colocalization of AtDCP1 and AtDCP2 in macromolecular foci detectable by confocal microscopy is dynamically regulated by heat stress (Motomura et al., 2015). Based on mutant analyses, the factor VCS regulates seed dormancy and germination in Arabidopsis (Basbouss-Serhal et al., 2017) and functions in plant-fungal pathogen interactions in *Nicotiana benthamiana* (Petre et al., 2016). Additionally, AtDCP5, an Sm-like (LSM) domain-containing RNA-binding protein (RBP), interacts with DCP1 and DCP2. Unlike DCP1 and VCS, DCP5 does not directly regulate DCP2 activity; however, it is required for PB formation, mRNA decapping, and translational repression associated with mRNA decay. Attenuation of DCP5 function does not result in lethality but causes developmental defects similar to loss-of-function mutants of core complex proteins, including perturbation of germination and leaf venation (Xu and Chua, 2009), indicating that these developmental processes require tight regulation of mRNAs mediated by the decapping pathway.

Phosphorylation of specific residues of the core decapping proteins constitutes a crucial mechanism for the osmotic stress response in plants. Under this stress, Arabidopsis DCP1 is phosphorylated by MAPK6 (MPK6), leading to enhancement of its association with DCP5, which, in turn, promotes the RNA-binding capacity of DCP5 and the mRNA-decapping activity of DCP2 (Xu and Chua, 2012). By contrast, VCS is phosphorylated by the abscisic acid (ABA)-unresponsive osmotic stress-activated subclass I of SUCROSE NONFERMENTING1-RELATED PROTEIN KINASE2s (SnRK2s). Osmotic stress triggers SnRK2 localization in PBs, where they appear to phosphorylate and regulate VCS function (Soma et al., 2017). Mutations that prevent DCP1 or VCS phosphorylation render Arabidopsis plants susceptible to osmotic stress (Xu and Chua, 2012; Soma et al., 2017). These observations firmly suggest that transcriptome adjustments mediated by mRNA decapping are relevant to stress resilience.

In yeast and metazoa, the heptameric LSM1-7 complex, in association with PROTEIN-ASSOCIATED WITH TOPOISOMERASE1 (PAT1), binds to the 3′ end of deadenylated mRNAs and promotes decapping (Tharun, 2009; Haas et al., 2010). Simultaneously, PAT1 interacts with the DEAD-box RNA helicase DHH1/DDX6. Both PAT1 and DDH1 play a role in translational inhibition as well as PB formation (Coller and Parker, 2005; Ozgur et al., 2010; Sharif et al., 2013). This links deadenylation with translational repression and decapping. The LSM1-7 complex has been characterized in Arabidopsis. Genetic analysis of the paralogs *AtLSM1A* and *AtLSM1B* revealed their functional redundancy and importance in normal development (Perea-Resa et al., 2012; Golisz et al., 2013). Similar to DCP1, DCP2, and VCS, both LSM1A and LSM1B accumulate in PBs under heat, cold, drought, and salt stress and are required for conditional PB assembly under these conditions (Perea-Resa et al., 2012, 2016). Intriguingly, the Arabidopsis LSM1s differentially regulate tolerance to abiotic stresses by dynamically controlling the decapping and degradation of a select group of stress-responsive transcripts, including those involved in ABA biosynthesis (Perea-Resa et al., 2016). Mutant analysis shows that the LSM5 component of the LSM1-7 complex is essential for heat tolerance in Arabidopsis, targeting both functional and aberrant transcripts for degradation during heat stress (Okamoto et al., 2016). A proteomic analysis revealed that AtLSM1A forms complexes with VCS, PAT1, DHH1/DDX6-like, and NOT1-like proteins (Golisz et al., 2013), so its interaction with the deadenylation machinery or the 3′ deadenylated mRNA remains somewhat unclear.

