



Review

The role of eukaryotic initiation factor 3 in plant translation regulation

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ABSTRACT

Regulation of translation represents a critical step in the regulation of gene expression. In plants, the translation regulation plays an important role at all stages of development and, during stress responses, functions as a fast and flexible tool which not only modulates the global translation rate but also controls the production of specific proteins. Regulation of translation is mostly focused on the initiation phase. There, one of essential initiation factors is the large multisubunit protein complex of eukaryotic translation initiation factor 3 (eIF3). In all eukaryotes, the general eIF3 function is to scaffold the formation of the translation initiation complex and to enhance the accuracy of scanning mechanism for start codon selection. Over the past decades, additional eIF3 functions were described as necessary for development in various eukaryotic organisms, including plants. The importance of the eIF3 complex lies not only at the global level of initiation event, but also in the precise translation regulation of specific transcripts. This review gathers the available information on functions of the plant eIF3 complex.

1. Introduction

Translation is an essential step for the expression of a gene, where the information stored in nucleic acids is translated to a functional polypeptide. The complex process of translation requires not only a large amount of cell energy, different species of RNA molecules and many ribosomal proteins, but also precise regulation. In plants, expression of several key developmental regulators, stress factors and some other important groups of proteins is controlled at the translational level (Reviewed in Merchante et al., 2017). The amount of examples of such translationally regulated genes is currently rapidly expanding, as the number of methods for measuring translation is getting higher and these methods are constantly being improved and uncover the translation universe in more detail (Reviewed in Mazzoni-Putman and Stepanova, 2018).

Translation of mRNA on two-subunit ribosomes is a conserved process amongst all organisms, requiring different kinds of RNA molecules and proteins with structural, enzymatic and regulatory function. Complex series of processes within three main phases of translation; initiation, elongation and termination, ensure the precise start, rapid course and correct end of translation. While every step of translation is potentially regulated, most of the regulatory mechanisms is centered in the initiation phase where numerous translation initiation factors (eIFs)

(Table 1) ensure the mRNA-ribosome association, scanning of the mRNA and start codon selection.

Initiation is the opening step of translation, achieved by the scanning mechanism in eukaryotes (Reviewed in Hinnebusch, 2017, 2014; Merrick and Pavitt, 2018), a process of subsequent steps that includes many factors (Table 1), which undergo several structural rearrangements within (Guca and Hashem, 2018). Initiation starts with formation of the Ternary Complex (TC) from eIF2-GTP and initiating Met-tRNA^{Met}. The TC is then bound to a free 40S ribosomal subunit alongside with eIF1, eIF1A, eIF3 and eIF5 to form the 43S pre-initiation complex (43S PIC). In addition, eIF1, eIF2, eIF3 and eIF5 could pre-assemble, independently on 40S subunit, forming the so-called multi-factor complex (MFC). Free cytoplasmic MFC was observed in different organisms, including plants (Dennis et al., 2009). Activated mRNA then joins the 43S PIC along with associated proteins; eIF4E, eIF4A, eIF4B, PABP and eIF4G, to form 48S pre-initiation complex (48S PIC) (Villa et al., 2013). The 48S PIC starts then the scanning of the 5'UTR until the start codon is reached in the favorable Kozak consensus of surrounding nucleotides (Kozak, 1987). The following release of the majority of initiation factors sets the 48S PIC ready to be bound with the 60S subunit. The 60S subunit joining is facilitated by eIF5B, resulting in the 80S Initiation Complex (80S IC), which proceeds to subsequent rounds of elongation.

Abbreviations: eIF, eukaryotic translation initiation factor; IC, initiation complex; IRES, internal ribosome entry site; MFC, multi-factor complex; ORF, open reading frame; PABP, Poly-A binding protein; PIC, pre-initiation complex; SAM, shoot apical meristem; TC, ternary complex; UTR, untranslated region

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Table 1

Overview of eukaryotic translation factors and their function in canonical translation. Simplified from the list of *Arabidopsis thaliana* translation factors in (Browning and Bailey-Serres, 2015).

Protein	Function
Initiation factors (eIFs)	
eIF1	PIC formation, scanning, AUG selection, controls eIF5 activity, promotes 40S open conformation
eIF1A	PIC formation, scanning, AUG selection, promotes 40S open conformation
eIF2	subunits α , β , γ
eIF2B	Small GTPase, forms ternary complex with GTP and Met-tRNA _i ^{Met}
eIF3	12 subunits
eIF3j	GDP-GTP recycling factor for eIF2
eIF4A	Formation of PIC, scanning and AUG recognition, mRNA joining
eIF4B	eIF3 associated factor, promotes eIF3 binding to 40S
eIF4F	ATP-dependent helicase, unwinds secondary structure of mRNA, binds mRNA to 40S
eIF4E	Cofactor of eIF4A
eIF4G	5'cap binding protein
eIF5	Scaffold protein
eIF5B	GTPase activating protein for eIF2, Met-tRNA _i ^{Met} placement on AUG
PABP	Joining of 60S subunit, GTPase
	Binds poly (-A) tail, interacts with eIF4G
Elongation factors (eEFs)	
eEF1A	subunits α , β , γ
eEF1B	small GTPase, binds aminoacyl tRNA and GTP
eEF2	Recycling factor of eEF1A
	tRNA and mRNA translocation
Release factors (eRFs)	
eRF 1	Termination/peptide release
eRF 3	Termination/peptide release
ABCE1	Ribosome recycling

