About non – coding RNAs

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Abstract— *The central dogma of molecular biology states that DNA makes RNA and RNA makes protein. Recently, a large number of RNAs have been identified in animal and plants that have little or no protein – coding potential. Such RNA molecules have been discovered by the extensive applications of high – throughput sequencing technology. Non – coding RNAs (ncRNAs), which comprise a significant output of the genomes of prokaryotes and especially eukaryotes, are increasingly implicated in the molecular mechanisms that are being used for responding to biotic and abiotic stresses that occurred in living things life. The ncRNAs are a heterogeneous group of RNA molecules, which can be classified in different ways according to their location, length, and biological functions. In this review a brief description about non – coding RNAs will be brought especially in plants.*

Keywords— Gene regulation, Non – coding RNAs, Plants.

I. INTRODUCTION

DNA makes RNA and RNA makes protein. This phrase has ruled as a dogma in biology for many years. But what rules in biology and or molecular biology is not so simple. In fact majority of the genetic material is transcribed into RNAs that don't make protein. Studies of genome suggest that the protein coding regions represent only around 1 – 2% of the genome [158]. Non – coding RNAs (ncRNAs), which comprise a significant output of the genomes of prokaryotes and especially eukaryotes, are increasingly implicated in the molecular mechanisms that are being used for responding to biotic and abiotic stresses that occurred in plant life. Indeed, regulatory RNAs are part of genetically encoded response networks and also underpin epigenetic processes, which are emerging as key mechanisms of adaptation and transgenerational inheritance [112]. Non – coding RNAs also capable of changing the conformational activity of many critical proteins [113]. Subcellular localization of proteins that mediated by non – coding RNAs has been described in plants as well [4]. Immune related diseases are controlled by lncRNAs (one of the types of non – coding RNAs) in both human and plants [158] and many other examples of roles played by non – coding RNAs in (Plants).

II. CLASSIFICATION OF NON – CODING RNAS

Non – coding RNAs are divided on different bases. Based on a general division they are roughly classified into either short ncRNAs with less than 200 nucleotides or long ncRNAs (lncRNAs) with more than 200 nucleotides. But the number and the variety of non – coding RNAs is more than for this classification. So that the percentage of non – coding RNA counts for more than 98% of total transcripts [20]. Increasing data showed that noncoding portions of RNA have been broadly involved in regulating the complexity of organisms and the complexity of RNA sequence increases the ability of cells to store the huge information in genome [78 and 81]. In addition to the long and short those non – coding RNAs with less than 200 nucleotides classified into microRNA (miRNA), small interfering RNA (siRNA), and piwi – interacting RNA (piRNA) [50]. As already mentioned non – coding RNAs are divided on different bases for example lncRNAs could be grouped by its position of their target genes: overlap, when it share same sequence with protein coding transcripts; intergenic, when the lncRNA located between the coding regions of two protein; intronic, when it sits in between two genes of one protein [79]. In addition to the position, the directions of transcripts and lncRNA also play an essential function for lncRNA's regulation. Therefore, it could be further divided to sense; antisense and bidirection three types [109].

Non – coding RNAs can also be considered as a large and diverse collection of polyadenylated or nonpolyadenylated transcripts with low protein – coding potential. Although housekeeping RNAs (e.g. ribosomal RNAs) and primary transcripts of microRNAs (miRNAs) also fall into this definition [68]. Most of the intergenic regions of Arabidopsis, rice and corn encode lncRNAs that become polyadenylated and their encoding genes are thought to be transcribed by polymerase II with some being transcribed by PolIV and/or PolV [37; 136; 80; 89; 67; 140; 151]. In addition, various types of unstable lncRNAs can also be transcribed from the genomic regions around transcription start sites, enhancer regions, intron splicing sites and/or transcription termination sites [35; 119; 138; 53; 117; 41].

A widely accepted view considers only stable lncRNAs transcribed by RNA polymerase II as 'typical lncRNAs' [57].

Nonpolyadenylated can be classified as a group of novel transcripts which are 50 – 300 nt in length that have been detected in the model plants Arabidopsis and Rice [143and 149] and they are named intermediate – sized ncRNAs (im – ncRNAs) [149].

Nonpolyadenylated ncRNAs can be circular in structure, and indeed, plant viroids were the first to be characterized as circular RNA (cRNA) molecules some 38 years ago [51]. Since then, several cRNAs have been found to naturally exist in other viroids and eukaryotes [19; 23; 11). A recent report identified thousands of cRNAs in human, which were generated from back – spliced exons [130; 76; 77; 149]. Circular RNAs have been suggested to function as target mimics of microRNAs (miRNAs) to compete with endogenous RNA – p lants [72; 97; 157; 48]. Although cRNA and target mimicry mechanism were originally discovered in plant viroids and plants, respectively [72] and 51), to date, cRNAs have not yet been identified on a genome wide scale in plants.

III. BIOGENESIS OF NON – CODING RNAS

As previously mentioned the main basis for the division of non – coding RNA is their length. Accordingly a brief explanation of the biosynthesis of each of these is given.