Arabidopsis PAT1 interacts with LSM1B and regulates the decapping of select transcripts. It is an MPK4 phosphorylation target that accumulates in PBs in response to the bacterial pathogen-associated molecular pattern flagellin22. PAT1 and MPK4 suppress plant autoimmunity, as loss of their function results in the ENHANCED DISEASE SUSCEPTIBILITY1-mediated constitutive immune response through a pathway downstream of the immune receptor SUPPRESSOR OF MKK1 MKK2 2 (Roux et al., 2015). Studies of the Arabidopsis LSM1-7-PAT1 complex extend the contribution of mRNA decapping from abiotic to biotic stress signaling and suggest that both components and architecture of the mRNA-decapping complex of yeast and metazoa are conserved in plants. An Arabidopsis DHH1-like protein has been identified and shown to localize in DCP1 and DCP2 granules (Xu et al., 2006; Bhullar et al., 2017), but whether this protein interacts with PAT1 and functions in translational repression and mRNA decapping has yet to be elucidated.

Arabidopsis also possesses noncanonical, condition-specific decapping activators important for abiotic and biotic stress responses. For example, the BEACH domain-containing protein SPIRRIG (SPI) is a regulator of cellular membrane dynamics that localizes into PBs under salt stress via its interaction with DCP1. SPI function is required for salt stress-triggered PB assembly, and it selectively stabilizes and destabilizes a subset of salt-responsive transcripts by regulating their translocation into PBs (Steffens et al., 2015). ASYMMETRIC LEAF2 (AS2) is a transcription factor playing a role in leaf development. Intriguingly, AS2 colocalizes with PBs as a result of its trafficking there by the geminivirus nuclear shuttle protein BV1 (Ye et al., 2015). This apparently promotes DCP2 decapping activity to accelerate host mRNA decay, leading to the suppression of host antiviral gene silencing. There are numerous examples of viral conscription of the translational apparatus (Browning and Bailey-Serres, 2015); this example illustrates a bizarre means by which a virus manipulates mRNA turnover.

5′-3′ Degradation

In eukaryotes, the hydrolysis of 5′-monophosphorylated (uncapped) transcripts into nucleotides is executed by

Mg^{2+}-dependent 5′-3′ exoribonucleases of the XRN family, with XRN4 functioning as the cytoplasmic enzyme in Arabidopsis (Kastenmayer and Green, 2000). Unlike the core decapping proteins, disruption of AtXRN4 function only results in mild morphological defects under standard growth conditions. This may reflect reliance on AtXRN4 for the degradation of specific transcripts (Rymarquis et al., 2011). Nevertheless, XRN4-mediated translational repression and mRNA decay play a role in seed dormancy and germination (Basbouss-Serhal et al., 2017), ethylene signaling (Li et al., 2015; Merchante et al., 2015), heat stress response and tolerance (Merret et al., 2013; Nguyen et al., 2015), and viral defense (Jaag and Nagy, 2009; Peng et al., 2011; Lee et al., 2016). An alternative explanation is that, in the absence of XRN4 function, the 3′-5′ degradation pathways described below may maintain homeostasis.

3′-5′ Degradation

After deadenylation, the 3′ end of mRNAs can be hydrolyzed directly by an evolutionarily conserved complex of multiple 3′-5′ exoribonucleases called the exosome. In Arabidopsis, as in other eukaryotes, the exosome core complex is composed of nine subunits. Six are RNase PH domain-containing proteins (RIBOSOMAL RNA PROCESSING PROTEIN41 [RRP41], RRP42, RRP43, RRP45, RRP46, and RRP41L/MTR3) that together form a hexameric core ring that is stabilized by the attachment of a cap of three S1/KH-domain proteins (RRP4, RRP40, and CSL4; Lange and Gagliardi, 2010). Whereas all nine core exosome subunits have equal contributions to the structural and functional integrity of the yeast and mammalian exosome, each Arabidopsis exosome subunit appears to play a distinct and, in some cases, dispensable role suggesting target specificity (Table I). For example, AtCSL4 is apparently dispensable and AtRRP4 alone provides the 3′-5′ exoribonuclease activity (Chekanova et al., 2002, 2007), whereas in yeast and mammals, exosome core subunits are catalytically inactive and additionally require RRP6 and/or RRP44 for the 3′-5′ exoribonuclease activity.