A multisubunit complex of eukaryotic translation initiation factor 3 is the largest of all eIFs. The eIF3 complex was first isolated from rabbit reticulocytes in the 1970's and since then, 12 non-identical eIF3 subunits have been identified (Benne and Hershey, 1976; Reviewed in Cate, 2017). In the beginning of the 21st century, a unified letter nomenclature for eIF3 subunits was proposed instead of using their respective molecular weight (Browning et al., 2001; Burks et al., 2001). In canonical translation initiation, eIF3 plays the role of a scaffold protein that binds and interacts with many other initiation factors. eIF3 participates mainly in promoting the formation and assembly of the MFC, 43S PIC and 48S PIC, and is involved in the scanning and precise start codon selection. The role of the eIF3 complex reaches further from the translation initiation process to its regulation at global and specific levels and in some other phases of translation as well (Valášek et al., 2017). In the majority of studies, mammalian eIF3 and budding yeast eIF3 complexes were examined. Described features from such research

are applicable to other organisms as well, as high similarity homologues of at least the minimal functional core of the eIF3 complex are present in most, if not all eukaryotic organisms (Valášek et al., 2017).

Plant eIF3 complex architecture is similar to that of the mammalian eIF3 (Browning et al., 2001; Burks et al., 2001; Li et al., 2016). Several plant eIF3 subunits have been analyzed during the last 20 years using mainly *Arabidopsis* as a model organism. Single subunit mutants pointed to the importance of the eIF3 in translation regulation, being essential for different stages of plant development or proper stress response. Moreover, eIF3 is also an interacting partner of many viral proteins of plant viruses that recruit the host translational machinery. However, the knowledge about the exact regulation mechanisms pertained by eIF3 in plants is still mostly unknown. This review gathers the current knowledge for eIF3 complex and its subunits and their involvement in the regulation of translation in flowering plants. Because of the lack of precise structural eIF3 data from plants, preceding description of the mammalian eIF3 structure and its function is presented for better understanding of the molecular context.

2. eIF3 complex

The eIF3 complex was found present in all eukaryotic organisms so far. Although the overall conservation of the eIF3 is high, not all organisms kept the complete set of twelve subunits (Table 2). *Saccharomyces cerevisiae* (*S. cerevisiae*) possess the most reduced eIF3 complex identified so far consisting of five subunits (eIF3a, -3b, -3c, -3i, and -3g) (Asano et al., 1998; Khoshnevis et al., 2012; Phan et al., 1998). Even though so reduced, the yeast complex is still capable of performing the eIF3 functions. In *S. cerevisiae*, protein named eIF3j is necessary for eIF3 binding to 40S, but is only loosely attached to the eIF3 complex and not present in the purified yeast eIF3 complex (ElAntak et al., 2010; Valášek et al., 2001). Therefore, it is considered an eIF3-associated factor (Valášek et al., 2017). In higher eukaryotes, homologues of all five yeast eIF3 subunits are found in the purified eIF3 complex, together with seven additional subunits eIF3d, -3e, -3f, -3h, -3k, -3l and -3m (Smith et al., 2013; Zhou et al., 2008). eIF3-associated protein eIF3j seems to have similar functions in mammals as its respective *S. cerevisiae* orthologue (Fraser et al., 2004; Smith et al., 2013). The composition of 12 subunits in the eIF3 complex was found to be similar in *Neurospora crassa*, mammals and plants (Valášek et al., 2017). In evolutionary diverged taxonomical supergroup *Excavata*, eIF3 composition resembles the mammalian model in general, yet there is no evidence of presence of some eIF3 subunits in several inspected *Excavata* species (Han et al., 2015; Meleppattu et al., 2015; Rezende et al., 2014). *Archaea* lack evidence for most eIF3 subunits, except of found homology with eIF3i in *Methanocaldococcus jannaschii* (Rezende et al., 2014). No homology for any eIF3 subunit has been found in *Bacteria* (Benelli and

Table 2

eIF3 subunit composition in different organisms. eIF3-associated protein eIF3j is not included, as it is not considered a canonical eIF3 subunit. Modified from (Valášek et al., 2017), with respect to (Li et al., 2016) and (Li et al., 2017).

Subunit	Domains, motives	Organism					
		<i>S.cerevisiae</i>	<i>S.pombe</i>	<i>T.brucei</i>	<i>H.sapiens</i>	<i>A.thaliana</i>	<i>O.sativa</i>
eIF3a	PCI	x	x	x	x	x	x
eIF3b	WD40, RRM	x	x	x	x	x	x
eIF3c	PCI	x	x	x	x	x	x
eIF3d	5'cap binding?		x	x	x	x	x
eIF3e	PCI		x	x	x	x	x
eIF3f	MPN		x	x	x	x	x
eIF3g	RRM, Zn finger	x	x	x	x	x	x
eIF3h	MPN		x	x	x	x	x
eIF3i	WD40	x	x	x	x	x	x
eIF3k	PCI			x	x	x	x
eIF3l	PCI			x	x	x	x
eIF3m	PCI		x		x	x	x

