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Molecular Surveillance and Cellular Homeostasis

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ABSTRACT

A web of events which are inter-related and highly regulated determines the fate of gene expression. Essentially, these vital events are broadly categorized into two types, namely, post-transcriptional and post-translational events. Primarily, processing mechanisms of pre-mRNA including polyadenylation, capping, splicing and modifications of RNA through changes in chromatin [Small interfering RNAs (siRNA), long non-coding RNAs, micro RNAs (miRNA)] are included under post- transcriptional events. Protein modifications including sumoylation, ubiquitination and phosphorylation are some of the events which occur at post-translational level. Both post-transcriptional and post-translational events are considered to be constitutive and also are aggravated by endogenous and exogenous factors. Particularly, in plants, regulation of gene expression is yet to be fully understood. These molecular events ensure proper occurrence of the factor(s) required which would ultimately modulate several downstream cellular processes. This review primarily focuses on some of the key post-transcriptional and post-translational events which are significant in deciding the fate of eukaryotic gene expression.

KEY WORDS: REPLICATION, MESSENGER RNA, POST-TRANSCRIPTIONAL MODIFICATIONS, PROTEIN MODIFICATIONS.

INTRODUCTION

Exterior framework of an organism typically referred to as the phenotype, is generally determined by the functional proteins, though their sequence is encoded in DNA. The genetic expression is regarded as one of the elemental process which plays a vital function in the changeover of the complex genome to a substantial life. Since genetic expression process is a strongly regulated event, so any sort of mis-regulation may escort to distorted physical life which includes a variety of genetic diseases. Till date, it is pretty well recognized that the genetic expression is synchronized at a variety of levels and these miscellaneous mechanisms are well included as a food web. The regulatory mechanisms controlling gene expression is primarily divided into two main types (1) post-transcriptional mechanism and (2) post-translational mechanism. Additionally, upstream of these two events, DNA is mostly synchronized at the transcriptional level prior to entering into the transcription event.

Quality control of RNA at the post-transcriptional level is a very important concern for all organisms to ensure precise gene expression, both qualitatively and quantitatively (Ohtani and Wachter 2019).Transcriptional process has been expansively premeditated as compared to that of post-transcriptional and post-translational events for the reason that of scientific aspects. It is apparent that transcription is one of the essential and instinctively imperative steps within the multistep processes involved in regulation of gene expression and also the scientific methods to decode transcriptional regulation are very well recognized.Post-transcriptional regulation mechanisms engage diverse events such as

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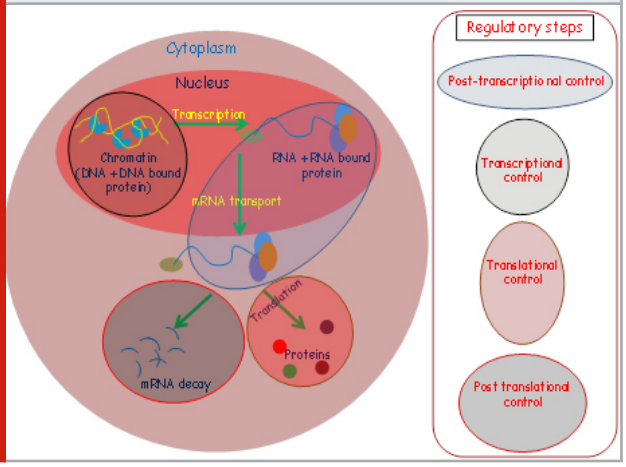
messenger RNA processing which includes 5 end capping, polyadenylation and intron splicing. Export as well as localization of messenger RNA, messenger RNA decay, and translation of messenger RNA are also included (Fig. 1).