The Arabidopsis genome encodes three *RRP6* paralogs: *AtRRP6L1*, *AtRRP6L2*, and *AtRRP6L3*. Of these gene products, only RRP6L3 was shown to be cytosolic, but its role in mRNA degradation is unknown (Lange et al., 2008). There are two *AtRRP44*-like genes: *AtRRP44A* and *AtRRP44B/SUPPRESSOR OF VARICOSE* (*SOV*). RRP44A is an active nucleus-localized RNase that functions in rRNA processing (Kumakura et al., 2016), whereas RRP44B is a cytosolic RNase that forms microscopic PB-like particles. AtRRP44A and RRP44B/SOV fall into distinct phylogenetic clades present across the animal and plant kingdoms (Zhang et al., 2010). The latter lacks the N-terminal PIN domain required for binding to the exosome core. It is suggested that RRP44A is a component of the nuclear exosome whereas RRP44B/SOV is a solo cytoplasmic exoribonuclease (Kumakura et al., 2013). Notably, RRP44B/SOV can partially complement the function of VCS in cytoplasmic mRNA degradation in some Arabidopsis ecotypes (Zhang et al., 2010). This indicates a general functional redundancy of the 3′-5′ decay apparatus, although it seems possible that the different complexes may have some specificity with respect to individual mRNAs, developmental stages, or growth conditions.

The activity of the cytoplasmic exosome is dependent on the SKI complex, a tetrameric assembly of a SKI8 dimer and the RNA helicase SKI2 connected by their mutual interaction with the scaffold protein SKI3, which unwinds and threads RNA substrates into the exosome for degradation (Halbach et al., 2013). Arabidopsis SKI2, SKI3, and SKI8 form a stable complex in vivo, with SKI2 and SKI3 also present in cytoplasmic foci (Dorcey et al., 2012; Zhang et al., 2015; Zhao and Kunst, 2016). Disruption of *AtSKI8* function results in the stabilization of mRNAs targeted for degradation by the exosome (Dorcey et al., 2012). Similar to the exosome core components RRP45A and RRP45B, all three SKI proteins are required for the exosomal degradation of the *AtECERIFERUM3* transcript during stem wax deposition (Zhao and Kunst, 2016).

mRNA SEQUESTRATION IN SGS: A TRANSIT DEPOT BETWEEN TRANSLATION, STORAGE, AND DECAY?

Polysome disassembly as a consequence of translational repression induces the sequestration of mRNAs into translationally inactive mRNPs. SGs are one type of mRNPs that form in response to stress-induced inhibition of translation initiation, serving as triage centers for mRNA sorting to PBs or protection from degradation (Protter and Parker, 2016; see Box 1). These heterogenous complexes are physically, compositionally, and functionally linked with PBs (Buchan and Parker, 2009). Typically, mRNAs stored in SGs are translationally competent and can reenter the translational pool once released. In plants, this is exemplified by Arabidopsis mRNAs encoding ribosomal proteins that are preferentially stored in SGs under heat shock stress and released and translated during recovery through a mechanism that requires HEAT SHOCK PROTEIN101 (HSP101; Merret et al., 2017).

In yeast and humans, SGs contain a diverse proteome (Jain et al., 2016). Some RBPs are essential for SG formation in these species, such as T-cell-restricted intracellular antigen-1 (TIA-1) and TIA-1-related (TIAR) proteins (Gilks et al., 2004), Ras-GTPase-activating protein SH3-domain-binding proteins (G3BPs; Aulas et al., 2015), and Tudor staphylococcal nucleases (TSNs; Gao et al., 2015). Recent studies have revealed the roles of related proteins in plants (Fig. 2; Table II).