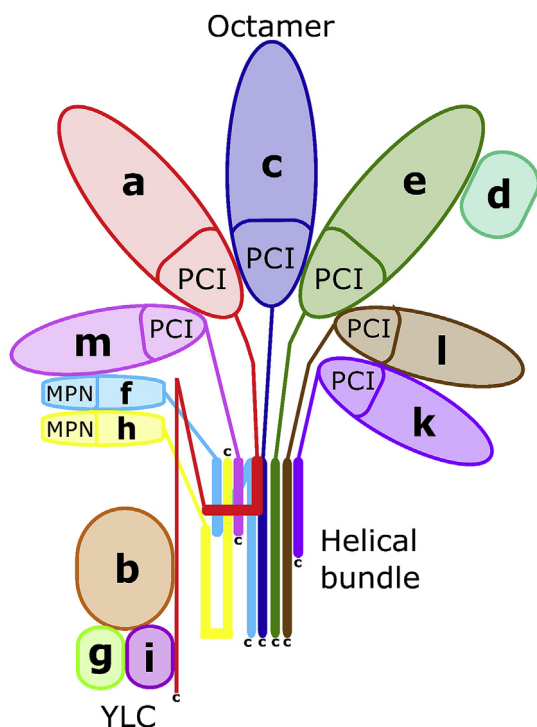


Fig. 1. Simplified 2D cartoon model of the mammalian eIF3 relative subunit position and interaction. The model shows the PCI/MPN domain Octamer, the helical bundle interaction hub and the flexible YLC that is connected to the Octamer module via eIF3a C-terminal end. Modified from (Wagner et al., 2016).

Londei, 2011; Rezende et al., 2014), corresponding well with the fact that neither *Bacteria* nor *Archaea* initiate translation by the scanning mechanism as eukaryotes.

In recent years, the structure of eIF3 has been solved in contexts of PIC in various stages of initiation in yeast (Aylett et al., 2015; Erzberger et al., 2014; Korostelev, 2014) and in mammals (des Georges et al., 2015; Eliseev et al., 2018; Hashem et al., 2013a; Querol-Audi et al., 2013; Simonetti et al., 2016), together with the biochemical data of proposed eIF3 subunit assembly and mutual interactions (Herrmannová et al., 2012; Khoshnevis et al., 2012; Masutani et al., 2007; Sun et al., 2011; Wagner et al., 2016, 2014; Zhou et al., 2005, 2008). The mammalian model of eIF3, considered similar to the plant eIF3 complex, is divided into two structural modules: a PCI/MPN Octamer and a Yeast-Like Core (YLC) (Fig. 1). The PCI/MPN octamer is formed from eight subunits; eIF3a, -3c, -3e, -3f, -3h, -3k, -3l and -3m. The formation of the Octamer is enabled by a scaffold structure of 6 subunits (eIF3a, -3c, -3e, -3k, -3l and -3m) containing a PCI (Proteasome, CSN, eIF3) domain and 2 subunits (-3h and -3f) containing a MPN (for Mpr1-Pad1-N-terminal) domain (Querol-Audi et al., 2013; Siridechadilok et al., 2005). The structure of the Octamer is stabilized by two interaction hubs; first being the PCI domains forming a structure known as β -sheet arc, and second being a helical bundle in which every subunit of the octamer joins with one of its C-terminal α -helix (des Georges et al., 2015). Similar structure of PCI/MPN domains and helical bundle is shared between two other large protein complexes; COP9 signalosome (CSN) and the 26S proteasome lid (Ellisdon and Stewart, 2012; Enchev et al., 2010; Pick et al., 2009). The second module, YLC, consists of subunits eIF3b, -3i and -3g. All these three subunits are present in the reduced *S. cerevisiae* eIF3 complex. Both modules are connected via the interaction of -3a and -3b subunits. Recent structural study done with the reconstituted yeast eIF3 complex suggest that the N-terminal part of eIF3c interacts with eIF3b as well, which would mean that eIF3 could form, at least in some phase of the initiation process, a complete circle around the small ribosomal subunit (Llacer et al., 2018). The assembly of the

whole eIF3 has a hierarchical order, although different methodology approaches gave slightly different results. One assembly order was proposed by Wagner and co-workers in 2016 (Wagner et al., 2016). In this model, eIF3a binds eIF3b as the nucleation core, then subunits of the YLC module (-3i, -3g and -3b) join and form a subcomplex that alone is already able to bind to 40S and recruit activated mRNA *in vivo* in mammals (Wagner et al., 2014). Assembly of other PCI/MPN domain containing subunits of the Octamer proceeds. Twelfth subunit, eIF3d, was found to be bound to the eIF3e subunit (Wagner et al., 2016). Although in this model, the proposed nucleation core is the -3a/-3b dimer and the YLC is considered a prerequisite for the ongoing Octamer assembly, the whole human PCI/MPN Octamer was only reconstituted *in vitro* and the initial dimer of -3a/-3c was proposed as the main nucleation core (Sun et al., 2011). In this case, YLC subunits completed the whole complex when added later on. It could be elucidated that both modules might be formed independently on each other, and that the reduced *S. cerevisiae* complex probably represents the functional core needed for basal translation initiation. Moreover, variable functional eIF3 subcomplexes were observed in some of the aforementioned experiments as well as in recent reconstitution of *Neurospora crassa* eIF3 (Smith et al., 2016), increasing the possibilities of translation initiation modularity.