3.1 Biogenesis of small non – coding RNA

Small 21 – to 25 – nt, noncoding RNAs are important regulators of gene expression in both plants and animals [63; 30; 87]. These small RNAs can be divided into two classes: micro – RNAs (miRNAs) and short interfering RNAs (siRNAs). miRNAs are found in a number of multicellular eukaryotes [144; 63;30] and are generated from longer hairpin precursors by the Ribonuclease III – like enzyme Dicer. After incorporation into an Argonaute – containing RNA Induced Silencing Complex (RISC) [44; 43], base pairing between miRNAs and complementary target mRNAs guides sequence – specific translational inhibition or transcript cleavage [30]. miRNAs have a well – documented role in allowing developmental regulation of multigene families (65; 63; 30]. siRNAs differ from miRNAs in that they are generated from long double – stranded RNAs. siRNAs were first identified in plants undergoing posttranscriptional gene silencing (PTGS[8]), and subsequently diverse sets of endogenous siRNAs have been found in plants and animals (26; 125; 144; 2; 45; 21]. The biogenesis of small RNAs in plants is especially complex. In Arabidopsis, there are four Dicer – like (DCL) proteins [127], six predicted RDRs [116], and ten predicted Argonautes [60]. DCL1 is required for the production of 21 – nt miRNAs and trans – acting siRNAs (tasiRNAs) [147; 13; 40]. Allen *et al*. (2005) [32] demonstrated that an initial DCL1 – dependent, miRNA guided cleavage of tasiRNA primary transcripts sets the 21 – nt phase for accurate tasiRNA formation. DCL4 is responsible for the processing of 21 – nt tasiRNAs [145; 160; 108]. Generation of tasiRNAs also involves RNA – D EPENDENT RNA POLYMERASE 6 (RDR6) and SUPPRESSOR OF GENE SILENCING 3 (SGS3) [13 and 40]. DCL2 is involved in the production of some viral siRNAs [161] and may substitute for DCL3 or DCL4 when they are absent [145]. DCL3 and RDR2, as well as the RNA polymerase IV encoded by NRPD1A/SILENCING DEFECTIVE 4, cooperate in generating heterochromatin – associated 24 – nt siRNAs from various retroelements and transposes, 5S ribosomal RNA genes, endogenous direct and inverted repeats, and transgenes containing direct repeats [132; 161; 31; 155]. The appearance of these siRNAs has been correlated with DNA and histone methylation at the homologous chromatin [135].

3.2 Biogenesis of long non – coding RNAs

lncRNAs are similar to mRNAs in that many, but not all, lncRNAs are processed, 5' capped, and polyadenylated [102 and 146]. Most lncRNAs are named for the genes they are nearby or for the protein – coding genes that they regulate [96]. However, given the large quantity of proposed lncRNA transcripts, a debate has emerged about how to structure the naming convention in a logical and flexible format for cataloging newly discovered lncRNA transcripts [79 and 107]. lncRNAs are typically classified as overlapping when a protein – coding gene is encompassed by the intron of an lncRNA, bidirectional or divergent when the long intergenic noncoding RNA (lincRNA) and nearby protein – coding gene are transcribed on opposite strands, intronic when the entire sequence of the lncRNA falls within the intron of a protein – coding gene, intergenic when an lncRNA sequence falls between two genes as a distinct unit, and sense or antisense if the lncRNA is mapped between one or more exons of another transcript on the same (sense) or opposite (antisense) strand [79; 101; 70]. Finally, enhancer RNAs (eRNAs) are transcribed in one or two directions at genomic transcriptional enhancers, often times in close proximity to protein – coding genes [106].

lncRNAs are transcribed by RNA polymerase II or III, and additionally, by polymerase IV/V in plants [98; 100; 14]. They are processed by splicing or nonsplicing, polyadenylation or non – polyadenylation, and can be located in the nucleus or cytoplasm. Functional analyses of lncRNAs have shown that they are potent cis – and transregulators of gene transcription, and act as scaffolds for chromatin – modifying complexes. As potent regulatory components involved in gene regulation from various aspects, lncRNAs can exert their effects during tissue development and in response to external stimuli [33]. lncRNAs are classified primarily based on four major features, namely, genomic location, functions exerted on DNA or RNA, functioning mechanisms, and targeting mechanisms [92]. Although lncRNAs have received more attention in recent years, the research in this field is still in its infancy. Thus far, only a few lncRNAs have been sufficiently described [70; 61; 131]. In particular, research in this area in plants is far behind that in humans and animals [118;154; 153]. Nonetheless, studies available suggest that plant lncRNAs exert regulatory functions similar to those in animals [118 and 154].

IV. THE BIOLOGICAL ROLES OF NON – CODING RNAS

After a brief description of the non – coding RNAs and their division, from now on our focus will be on long non – coding RNA more, especially in plants.