TIA-1/TIARs are composed of three N-terminal RNA recognition motifs (RRMs) that provide RNA/DNA-binding specificity and a C-terminal prion-related domain that confers self-aggregation, both of

BOX 1. Heterogeneous Macromolecular Hubs of Cytoplasmic mRNA Translation, Turnover, and Sequestration

Polyribosome (polysome): A complex of a 5′-^{7}mG-capped and 3′-polyadenylated mRNA and multiple 80S ribosomes, typically undergoing translation (see main text). Cytoplasmic ribosomes are composed of 81 ribosomal proteins (RPs) and four rRNAs. They catalyze the peptidyl transferase reaction of elongation, interacting with numerous soluble translation factors (Browning and Bailey-Serres, 2015). Often considered invariant, ribosomes can be distinguished by RPs produced by distinct gene paralogs and post-translational modifications (i.e. phosphorylation; Hummel et al., 2015). In mammalian cells, ribosomes that can be distinguished by the presence or absence of certain RPs translate different subsets of mRNAs (Shi et al., 2017). Translation involves the phases of initiation, elongation, and termination that enable the ribosome to decode a transcript into a polypeptide (Browning and Bailey-Serres, 2015). In addition to global control of protein synthesis, the translation of individual mRNAs is regulated during development and as a rapid response to various internal and external cues (reviewed by Roy and von Arnim, 2013; Moore et al., 2016; Merchante et al., 2017). Because the major rate-limiting phase of translation is initiation, it has been thought that most polysomal mRNAs are actively undergoing decoding (Browning and Bailey-Serres, 2015). The discovery that mRNA decay can occur post-transcriptionally on poly(A) mRNAs indicates this interpretation is not fully accurate.

Processing body (PB): Dynamic cytoplasmic macromolecular assemblies of translationally inactive mRNAs and proteins involved in translation repression and mRNA turnover processes, including 3′-deadenylation, 5′-decapping, 5′ to 3′ exonucleolytic, nonsense-mediated decay, and miRNA-targeted gene silencing. PBs of > 0.1 μm are visible by imaging of fluorescent protein confocal microscopy (Eulalio et al., 2007). In plants, PB markers include DCP1, DCP2, VCS, and XRN4 (Maldonado-Bonilla, 2014). mRNP assemblies of DCP1 and other components of mRNA turnover can be detectable by confocal imaging under normal cellular states and are enlarged by a variety of stimuli. PB formation requires mRNA release from polysomes because cycloheximide, a drug that stalls translocation mRNAs on elongating ribosomes, can inhibit their assembly. Mobility of PBs involves the actin cytoskeleton through an interaction between myosin XI-K and DCP1 (Steffens et al., 2014). Since PBs are heterogenous, this term is best used along with the names of specific proteins, transcripts, and biological activities studied, as in many cases mRNAs targeted to PBs in plant cells are stabilized rather than degraded despite the presence of mRNA decay factors (Li et al., 2015; Merchante et al., 2015; Steffens et al., 2015; Scarpin et al., 2017). This is supported by the recent discoveries that mRNAs localized to PBs can be intact and not undergoing degradation in human cell lines (Horvathova et al., 2017; Hubstenberger et al., 2017), raising questions about the precise functions of visible PBs in mRNA fate.