The canonical eIF3 function in the translation initiation is to scaffold all the necessary factors, small ribosomal subunit and the mRNA together. This paragraph gives a description of the initiation phase from the perspective of the eIF3 in more detail. eIF3 alone is able to bind to 40S subunit as it prevents the precocious 40S and 60S association (Kolupaeva et al., 2005). After binding to the 40S subunit, eIF3 enhances joining of the TC, eIF1, eIF1A, eIF5 (Valášek, 2012). Moreover, eIF3 also participates in the forming of the MFC. The MFC then loads the Met-RNA^{Met} on the 40S (Sokabe et al., 2012). In the MFC assembly, the N-terminal domain of the eIF3c subunit facilitates interactions with other MFC factors (Karásková et al., 2012; Obayashi et al., 2017). In the assembling 43S PIC, eIF3 encircles the 40S subunit in a clamp-like fashion. The Octamer module is bound to the 40S on the solvent side with eIF3a N-terminal domain (NTD) reaching to the mRNA exit channel, and YLC module placed on the intersubunit side near the mRNA entry channel (des Georges et al., 2015), where interactions with the 40S are maintained by a 9-bladed β -propeller structure of eIF3b (Liu et al., 2014). Then, eIF3 is necessary for loading the mRNA to the 43S PIC (Mitchell et al., 2010). The recruitment of mRNA to PIC is enabled by the direct binding of the eIF4G to a surface made from eIF3 subunits; -3c, -3d, -3e (Villa et al., 2013). eIF3a interacts directly with the mRNA at the mRNA exit channel (Pisarev et al., 2008), thus stabilizing the mRNA on both entry and exit channels (Aitken et al., 2016). The processivity of scanning and stringent AUG recognition seems to also be enhanced by eIF3, presumably by stabilizing the mRNA conformation in the scanning (Aitken et al., 2016; Chiu et al., 2010; Cuchalová et al., 2010; ElAntak et al., 2010; Karásková et al., 2012; Obayashi et al., 2017; Valášek et al., 2017). Having been analyzed by recent structural studies, the whole YLC module undergoes structural rearrangements on 40S during mRNA binding, relocating from the solvent exposed site to the intersubunit surface, thus stabilizing the interaction of the scanning complex (Eliseev et al., 2018; Llacer et al., 2018; Simonetti et al., 2016). Upon AUG recognition, YLC is relocated back to the solvent exposed site. This rearrangement seems to be triggered by a conformational change of eIF2 (Eliseev et al., 2018).

Apart from translation initiation, additional functions were described for eIF3 during translation termination, recycling and some non-canonical translational events (Valášek et al., 2017), such as reinitiation after upstream open reading frames (uORFs) (Mohammad et al., 2017). In *S. cerevisiae*, eIF3a promotes reinitiation after the recognition of the secondary structure on the uORF (Gunišová et al., 2018; Szamecz et al., 2008), while eIF3h promotes reinitiation in mammals (Hronová et al., 2017) and plants (Kim et al., 2007; Zhou et al., 2014). In yeast, eIF3 participates in stop codon read-through

(Beznosková et al., 2013), ribosome recycling (Pisarev et al., 2007) or the nonsense-mediated mRNA decay (Celik et al., 2017; Gupta and Li, 2018). Under stress conditions, eIF4F activity is inhibited and eIF3 is able to bind the 5' cap itself via eIF3d and eIF3l subunits (Kumar et al., 2016; Lee et al., 2016). Moreover, eIF3 can bind transcripts encoding cell growth, differentiation or apoptosis proteins (Lee et al., 2015), and transcripts containing N⁶-methyladenosine (m⁶A) in their 5' UTR (Meyer et al., 2015). Internal ribosome entry site-like (IRES-like) containing transcripts also frequently need eIF3 for translation initiation (Hashem et al., 2013b; Sun et al., 2013). DHX29 helicase interacts with the RNA recognition motif (RRM) of eIF3b and C-terminal domain of eIF3a to cooperate in scanning on complicated secondary structures in 5'UTRs (Pisareva and Pisarev, 2016).

3. The plant eIF3 complex

The plant eIF3 complex is a complex of 12 subunits in *Arabidopsis thaliana*, *Triticum aestivum* and *Oryza sativa* (Browning et al., 2001; Burks et al., 2001; Li et al., 2016), resembling the mammalian complex, suggesting from similarities in stoichiometric subunit composition, domain conservation and overall conservation of the eIF3 complex in the eukaryotic kingdom. However, as plants diverged in the evolution, additional specific functions of individual eIF3 subunits might have diverged. And indeed, studies of some of the individual plant eIF3 subunits already presented several regulatory functions that are additional to the basic function in translation initiation.

Arabidopsis thaliana, a model for plant eIF3 research, contains 19 coding sequences for eIF3 complex subunits in its genome (Table 3). Five eIF3 subunits are encoded by a single gene; eIF3a, -3e, -3f, -3h, -3k, and the remaining seven subunits are encoded by two genes; eIF3b, -3c, -3d, -3g, -3i, -3l, -3m (Browning and Bailey-Serres, 2015). The following section summarizes available information about eIF3 in plants. The general expression pattern of eIF3s resembles that of a house-keeping gene with highest expression in proliferating tissues (e.g. apical meristems, leaf primordia, inflorescences, developing anthers and germinating seeds) that demand new pool of translational machinery.