Figure 1: Multiple layers of regulatory events meant for gene expression



Regardless of this array of regulatory mechanisms, lone thing in general is that they eventually control where and when a messenger RNA is translated to protein. As a result, translation and its regulation are extremely fundamental to post-transcriptional regulation of gene expression (Panigrahi et al., 2021). The regulatory mechanisms controlling post-translational events are known as Post-Translational Modification (PTM), essentially which refers to several types of covalent and enzymatic modifications of proteins occurring following to their synthesis. Post-synthesis of proteins through ribosomes, they endure PTM in order to shape the mature and functional protein product. PTMs may arise on the side chains of amino acid or else at the N- or C- terminal of proteins (Pratt et al., 2006). Phosphorylation is quite a regular mechanism for modulating the enzymatic activity and is also most common PTM (Khoury et al., 2011).

Countless eukaryotic proteins harbourcarbohydrates attached through a process called as glycosylation, which mostly induces stabilization and protein folding, thus allowing the newly synthesized proteins to perform regulatory functions. Alliance of lipids commonly recognized as lipidation, chiefly aim a specific protein or a part of it which is adhered into the cellular membrane. Additional forms of PTMs comprises of cleavage, as in the case of synthesizing a mature form of protein by processing a given pro-peptide. Occurrence of disulfide bonds, formed due to cysteine residues, also is referred to as a type of PTM (Lodish 2000). PTMs also occur as a result of oxidative stress (Dalle et al., 2006, Panda et al., 2016, Panigrahi et al., 2016, Panigrahi and Sahoo 2016). Protein aggregates formed post protein degradation may be referred to as carbonylation which primarily targets the newly synthesized protein. Modifications in unambiguous amino acids can thus be applied as biomarkers signifying oxidative dent (Grimsrud et al., 2008).

RNA processing and export: Prior to the transfer of mRNA from nucleus to the cytoplasm for getting accessible to the translational apparatus, it needs to experience a sequence of dispensation steps: firstly, at the 5' end, the messenger RNA bears a cap like structure, then, splicing event initiates leading to the splicing out of introns harbouring in the pre-messenger RNA, finally a specific 3' end of the mRNA is synthesized, usually referred to as polyadenylation. Every event advance co-transcriptional and influences each other (Proudfoot et al., 2002). Initially, m7G cap is added at the 5' end of the budding mRNA and occurs following synthesis of 20-30 nucleotides. This event primarily is a complex process and occurs in a three-step process. At first, the guanosine mono phosphate (GMP) domain from the GTP is supplemented into the foremost nucleotide present in the pre-mRNA and then, GMP is methylated specifically at location N7.

For the stability of mRNA and translation process, the m7G cap is imperative. Inside the nucleus, the m7G cap gets associated along with the cap binding complex (CBC). CBC contains two subunits and after being moved into the cytoplasm, it forms a complex with the translation initiation factor 4E (eIF4E), which is essentially an indispensable tread in the initiation process of translation. Since the coding sequences (exons) of a large amount messenger RNAs incase of the higher eukaryotes are broken up by the presence of introns, thus these group of introns needs to be chopped off of the pre-messenger RNA to create functional messenger RNA. Consensus and conserved sequences are required for splicing of the mRNA, which primarily marks the exon-intron limits, and the spliceosome, commonly referred to as the catalytic complex carries out the enzymatic reactions to eliminate the introns and ultimately ligate the flanking exons. Five small ribonucleoprotein particles (snRNP U1, snRNP U2, snRNP U4, snRNP U5 and snRNP U6) make up the spliceosome unit. Usually, snRNPs are made up of a small nuclear RNA, commonly referred to as snRNA, and associated proteins, many of which are accessory proteins.

Preferably, almost hundred of proteins are believed to be engaged as factors, primarily involved in splicing event (Jurica and Moore 2003). Splicing reaction undergoes catalysis process and this event is reliant on RNA-RNA, protein-protein and RNA-protein interactions. Moreover, the unconventional use of exons, referred to as alternative splicing can also add to the formation of protein diversity by allowing a single gene to fabricate manifold isoforms (Matlin et al., 2005). The majority of messenger RNAs also bear a definite structure, a poly (A) tail at the 3' end. In higher eukaryotes, mRNAs coding for histone proteins lack poly (A) tail, but this is absent in yeast (Fahrner et al 1980). Polyadenylation at the 3′ end occurs in two steps: firstly, the newly synthesized messenger RNA is cleaved at the site mostly where the polyadenylation is destined to initiate, and then processed for poly (A) creation. In

resemblance to the splicing, the polyadenylation protein complex is required for poly (A) tail configuration and also explicit sequence-elements above the pre-messenger RNA. In case of mammalian cells, the position of cleavage mostly lies flanked by ahexamer motif (AAUAAA) along with a GU-rich downstream element, DSE.