Stress granule (SG): Multimolecular cytoplasmic complexes associated with mRNAs not undergoing translation that are ultimately stabilized or targeted for decay during stress. SGs are not typically discernable by confocal imaging unless cells or plants are exposed to acute environmental stresses, such as heat (Weber et al., 2008) and hypoxia (Sorenson and Bailey-Serres, 2014). SG assembly occurs through a mechanism that requires microtubule dynamics (Gutierrez-Beltran et al., 2015). Like PBs, this process is completely dependent on mRNA release from polysomes. SGs contain full-length polyadenylated mRNAs together with RNA-binding proteins, such as RBP47B, UBP1, and PABP. Although not well characterized in plants, SGs with stabilized mRNAs can include translation initiation factors (e.g. eIF3, eIF4E, eIF4A) and the 40S ribosomal subunit, indicating these complexes are in dynamic equilibrium with translating ribosomes. SG markers can overlap with other mRNPs, e.g. PBs or siRNA bodies, depending on the process of mRNP remodeling and environmental conditions (Jouannet et al., 2012; Gutierrez-Beltran et al., 2015). As for PBs, it is helpful to describe SGs in terms of the proteins and mRNAs under study.

which are required for SG formation (Waris et al., 2014). In plants, RBP45/47 and OLIGOURIDYLATE BINDING PROTEIN1 (UBP1) are the triple RRM families most closely related to the animal TIA-1/TIARs. Of the Arabidopsis RBP45/47 family, RBP47B is discernible in the nucleus under normal conditions and relocates to cytoplasmic foci detectable by confocal microscopy in response to heat, salt, and hypoxia stress (Weber et al., 2008; Yan et al., 2014; Gutierrez-Beltran et al., 2015; Lokdarshi et al., 2016). The Arabidopsis *UBP1* family is composed of three members, namely *AtUBP1A*, *AtUBP1B*, and *AtUBP1C*. UBP1A and UBP1C reversibly aggregate

Table II. *Proteins associated with SGs and PBs in plants*

CCR4s, CAF1s, XRN4, and components of the mRNA-decapping complex are localized PBs but are only presented in Table I. AtLARP1A, a heat-specific cofactor of XRN4-mediated cotranslational decay, also accumulates in SGs and PBs under heat shock stress and is presented in Table I. All 11 Arabidopsis tandem zinc finger proteins are localized to cytoplasmic granules; however, only those with demonstrated colocalizations with known SG and/or PB components are included. AtSGS3 and AtAGO7 are typically present in distinct siRNA bodies but become positive for SG markers during heat stress. At, *Arabidopsis thaliana*; Os, *Oryza sativa*.