3.1. eIF3a

eIF3a is the largest plant eIF3 subunit with a conserved PCI domain, considered essential in mammals and yeast (Valášek et al., 2017). In *Arabidopsis*, eIF3a is encoded by a single gene. Up to date, no evidence of any plant mutant of the eIF3a subunit has been reported. AtEIF3A protein was recognized in several high throughput studies as an interacting partner of histone deacetylase GCN5 (Servet et al., 2008), substrate of phosphorylation during the shift from light to dark (Boex-Fontvieille et al., 2013), a ubiquitin-conjugate protein (Kim et al., 2013), a mRNA binding protein (Reichel et al., 2016), and also as part of RNA storage particles in tobacco pollen (Hafidh et al., 2018; Honys et al., 2009). Another interaction of AtEIF3A was discovered with plant

reinitiation supporting protein (RISP), factor participating in the translational reinitiation after long translated segment on the *Cauliflower mosaic virus* (CaMV) mRNA (Thiébaud et al., 2009). A Chinese study presented OsEIF3A as a gene expressed in various *Oryza sativa* tissues, strongly in root tips, leaf or in stigma, and its expression being induced by auxin (Li et al., 2003). As the eIF3a subunit has not been fully characterized in plants, from the number of modifications described we can only suggest on a strict regulation of the AtEIF3A.

3.2. eIF3b

eIF3b subunit is a part of the YLC module and is necessary for its complete assembly. In *Arabidopsis*, eIF3b is encoded by two genes, AtEIF3B1 and AtEIF3B2. Expression profiles of both genes follow the general eIF3 pattern, with high transcript level in growing and proliferating tissues (Linhardt, 2017). Overall, the expression of AtEIF3B1 is higher in tissues when compared to the AtEIF3B2. Homozygous *ateif3b2* insertion mutant plants were delayed in plant development of the plant (Linhardt, 2017; Roy, 2010). On the contrary, *ateif3b1* insertion mutant plants were obtained only as heterozygote. Heterozygous *ateif3b1* plants showed a higher frequency of aborted embryos and couldn't be fully complemented by the weaker expression of the paralogue AtEIF3B2 (Linhardt, 2017). Double mutant hasn't been characterized yet. Both *Arabidopsis* eIF3b subunits were found as substrates of phosphorylation in the light to dark shift response (Boex-Fontvieille et al., 2013), and as part of RNA storage particles in tobacco pollen (Hafidh et al., 2018; Honys et al., 2009).

3.3. eIF3c

eIF3c is another PCI domain containing subunit that is also part of the yeast minimal eIF3 core. In *Arabidopsis*, eIF3c is encoded by two genes, AtEIF3C1 and AtEIF3C2. Expression profile of the AtEIF3C1 is similar with the common eIF3 expression pattern, whereas AtEIF3C2 is generally expressed very low, except for expression during pollen development and in the endosperm, where its expression is increased. Characterization of eIF3c in *Arabidopsis* suggests that AtEIF3C1 is dispensable during the male gametophyte development, where it is presumably complemented by higher expression of AtEIF3C2. The heterozygous insertion mutant *ateif3c1* also showed defects in the embryo development, leading to higher rate of seed abortion (Roy, 2010). *Arabidopsis* and wheat eIF3c were shown to be phosphorylated on multiple sites by CK2 kinase (Dennis et al., 2009), an essential and highly conserved serine/threonine kinase that is involved in cell cycle regulation, cell proliferation and apoptosis (Nuñez de Villavicencio-Díaz et al., 2017). In plants, CK2 is under control of plant hormones and affects plant development (Mulekar and Huq, 2014; Vilela et al., 2015). Amongst other substrates, plant CK2 phosphorylates also eIF2, eIF5 and eIF3c; which altogether enhances the interaction affinity between these factors to increase the rate of MFC formation in cytoplasm (Dennis et al., 2009). Another interaction discovered for *Arabidopsis* eIF3c was its interaction with the RISP protein, a protein that increased the reinitiation on CaMV mRNA (Thiébaud et al., 2009).

3.4. eIF3d

eIF3d is bound to the Octamer module via the interaction with eIF3e. There are two genes encoding eIF3d in *Arabidopsis*, AtEIF3D1 and AtEIF3D2. Insertion mutants for single subunit caused no apparent phenotype defects. However, in the *ateif3d1* insertion line, the T-DNA insertion was located in the 3' UTR and its expression was not affected at all (Roy, 2010). Both genes show similar expression patterns in *Arabidopsis*, peaking during microgametogenesis.

Table 3

Arabidopsis eIF3 subunits and their gene codes.

eIF3 subunit	MW [kDa]	Genes in <i>Arabidopsis</i>	Gene codes
a	114.0	1	At4g11420
b	85.0	2	At5g27640, At5g25780
c	103.0	2	At3g56150, At3g22860
d	67.0	2	At4g20980, At5g44320
e	52.0	1	At3g57290
f	32.0	1	At2g39990
g	36.0	2	At3g11400, At5g06000
h	38.0	1	At1g10840
i	36.0	2	At2g46280, At2g46290
k	26.0	1	At4g33250
l	60.2	2	At5g25754, At5g25757
m	50.0	2	At3g02200, At5g15610