This hexamer is essentially associated by the cleavage and polyadenylation specificity factor (CPSF). The downstream elements associate with the cleavage stimulatory factor:cleavage factor I and cleavage factor II are also obligatory. While both the poly(A) polymerase (PAP) and the cleavage and polyadenylation specificity factor are mandatory for cleavage of the pre-mRNA and poly(A) addition respectively, the cleavage stimulatory factor(CstF) is also indispensable for the endonucleolytic cleavage to occur, and CstF together with the CPSF are indulged for recruiting CF I and also the CF II. The synthesis of poly (A) tail occurs in the same way both in the case of yeast and mammalian cells. The protein factors concerned largely bear orthologous components, but also explicit accessory machinery that are specifically found in any one of the species. Additionally, in case of yeast cells, the AAUAAA hexamer pattern is replaced by an erratic A-rich element and instead 3 polyadenylation complexes are present. Cleavage Polyadenylation Factor (CPF), which bears numerous factors which are homologous to CPSF and also the cleavage factor IA (CF IA), poly(A) polymerase and cleavage factor IB (CF IB).

The rising poly (A) tail is associated by the poly (A)-binding protein (PAPB). The PABP is mainly thought to persuade the ultimate length of the poly (A) tail, positively by invigorating the processivity of poly (A) polymerase, and negatively by associating with the poly (A) nuclease (PAN) (Magnus et al., 2003). Moreover, PABPs are concerned with nuclear export and are also imperative for the launch of translation. The poly (A) tail is critical for quite a lot of superfluous mechanisms regulating post-transcriptional events, occurring in the cellular cytoplasm. The translational state can also be standardized via cytoplasmic polyadenylases and steadiness of a range of target messenger RNAs by manipulating the length of the poly (A) tails. The preeminent illustration is most likely that of translational regulation of the maternal messenger RNAs in case of oocytesof Xenopus, stockpile in a translationally subdued state with extremely petite poly (A) tails, which become polyadenylated when activated and as a outcome of which, translated messenger RNA undergoes decay by several exonucleolytic events which is usually preceded by a reduction of the 3 end poly (A) tail (Parker and Song 2004).

In recent times, poly (A) tails deadenylation has also been exposed to ensue in micro RNA-mediated regulation (Giraldez et al., 2006, Wu et al., 2006). The very last component in the expedition from the nucleus (space of transcription process) into the cytoplasm is the nuclear export of the mature messenger RNA. Export occurs through the nuclear pore complex and happens in the perspective of messenger ribonuleoprotein complexes (mRNPs). Messenger ribonuleoprotein complexes embrace messenger RNA and several associated RNA-binding proteins, which associate to the messenger RNA during the progressing steps (Aguilera et al., 2005). Separately from the aforesaid, Cap binding complex or poly (A) binding proteins, like RNA-binding proteins consist of SR (serine/arginine rich) and hnRNP(heterogeneous nuclear RNP) proteins, the exon junction complex (EJC), which are a group of proteins encumbered onto the messenger RNA, mainly at the upstream region of exon-exon junctions, as a end result of the pre-messenger RNA splicing.

These protein components are imperative for the organization of the mRNP complex with the nuclear pore complex and the shuttling from nucleus into the cytoplasm, and a few of them settle, allied with the messenger RNA as it is moved out, whereas others are constrained within the nucleus. Moreover, nuclear export is an central step in quality control, as damaged or un-processed messenger RNAs are not only ineffective, but also potentially detrimental, if incase gets translated within the cytoplasm. Only physiological messenger RNAs are transferred into the cytoplasm from their site of synthesis and particularly this surveillance step is very closely united to RNA processing and the composition of mRNP. Yet again, it needs to be highlighted that, regardless of the introduction of messenger RNA transcription and other downstream chronological events occurring in the cell are well integrated among each other and are not independent in temporal and spatial perspective (Proudfoot et al., 2002, Aguilera et al., 2005).