Protein	Symbol	Gene Identifier	mRNP	Biological Functions	References
Eukaryotic translation initiation factors	AteIF4E	AT4G18040	SG	Heat stress response	Weber et al. (2008)
	AteIF3b1	AT5G27640	SG		Suzuki et al. (2015)
Poly(A)-binding proteins	AtPABP2	AT4G34110	SG	Hypoxia stress response	Weber et al. (2008); Sorenson and Bailey-Serres (2014)
	AtPABP8	AT1G49760	SG	Heat stress response	
RNA-binding proteins45 and -47	AtRBP47B	AT1G19130	SG	Heat stress response	Weber et al. (2008)
Oligouridylate binding proteins1	AtUBP1A	AT1G54080	SG	Hypoxia stress response	Sorenson and Bailey-Serres (2014)
	AtUBP1B	AT1G17370	SG	Salt, osmotic, and heat stress response/tolerance; ABA sensitivity	Weber et al. (2008); Nguyen et al. (2016, 2017)
	AtUBP1C	AT3G14100	SG	Hypoxia stress response/tolerance; Suc-reversible seedling growth arrest	Sorenson and Bailey-Serres (2014)
Ras-GAP SH3 domain-binding protein	AtG3BP-like	AT5G43960	SG	Plant-virus interaction	Krapp et al. (2017)
Tudor staphylococcal nucleases	AtTSN1	AT5G07350	SG, PB	GA-mediated growth response under salt stress; heat stress response	Yan et al. (2014); Gutierrez-Beltran et al. (2015)
	AtTSN2	AT5G61780	SG, PB		
Tandem zinc finger proteins	AtTZF1	AT2G25900	SG, PB	Sugar and ABA-mediated stress response; GA-dependent growth response	Pomeranz et al. (2010b); Lin et al. (2011)
	OsTZF1	Os05s10670	SG, PB	Salt and drought stress tolerance	Jan et al. (2013)
	AtTZF4	AT1G03790	SG, PB	ABA-, GA-, and phytochrome-mediated seed germination	Bogamuwa and Jang (2013, 2016)
	AtTZF5	AT5G44260	SG, PB		
	AtTZF6	AT5G07500	SG, PB		
	AtTZF9	AT5G58620	PB	Pathogen-associated molecular pattern-triggered immunity	Maldonado-Bonilla (2014)
Mediator of ABA-regulated dormancy1	AtMARD1	AT3G63210	SG, PB	Interacting partner of AtTZF4, AtTZF5, and AtTZF6	Bogamuwa and Jang (2016)
Responsive to dehydration21A	AtRD21A	AT1G47128	SG, PB	Interacting partner of AtTZF4, AtTZF5, and AtTZF6	Bogamuwa and Jang (2016)
Calmodulin-like38	AtCML38	AT1G76650	SG	Hypoxia response/tolerance	Lokdarshi et al. (2016)
Vascular plant one-zinc-finger protein2	AtVOZ2	AT2G42400	SG, PB	Heat stress response	Koguchi et al. (2017)
Heat shock protein101	AtHSP101	AT1G74310	SG	Heat stress response	Merret et al. (2017)
Suppressor of gene silencing3	AtSGS3	AT5G23570	SG	Heat stress response	Jouannet et al. (2012)
Argonaute7	AtAGO7	AT1G69440	SG	Heat stress response	Jouannet et al. (2012)
BEACH domain-containing protein	AtSPIRRIG/AtSPI	AT1G03060	PB	Salt stress tolerance	Steffens et al. (2015)
GW-repeat protein	AtSUO	AT3G48050	PB	miRNA-mediated translational repression; control of vegetative phase change	Yang et al. (2012)
TBP-associated factor1b	AtTAF15b	AT5G58470	PB	TNL-mediated plant immunity	Dong et al. (2016)
Plant SMY2-type ILE-GYF domain-containing protein1	AtPSIG1	AT5G42950	PB	Regulation of cell death during plant-pathogen interaction	Matsui et al. (2017)
Polypyrimidine tract-binding proteins	AtPTB1	AT3G01150	PB	Pollen germination	Wang and Okamoto (2009); Stauffer et al. (2010)
	AtPTB2	AT5G53180	PB		
Ethylene insensitive2	AtEIN2	AT5G03280	PB	Ethylene response	Li et al. (2015); Merchante et al. (2015)
Up frameshift1	AtUPF1	AT5G47010	PB	Nonsense-mediated decay; ethylene response	Kerényi et al. (2013); Merchante et al. (2015)
Suppressor with morphological effect on genitalia7	AtSMG7	AT5G19400	PB	Nonsense-mediated decay; TNL-mediated plant immunity	Mérai et al. (2013); Gloggnitzer et al. (2014)

into cytoplasmic poly(A) mRNA granules upon hypoxic and heat stress (Sorenson and Bailey-Serres, 2014). Similarly, UBP1B reversibly forms SGs under heat stress and plays a crucial role in ABA signaling and heat stress tolerance (Nguyen et al., 2016, 2017). An analysis of RNA decay kinetics suggested that UBP1B complexes (UBP1B-SGs) protect stress-related mRNAs from degradation during heat stress (Nguyen et al., 2016). Likewise, UBP1C is required for plant survival of low-oxygen stress. UBP1C dynamically relocalizes from the nucleus to form cytoplasmic foci that are disassembled upon reoxygenation. Intriguingly, RNA-ribonucleoprotein immunoprecipitation followed by microarray analysis determined that AtUBP1C preferentially associates with mRNAs with U-rich 3′ UTRs under control conditions, but UBP1C-SGs collect mRNAs that are either stored or degraded as opposed to preferentially translated during hypoxia (Sorenson and Bailey-Serres, 2014).