3.5. eIF3e

eIF3e is a PCI domain containing subunit, encoded in *Arabidopsis* by a single gene. The strongest expression of its transcript is observed in rapidly growing tissues of SAM, leaf primordia, flowers, imbibed seeds or during microsporogenesis (Linhart, 2017). The *ateif3e* insertion mutant showed impaired pollen germination but not pollen development where pollen grains carrying the mutation rarely germinated (Linhart, 2017; Roy, 2010; Roy et al., 2011). Also, the fitness of female gametophyte was decreased in *ateif3e* mutant (Linhart, 2017). Interestingly, the overexpression of the eIF3e lead to retardation defects during seedling, vegetative and floral development. AtEIF3E was found interacting with subunits of the 26S proteasome lid and COP9 signalosome (CSN) in plants (Karniol et al., 1998; Pick et al., 2009; Yahalom et al., 2001), which is a relatively common phenomena, as its respective orthologues suggest interactions between subunits of both these complexes in fission yeast (Yen et al., 2003) or mammals (Hoareau Alves et al., 2002). In *AtEIF3E* overexpressing lines, observed defects were even similar to the mutations of COP9 signalosome (CSN) (Yahalom et al., 2008). Moreover, AtEIF3E was not only shown to interact with CSN subunit 7, but was also localized to the nucleus in photosynthetically active tissues (Yahalom et al., 2001). Based on these similarities between *ateif3e* and *csn7* mutants, overexpression and *in vitro* analyses, AtEIF3E was proposed a substrate for CSN-dependent degradation in the 26S proteasome and that it is a negative regulator of translation in plants (Yahalom et al., 2008). Authors of this study suggested that AtEIF3E is normally a part of the eIF3 complex and contributes to the binding of eIF4G to the PIC. However, the excess of free monomeric AtEIF3E inhibits the translation rate *in vitro*, presumably by binding to the 40S alone, impairing the ability of the whole eIF3 complex to bind to the 40S subunit (Paz-Avram et al., 2008; Yahalom et al., 2008).

Rice *OsEIF3E* has very similar expression pattern to the *Arabidopsis* orthologue, and shows an increased level of its transcript during cold stress and in the ABA response. RNAi knockdown plants were mannitol sensitive and had slower and dwarfish development, defects in pollen maturation, reduced reproductive organ size and lowered seed biomass (Wang et al., 2016). Moreover, *OsEIF3E* was found to form homodimers and it was proposed that a possible self-regulating mechanism of dimerization might decrease the inhibition effect of a monomer on translation (Wang et al., 2016). *OsEIF3E* also interacts with inhibitors of cyclin dependent kinases *in vitro*, also suggesting an unknown role in cell cycle regulation (Wang et al., 2016). However, no further study provides more detailed answers for these suggestions to be true.

3.6. eIF3f

eIF3f is an MPN domain containing subunit. eIF3f was characterized in *Arabidopsis thaliana* and *Oryza sativa*, where is encoded by a single gene (Li et al., 2016; Roy, 2010; Xia et al., 2010). In *Arabidopsis*, expression of *AtEIF3F* was observed in all tissues, the strongest expression in pollen grains, inflorescences, root tips, developing embryos and ovules (Xia et al., 2010). In a knockdown insertion *ateif3f*, pollen grains were unable to germinate, although microsporogenesis and microgametogenesis was unaffected (Xia et al., 2010). The embryo development of the homozygous mutant, obtained by pollen rescue, showed higher rates of abortion at different developmental stages. However, some abnormal embryos still formed seeds and seedlings. These seedlings were malformed in stem shape and root system, lacked chlorophyll, and were sensitive to sugar (Xia et al., 2010), very similarly to the second MPN domain containing subunit mutant, *eIF3h* (Kim et al., 2004), which is discussed in its respective chapter (3.8). Xia et al. further analyzed the transcriptome of homozygous mutant seedlings to identify 3100 genes with significantly altered expression. The mutant phenotype could then be at least partially explained by the down-regulation of some genes important for sugar response (*ASN1*, *ProDH2*),

normal pollen tube growth and embryo development (*CSLA7*) or plastid differentiation and chlorophyll synthesis (*SCO1*, *NAP7*, *CAO*) (Xia et al., 2010). Authors in the study then conceded a lack of plant material from homozygous seedlings to perform any protein analyses to compare the transcript and protein level of the possible target genes (Xia et al., 2010).

In rice, expression of *OsEIF3F* was the strongest in immature florets and during anthers, pollen and seed development. RNAi knockdown of *OsEIF3F* caused reduced seed production and male sterility but showed no abnormalities in vegetative growth. Male sterility was a consequence of decreased pollen viability. In contrast to the reduced pollen germination observed in *Arabidopsis ateif3f*, mutant rice *oseif3f* pollen grains were arrested at various stages of microgametogenesis (Li et al., 2016). Surprisingly, *OsEIF3F* expression analysis showed novel localization of the *OsEIF3F* protein to the endoplasmic reticulum, leaving another question mark for future research (Li et al., 2016).

3.7. eIF3g

eIF3g is a subunit that is part of the YLC module. *Arabidopsis* eIF3g is encoded by two paralog genes, *AtEIF3G1* and *AtEIF3G2*. Both paralogs are expressed in all plant tissues and follow the pattern of higher expression in active proliferating tissues. *AtEIF3G1* transcript level is higher than *AtEIF3G2*. No defects have been observed in single gene insertion lines for both genes, suggesting possible redundancy (Roy, 2010). However, no characterization of double mutant line has been described up to date.

The *Triticum aestivum TaEIF3G* has been shown to play an important role in abiotic stress response and tolerance. *TaEIF3G* expression was highly increased during drought, cold, high osmolarity and high salinity stress and induced by brassinosteroids and salicylic acid (Singh et al., 2013, 2007). *TaEIF3G* overexpression in *Arabidopsis* increased the tolerance to drought, osmotic and salinity stress, increased concentration of soluble proteins and stress hormone abscisic acid, provided better stability of PSII under stress conditions and decreased levels of oxidative membrane damage stress (Singh et al., 2013). Stress resistance transcripts are extensively translated in the presence of high eIF3g protein levels. However, similar increase of general stress tolerance was found by just increasing global translation rate or when other initiation factors were overexpressed (Sun and Hong, 2013; Wang et al., 2012).