Significance of translational regulation: A varied number of reasonable benefits do occur since the translational regulation is perfectly fitted. Most importantly, the translational regulation happens as an immediate retort without the requirement of undergoing the several processes involved in regulating gene expression such as transcription, processing of messenger RNA or even export of messenger RNA. Moreover, the regulatory mechanism of translation is a reversible in nature since it involves quite a lot of reversible protein structure alterations like, the phosphorylation of several initiation factors. Control of translational machinery is very much inevitable, particularly in the systems where transcriptional regulation is not promising like in the case of reticulocytes; they lack nucleus, RNA viruses or oocytes.

Most importantly, the translational regulation is primarily, spatial control of gene expression inside the cell (Johnston 2005, Sahoo et al., 2020a,b,c,d,e,f). The significance of dedicated translational regulation is realized especially for localized protein assembly within neurons or else throughout the development process, since transcriptional regulation is limited to the cellular nucleus. For regulating gene expression, translational regulation is a superior alternative owing to its flexible nature. There are numerous molecular targets for regulation of translational process, which

ultimately affects the efficiency of translational event for numerous or a few messenger RNAs. Most remarkably, for fine tuning of gene expression cells regulate the translational machinery, as there are several number of genes such as GADD45α or TNF-α which are regulated at the transcriptional and translational level.

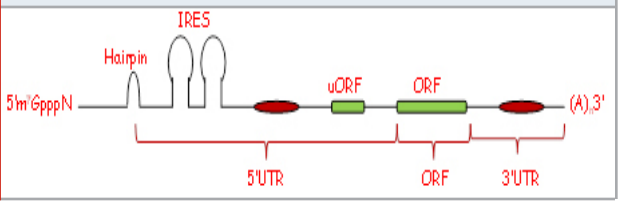
Effectors for regulation of translation: Initiation factors, messenger RNA (mRNA) and the ribosome: Translational control is well regulated at a comprehensive level as well as in a messenger RNA specific manner (Gebauer and Hentze 2004). Primarily, large-scale regulation affects the effectiveness of translation machinery of many messenger RNAs through a common switch-on and switch-off of translation process. The translation of a subset of mRNA is affected by mRNA-specific regulation. Mainly, translational regulation allows or forbids the union of the messenger RNA with that of the translational apparatus. A fundamental target in several regulatory mechanisms is the cap binding protein, eIF4E which binds to many inhibitory proteins, resulting in the unavailability of the messenger RNA.

Comprehensive regulation of translation is universally mediated through such modifications, especially of the translation initiation factors. An additional target for translational regulation is the messenger RNA itself. The cis-regulatory elements associate with trans-acting factors (Fig. 2). The cis-regulatory elements present on the messenger RNA could be present anywhere along the messenger RNA, but typically for the translational regulatory factors, these vital elements are present in the 5' UTR or 3'UTR. Translational regulatory events mediated by messenger RNA, occurs mostly by numerous regulatory proteins, which primarily bind to the cis-regulatory elements of a given messenger RNA.

The ribosome itself may also become one of the targets of translational regulation. Quite a lot of its protein constituents undergo post-translational modifications. An exemplar is the phosphorylation process of ribosomal protein S6 mediated by ribosomal S6. It has been reported that the phosphorylation of ribosomal protein S6 fallout in an augment in translation initiation. Ribosomal proteins also undergo a post-translational modification, ubiquitinationand methylation. Many studies points towards the heterogeneity of ribosomes; the cell is able to construct a range of different kinds of ribosomes, which essentially differs in terms of paralogue composition and post-translational modifications, and many a times dedicated ribosomes could also play a role in the translational regulation of specific subsets of messenger RNAs (Yu et al., 2004).