G3BPs are phosphorylation-dependent, sequence-specific endoribonucleases that interact with Ras GTPase-activating proteins. In mammalian cells, G3BP1 is a potent SG-nucleating protein that constitutes stable cores of SGs (Jain et al., 2016). As such, G3BP1 is targeted and sequestered by several viral proteins to prevent SG assembly/sequestration of viral RNAs during infection (Reineke and Lloyd, 2013). The first plant G3BP-like protein was isolated from *N. benthamiana* together with other SG components as targets of the viral nonstructural protein3 of *Semliki Forest virus* (Krapp et al., 2017). This protein is closely related to the NUCLEAR TRANSPORT FACTOR2 (NTF2) family in Arabidopsis. This G3BP-like NTF2-RRM aggregates into SGs and interacts with the nuclear shuttle protein of the begomovirus *Abutilon mosaic virus* and *Pea necrotic yellow dwarf virus* upon heat stress (Krapp et al., 2017). The roles of plant G3BP-like proteins in SG nucleation and mRNA stabilization await further studies.

TSNs are evolutionarily conserved cytoskeleton-associated RBPs characterized by four complete N-terminal staphylococcal nuclease domains followed by a central Tudor domain and a partial SN domain at the C terminus (Gutierrez-Beltran et al., 2016). A plant TSN was first described in rice as an RBP required for the transport of a subgroup of seed storage RNAs to a subdomain of the endosperm endoplasmic reticulum (Tian and Okita, 2014). Arabidopsis encodes functionally redundant *TSN1* and *TSN2*, which play a pivotal role in seed germination and response to high salinity and heat stress (Frei dit Frey et al., 2010; Yan et al., 2014; Gutierrez-Beltran et al., 2015). Root transcriptome and mRNA decay data suggest that TSN1 and TSN2 protect a specific set of transcripts from degradation during salinity stress, including mRNAs encoding GA 20-OXIDASE3, a key enzyme in GA biosynthesis (Yan et al., 2014). In contrast to animal TSNs that seem to localize exclusively to SGs (Gao et al., 2015), the Arabidopsis TSNs are targeted to both SGs and PBs and function in mRNA decapping during heat stress, suggestive of a crucial role in the structural integrity as well as the molecular identity of both SGs and PBs (Gutierrez-Beltran et al., 2015).

Tandem CCCH zinc finger (TZF) proteins constitute another RBP family that associates with SGs and PBs. Plant TZFs are characterized by two zinc-binding CCCH motifs arranged in tandem, with an Arg-rich motif upstream of the TZF motifs (Bogamuwa and Jang, 2014). Arabidopsis encodes 11 *TZFs*, encoding proteins localized to cytoplasmic granules when expressed heterologously in maize (*Zea mays*) mesophyll protoplasts (Pomeranz et al., 2010a). AtTZFs play diverse roles in growth, development, and stress responses (Pomeranz et al., 2010b; Lin et al., 2011; Bogamuwa and Jang, 2014). AtTZF1 shuttles between the nucleus and PBs under ambient temperatures but relocalizes into SGs after heat shock (Pomeranz et al., 2010b). Through its Arg-rich and TZF motifs, AtTZF1 binds poly(U) RNAs in the presence of zinc and triggers the decay of AU-rich element-containing mRNAs (Qu et al., 2014). In rice, OsTZF1 is a negative regulator of leaf senescence under stress and also binds poly(U) RNAs. Its colocalization with SG and PB markers was enhanced after ABA and NaCl treatment (Jan et al., 2013). *AtTZF4*, *AtTZF5*, and *AtTZF6* are expressed specifically in seeds and involved in seed germination (Bogamuwa and Jang, 2013). All three proteins interact physically in both SGs and PBs, along with MEDIATOR OF ABA-REGULATED DORMANCY1 and RESPONSIVE TO DEHYDRATION21A (Bogamuwa and Jang, 2016). The dual localization of these proteins in SGs and PBs hints that they could be involved in the selective sorting of transcripts from a stable state to en masse degradation.