Plant eIF3g is also a target of several viral proteins. The CaMV trans-activator protein (TAV) controls reinitiation after long uORF on the viral transcript by recruiting eIF3 through interactions with eIF3g and plant specific reinitiation supporting protein (RISP) (Park et al., 2001; Ryabova et al., 2004; Thiébeauld et al., 2009). The *strawberry vein banding virus* (SVBV) trans-activator protein P6 also interacts with *Fragaria vesca* FvEIF3G, reducing the trans-activation activity of the P6 protein by this interaction (Li et al., 2018). In a *Papaya ringspot virus* (PRSV) study done with *Carica papaya*, *CpEIF3G* mRNA level was increased 2–4.5x during PRSV infection. Viral nuclear inclusion protein (Nia-Pro) of the PRSV virus also interacts with central domain of *CpEIF3G* and decreases the *CpEIF3G* availability for the eIF3 complex by this interaction (Gao et al., 2015). Overall, these studies suggest that plant eIF3g might also play a role in translation efficiency during biotic stress as well, where viral protein target specifically the eIF3g to decrease the eIF3g-mediated enhancement of the translation of defense proteins.

3.8. eIF3h

eIF3h is s MPN domain containing subunit. eIF3h is encoded by a single gene in *Arabidopsis*, and its product, *AtEIF3H* is dispensable for the basal eIF3 function in *Arabidopsis* (Kim et al., 2004). However, *ateif3h* insertion mutant has severe phenotype defects of pleiotropic postembryonic growth, female fertility, sugar sensitivity and pollen

fitness that altogether lead to seedlings lethality (Kim et al., 2004; Roy et al., 2011). Some of these growth defects also altered the response to auxin. To surpass the seedlings lethality, addition of sucrose to the growth media partially rescued the plants, enabling them to reproduce (Kim et al., 2004). The phenotype is caused by the loss of ability to stimulate the translation efficiency of specific transcripts, which contain one or more inhibitory uORFs in their 5' leader sequences by participating in reinitiation promotion on major ORF after termination event on short uORF. In *Arabidopsis*, over 30% of transcripts possess at least one uORF (Kim et al., 2007). A plant model for eIF3h translation regulation is the *ATB2* gene that encodes the *Arabidopsis thaliana* basic leucine zipper protein 11 (AtBZIP11), a sugar sensitive transcription factor that activates genes involved in amino acid and sugar metabolism (Hanson et al., 2008; Ma et al., 2011). The mRNA has a long 5' leader that contains five uAUGs in four uORF. uORF1 has a weak context start codon and is mostly skipped by leaky scanning. When uORF1 is skipped, uORF2a/2b is translated from strong uAUGs. Short translation event on uORF2 disables initiation on uORF3 and uORF4 because their start codons overlap with uORF2. After translation of uORF2 is terminated, ribosome reinitiate on mORF to produce AtBZIP11 (Roy et al., 2010). In *ateif3h* mutant, reinitiation events decrease after uORF2, as well as polysomal occupancy on AtBZIP11 transcript. As a consequence, downregulation of AtBZIP11 protein level is observed. Stalled ribosomes are found to be more associated with coding uORFs (Hou et al., 2016), suggesting this regulatory mechanism is used more widely. In over 250 genes translationally downregulated in *ateif3h*, gene classes of transcriptional regulators and protein modifying enzymes are enriched (Kim et al., 2007; Roy et al., 2010; Tiruneh et al., 2013). Several bZIP family genes are involved in low or high sugar responses and possess uORFs (Wiese et al., 2005), explaining why mutant seedlings were sensitive to various sugar levels (Kim et al., 2004). The eIF3h is also needed for the *CLAVATA3-WUSHEL* autoregulatory negative feedback loop, the well-known regulation of shoot apical meristem (SAM) size and functionality (Reviewed in Somssich et al., 2016). In this case, CLV1 receptor is restrained on the translational level. Four uORFs in the *CLV1* 5' leader inhibit mORF translation. With reinitiation events inhibited in *ateif3h* mutant, the CLV1 protein level is downregulated, disrupting the inhibition of *WUS* in the negative feedback loop., SAM is indeed enlarged in the mutant, quiescent and has a different dome-like shape than normal SAM (Zhou et al., 2014). Analogically, the translation rate of the auxin response factors (ARFs) class of transcription factors with diverse uORFs is downregulated in *ateif3h* mutant (Zhou et al., 2010), as well as the adaxializing transcription factor, *ASYMMETRIC LEAVES1* (*AS1*), that possess three inhibitory uORFs and whose mutant has similar defects in leaf morphology as in *ateif3h* mutant (Zhou et al., 2014). Ensuring control over such key developmental factors, AtEIF3H function is also controlled by Target of rapamycin kinase (TOR kinase). Stimulated TOR kinase binds to translation initiation complexes or polysomes and activates kinase S6K1, which then phosphorylates AtEIF3H to increase its ability to promote reinitiation after uORF (Schepetilnikov et al., 2013, 2011).

Taken together, plant eIF3h does not change global translational levels, but its presence is essential to overcome the inhibitory effects of uORFs in 5' leaders on specific genes that regulate metabolism, stem cell maintenance and organogenesis. Similar phenotypes and involvement in uORF regulated translation were found in some mutants of ribosomal proteins, RPL4A, RPL4D, RPL5A, RPL24B (Nishimura et al., 2005; Rosado et al., 2012; Tiruneh et al., 2013; Zhou et al., 2010), suggesting a tight cooperation between large ribosomal subunits and eIF3 in reinitiation.