Novel components in translational control: Processing bodies and micro RNAs: Recently, two novel ways to direct messenger RNA turnover at the post-transcriptional level have gripped an immense deal of consideration. The discovery of processing bodies localized in the cytoplasm of a cell, which were originally considered as foci inside the cell with a high concentration of enzymes meant for messenger RNA decay, has been a significant outreach in the scientific field (Bashkirov et al., 1997). The added detection is that of small RNAs, which may amend the permanence and translation of targeted messenger RNAs (Bartel 2004). Processing bodies are most likely a site of messenger RNA decay (Fig. 3). Processing bodies were first characterized by several groups using several scientific techniques such as microscopy, as factors involved for the perishing of messenger RNA decay and other factors like LSM, XRN1, DCP1 and DCP2 accumulate in the foci (Bashkirov et al., 1997).

Figure 2: Cis-acting sequences influence translation initiation of specific messenger RNAs.

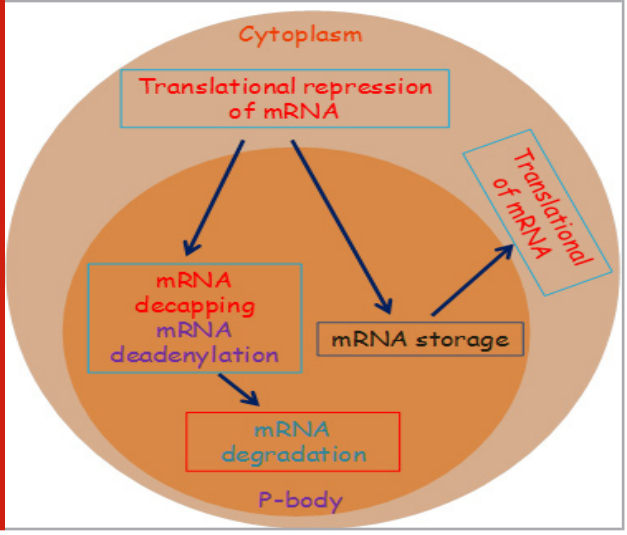


The messenger RNA decay in case of eukaryotes is mainly controlled in diverse ways mostly by exonucleolytic or endonuleolytic pathways.Degradation occurring through exonucleolytic pathway is typically initiated by deadenylation of the poly (A) tail of the messenger RNA. Then the transcripts will be tarnished from their 5′ ends mostly by the exonuclease such as XRN1, subsequent elimination of the 5' cap, known as decapping. On the other hand, the exosome complex can debase transcripts from their 3′ ends prior to decapping. Factors involved in the nonsense-mediated decay process, which are responsible for the hasty dilapidation of messenger RNAs with a untimely stop codon are also found in mammalian processing bodies (Conti and Izaurralde 2005). Nonsense-mediated messenger RNAdecay (NMD), which is possibly the best-known translation-dependent regulatory mechanism specifically in eukaryotes, selectively destroys messenger RNAs as a means of post-transcriptional gene control (Kim and Maquat 2019). Control can be for the purpose of ensuring the quality of gene expression.The relation between the processing bodies and messenger RNA turnover rate is still captivating.

The precise mechanism how messenger RNAs shuttle into the processing bodies and become repressed from translation is not yet clearly deciphered(Panigrahi and Satapathy 2020a).Small RNAs are mostly riboregulators that have significant roles in most of the eukaryotes. They inhibit the gene expression by acting either on DNA to direct sequence abolition and chromatin remodeling, or on the RNA to direct cleavage and eventually regulate the translation expression (Vaucheret 2006). Micro RNAs (miRNAs) and short interfering RNAs (siRNAs) are the two categories of small RNA molecules that appeared as regulating factors of messenger RNA stability and translation. Both the miRNAs and siRNAs are short RNAs ranging around 20-27 nucleotides and are differentiated based on their biogenesis.

miRNAs are principally derived from longer precursors that mostly comprise of a ~75 nucleotide improperly based hairpin segment. siRNAs are of comparable length but are derivative of absolutely complementary RNA precursors. During RNA interference (RNAi), siRNAs which are exogenously introduced target messenger RNAs for cleavage in an endonucleolytic manner (Tomari and Zamore 2005, Panigrahi and Satapathy 2020b). In case of animal cells, a large amount miRNAs are only partly complementary to their target messenger RNAs and the down-regulation of translational product of the target is typically greater than the down-regulation of its messenger RNA profusion, which suggests regulation at the stage of translation (Panigrahi and Satapathy 2020c).