Apart from RBPs, Arabidopsis studies have uncovered proteins with diverse cellular functions as constituents of SGs. These include the purported calcium sensor CALMODULIN-LIKE38 (CML38), which reversibly accumulates into SGs under hypoxic conditions in a Ca^{2+}-dependent manner (Lokdarshi et al., 2016), and the NAM (no apical meristem), ATAF (Arabidopsis transcription activation factor), and CUC (cup-shaped cotyledon) family transcription factor VASCULAR PLANT ONE-ZINC-FINGER2 (VOZ2), which translocates from the cytosol to the nucleus and SGs/PBs during heat stress (Koguchi et al., 2017). AtCML38 function contributes to hypoxia tolerance (Lokdarshi et al., 2016), but it remains to be discovered how AtVOZ2 incorporation into SGs/PBs under heat stress contributes to mRNA metabolism and if this influences heat stress tolerance.

CONCLUSION

The processes of mRNA translation, stabilization, and turnover are intrinsically linked via highly complex and dynamic interactions of the macromolecular complexes that govern the function and fate of each transcript within the cytoplasm of plant cells. Recent studies have uncovered remarkable regulation of these processes, underscored strong conservation of mechanisms across eukaryotes, and illuminated functions that may be limited to the plant lineage. As mRNAs are exported from the nucleus,

OUTSTANDING QUESTIONS

- Does ribosome translocation rate trigger cotranslational decay of mRNAs with paused or stacked ribosomes?
- Is targeted turnover of mRNAs prevalent under optimal growth conditions? What role does turnover play in modulating the abundance and translation of stress-responsive transcripts under stress and recovery conditions?
- What signaling pathways link translational repression to the nucleation/assembly of SGs and PBs?
- What factors determine the targeting and fates of mRNAs in SGs and PBs?
- Following polysome disassembly, what determines whether a transcript is stabilized or degraded under a particular stress condition?
- Is the presence of some mRNA decay factors and SG components in the nucleus relevant to their functions in the cytoplasm?
- What are the mechanisms of mRNA release from SGs and clearance of their components after disassembly?
- Does codon use or RNA modifications (e.g. uridylation and m^6A) impact cytoplasmic mRNA translation, sequestration, or turnover?

the pioneer round of translation appears to be the default quality-control pathway that licenses reiterative rounds of translation of a polysomal mRNA. It is now recognized that translation can be linked to mRNA decay or sequestration through cotranslational degradation or a more complex process involving the disassembly of a polysome complex and then advancement to decay or stabilization. Through mutant analyses, confocal microscopy, and omics technologies, the integration of mRNA translation, turnover, and sequestration has become recognized as a highly selective regulatory process of individual mRNAs. Due to space limitations, we did not delve upon how mRNA decay protects the cellular transcriptome from inappropriate posttranscriptional silencing of endogenous genes (for review, see Liu and Chen, 2016; Tsuzuki et al., 2017; Zhang and Guo, 2017). We also did not consider nuclear mechanisms of transcript turnover that can involve CBP80 (Yu et al., 2016). Nor did we consider N^6-methyladenosine and other modifications of specific nucleotides (the epitranscriptome; Luo et al., 2014; Vandivier et al., 2015; Zuber et al., 2016; David et al., 2017), which may influence RNA-protein interactions and, hence, the nuclear or cytoplasmic fates of individual transcripts. The wealth of new discoveries of the dynamic cytoplasmic mRNP triumvirate has unearthed new challenging questions (see Outstanding Questions) that may provide insights relevant to other eukaryotes or of value to crop improvement.

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