3.9. eIF3i

The eIF3i subunit contains a WD40 domain and is a part of the YLC module. eIF3i is also considered the most conserved subunit of the eIF3 complex, its respective homolog was found even in *Archaea* (Benelli and

Londei, 2011; Rezende et al., 2014). eIF3i is encoded by two duplicate genes in *Arabidopsis*, *AtEIF3I1* and *AtEIF3I2*, that form direct tandem repeat on the chromosome 2, with only 517 bp between them. The common eIF3 gene expression pattern was observed in gene expression analyses (Jiang and Clouse, 2001).

Arabidopsis atef3i knock down RNAi lines lead to severe developmental defects; seeds exhibited delayed germination, seedlings had dwarf phenotype and died before growing first true leaves. For some seedlings that survived, developmental malformations in leaf morphology, apical dominance and aberrant flower development were observed (Jiang and Clouse, 2001; Roy, 2010). However, any transcriptomic or proteomic data are missing to investigate the eIF3i impact on translation. It was also shown that eIF3i transcription is regulated by brassinosteroids (Jiang and Clouse, 2001). Adding brassinosteroids increased the level of the *Phaseolus vulgaris* *PVEIF3I* mRNA in bean, tobacco cells and *Arabidopsis* seedlings (Jiang and Clouse, 2001). Moreover, eIF3i was phosphorylated *in vitro* by BRASSINOSTEROID-INSENSITIVE 1 (BRI1) receptor serine/threonine kinase (Ehsan et al., 2005), suggesting brassinosteroids control eIF3i activity also post-translationally. In mammals, eIF3i is phosphorylated by transforming growth factor beta (TGF- β) receptor kinase and thereafter modulates TGF- β response (Choy and Derynck, 1998). Supporting to the role of eIF3i in translation regulation of proliferative genes, eIF3i dysregulation was shown in various types of cancer (Ali et al., 2017). The link between both mammalian and plant eIF3i orthologues is the similarity between cytoplasmic domains of both BRI1 and TGF- β receptor kinases, both having eIF3i as a substrate of phosphorylation. However, no study identified how brassinosteroids or eIF3i phosphorylation affects the function of eIF3i within the eIF3 complex and if that modulates the initiation in any way.

3.10. eIF3k, eIF3l and eIF3m

eIF3k, is a PCI domain containing eIF3 subunit encoded by a single gene in *Arabidopsis*. The insertion mutant of *ateif3k* had no effect on the phenotype or the translational efficiency of AtBZIP11, a marker for eIF3-mediated specific translational regulation (Roy, 2010; Tiruneh et al., 2013). AtEIF3K protein was identified as a ubiquitin-conjugate (Kim et al., 2013). eIF3l and eIF3m are the two remaining PCI domain subunits of the eIF3 complex, both encoded by two genes in *Arabidopsis*. AtEIF3L1 was identified as a ubiquitin-conjugate (Kim et al., 2013) but no characterization was done for any eIF3l gene in plants. Single insertion mutants and double mutants lacked any observable difference in the phenotype (Roy, 2010).

4. Conclusions

Recent studies have already outlined the vast complexity of translation regulation in plants (Merchante et al., 2017). However, in the contrast with the understanding and complexity of transcription regulation, our knowledge around translation and its regulation is still merely scratching the surface, being limited mostly by the available technology. More advanced methodologies to study the translation are therefore rapidly emerging and will answer more questions in the nearest future, as well as improving even more (Mazzoni-Putman and Stepanova, 2018). Across the eukaryotic kingdom, the eIF3 complex is mostly studied in yeast and mammals, where the individual subunits show essential regulatory roles in changing the translation efficiency of specific developmental regulators. Their mutations or protein level dysregulation, for example in human, cause numerous developmental dysfunctions and were found in various types of tumors (Reviewed in Gomes-Duarte et al., 2018). Although plants and mammals are evolutionary very distinct eukaryotic organisms, the general function and resemblance of the complex is conserved.

In plants, a similar role for the eIF3 subunits participating in post-transcriptional regulation is undoubtedly confirmed, but still only little

is known about the exact mechanisms. Several single subunit mutants were characterized in plants and proven to regulate translation during stress response and are affecting vegetative development, as well as the plant gametophytic generation. However, no studies tried to combine any single subunit mutants in the *Arabidopsis*. For the subunits encoded by two genes in *Arabidopsis*, there has been no evidence for any double mutant up to date. What differences will appear in multiple subunit dysfunction is a question for future research. A new detailed interaction and structural research on eIF3 in plants should bring out new understandings of mechanisms in the described regulatory function, and/or answers about the differences between the so far consistent eIF3 models from different organisms. Also, many post-translational modifications of the plant eIF3 subunits emerged from high-throughput studies and indicated that the additional regulatory functions are under control of phytohormones or might emerge during abiotic or biotic stress responses. To add more to the possible complexity of plant eIF3 and its specialized role in translation, an interesting field for future research is also the existence of distinct eIF3 subcomplexes, as they were found able to perform at least the general eIF3 functions. Whether such subcomplexes are just yet unassembled, or they do have non-identical functions in the translation during different developmental stages or stress, is not known.

CRedit authorship contribution statement

Karel Raabe: Writing - original draft, Conceptualization. **David Honys:** Writing - review & editing, Funding acquisition. **Christos Michailidis:** Writing - review & editing, Conceptualization, Funding acquisition.

Declaration of competing interest

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

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