Figure 3: Processing bodies (P-bodies): The site for mRNA decay.



Post-translational modifications of proteins: Post-translational modifications (PTMs) of proteins largely involve covalent alterations that occur subsequent to the translation process. The newly synthesized nascent proteins are eventually exposed to a string of specific enzyme-catalyzed alterations located on their backbones or side chains. Two extensive types of protein post-translational modifications occur. The first type includes every enzyme-catalyzed addition of a few kinds of chemical groups, typically an electrophilic part of a substrate, towards the side chain residue of a protein. This modified side chain is generally electron rich and act as a nucleophile in the transfer process. The second type of PTMs is covalent cleavage of the peptide backbones in proteins. It occurs either by protease action or less commonly mediated by autocatalytic cleavage. A lot of diversifications can be seen in the side chains of amino acids (Walsh et al., 2005).

Covalent modification of proteins: Fundamentally, there are five most frequent types of covalent additions occurring to proteins. They are acylation, phosphorylation, alkylation, oxidation and glycosylation, which are generally catalyzed by dedicated post-translational modification enzymes. Thus, the protein products obtained in this mode result into making up subsets of the complete proteome of an organism commonly referred to as the acyl proteome, the phosphoproteome, the alkyl proteome, the oxidized proteome and the glycoproteome. Most remarkably, every sub proteomes add to extensive diversity (Walsh et al., 2005, Ray et al., 2020, Behera et al., 2020, Jena et al., 2020, Das et al., 2020).

Post-translational modification: reversible and irreversible: Because of the cellular requirement of a meticulous covalent modification occurring in a protein, reversibility and irreversibility of the specific protein modification is critical. The epitome of reversible modification is mainly the protein phosphorylation, reliable with its advancement to the foremost role in protein-based signaling in eukaryotes. All PTMs apart from alkylation have committed enzymes. Mostly, large enzyme families mediate the amputation of several covalent modifications. The enzymes which are involved in acylation, reverse phosphorylation and glycosylation are mostly specific hydrolases, while cleavage of disulfide bonds is mediated by reductases(Walsh et al., 2005).

CONCLUSION

The self-fidelity and unswerving post-transcriptional and post-translational mechanisms make sure of a safe and sound pathway for the genetic makeup, primarily the DNA of an organism and carries out the critical changeover of the DNA into a functional protein which eventually results into an healthy physiological environment within the cell. This inter-relationship and interdependence prevailing among different molecular events similar to a spider's web provides the foundation for a fault free "Central Dogma" of molecular life. A number of events occurring within a cell irrespective of the nature of product to be formed, surveillance mechanisms ensure the fidelity. These molecular events are essentially very critical for maintaining the homeostasis within the cell. For instance, maximum number of immune related genes, both in plants and animals, are tightly regulated by the quality control mechanism, NMD.

NMD ensures that during normal and healthy conditions (pathogen unchallenged condition); these immune genes do not synthesize their protein counterparts. This regulation critically saves a lot of energy for the organism by not synthesizing unwanted protein factors. Whereas, the same NMD process shuts off when the organism is challenged with any sort of pathogen and allows the expression of protein factors responsible for defense mechanism. In a nutshell, understanding and deciphering the role of different post-transcriptional and post-translational events would be critical for future benefits.

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CRediT authorship contribution statement:
Annapurna Sahoo: conceived the idea, wrote the manuscript, have read and approved the final manuscript before submission. Kunja Bihari Satapathy: conceived the idea, have read and approved the final manuscript before submission.

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