4.1 Long non – coding RNAs in plants

Although lncRNAs have received more attention in recent years, the research in this field is still in its infancy. Thus far, only a few lncRNAs have been sufficiently described [70; 61; 131]. In particular, research in this area in plants is far behind that in humans and animals [118; 154; 153]. Nonetheless, studies available suggest that plant lncRNAs exert regulatory functions similar to those in animals [118 and 154]. In plants, as sessile organisms exposed to environmental influences, RNAs have been identified as major components in response to variations and stresses, such as to drought, changed light regimes and nutrient and salt stresses, involving long RNAs, miRNAs and other endogenous small RNAs [25; 18; 38; 66; 111; 125; 67; 95; 72; 64]. Environmental variations are part of plant natural life cycles and stresses can also be related to specific developmental processes. For example, the npc536 RNA promotes root growth under salt stress conditions [18], and at least two different lncRNAs are crucial in the phenomenon of vernalization in flowering species, which are exposed to prolonged periods of cold prior to flowering in spring. This involves the intersection of RNA regulation with chromatin – based epigenetic mechanisms, including the Polycomb silencing of the floral repressor FLOWERING LOCUS C (FLC). The intronic lncRNA Coldair, which is transcribed from the FLC locus, plays a role in the stable repression of FLC through specific recruitment of Polycomb components to target sequences [189], whereas the antisense transcript Cool air, which originates from the 30 – end of the FLC gene, has an early role in the silencing of FLC through a mechanism that involves antisense transcription [131]. More generally, given their extensive involvement in stress response and development, including through epigenetic mechanisms, ncRNAs have the potential to emerge as important molecules in the regulatory mechanisms that confer developmental and phenotypic plasticity in plants and other organisms [55 and 133].

Novel ncRNAs can be detected and discovered by both experimental and computational screenings [26]. Genome – wide approaches used for transcriptomic analyses such as microarrays and RNA sequencing in model organisms have revealed that non – protein coding transcripts occupy most of the eukaryote transcriptome, much higher than that previously believed [67; 89; 59]. Especially, next – generation sequencing (NGS) – based technology provides us with a more complex perspective and a much closer and complete view of the RNA world. lncRNAs have been discovered in yeast and other higher eukaryotes [129 and 57]. For instance, genome – wide analyses have discovered more than 50,000 lncRNAs in the human genome [12; 88; 102]. About 6480 lncRNAs were identified from 200 *Arabidopsis thaliana* transcriptomic data sets, with either organ – specific or stress – induced expression profiles [67]. Wang *et al*., [148] discovered 37,238 long non – coding natural antisense transcripts (lncNATs) in *A. thaliana*, with antisense transcripts associated with 70% of annotated mRNAs [28]. Using a strand – specific RNA sequencing approach, Zhu *et al*. [118] identified lncRNAs in *A. thaliana* induced by *Fusarium oxysporum* infection.

Results showed that antisense transcripts existed in about 20% of the annotated genes, and most newly – identified transcriptionally – active regions (TARs) were adjacent to or located as an extension of the annotated genes. Besides poly(A)$^+$ lncRNAs, lncRNAs without poly(A) tails (poly(A)- lncRNAs) were also identified in plants]. In plants, the presence of poly(A)$^-$ lncRNAs was revealed in seedlings of *A. thaliana* under different stress conditions using RNA – seq [24]. Compared to poly(A)$^+$ lncRNAs, poly(A)- lncRNAs are shorter, have lower expression, and are more specific in response to stresses. Also small RNAs (usually transposon derived) in plants are implicated in epigenetic processes that underpin phenotypic differences between Arabidopsis ecotypes as well as in hybrid vigour and compatibility in different species. Remarkably, in fruit flies, transposon – derived piRNAs, which are important epigenetic regulators are also centrally

involved in the process of hybrid compatibility and dysgenesis [62 – and 137]. Moreover, small regulatory RNAs, including piRNAs and siRNAs, are closely implicated in transgenerational epigenetic inheritance in both plants and animals [137 and 75], which may represent a widespread adaptive phenomenon, including in stresses and defence against aggressions and parasites [1 and 5]. Given the strong connections of epigenetic mechanisms and responses to the environment, including to stresses [27], the investigations of the roles of regulatory RNAs and the possible evolutionary implications are warranted. Moreover, transposons, whose transcription and activity are developmentally regulated and strongly responsive to stresses (such as heat shock, DNA damage, oxidative stress and viral infection) [86], can be the source or integrate the sequence of regulatory small and long RNAs [28 and 6] and have large impact not only in genome evolution but also in several epigenetic regulatory effects [123]. As these links between regulatory RNAs and molecular phenomena recently associated with evolutionary processes, including epigenetic regulation, stress response [16 and 91] and transposition [86], grow increasingly stronger, it will become fundamental to consider the centrality of RNA regulation in these processes.

Genome – wide analysis of the Arabidopsis genome has identified the expression of overlapping NATs corresponding to a significant proportion of Arabidopsis transcriptome [47 and 148]. Although the role of NATs in translational induction by association with the sense mRNA as demonstrated in animals has yet to be described in plants. Studies of NATs in Arabidopsis have demonstrated other means of gene regulation in which the formation of double stranded RNA with the complementary sense RNA recruits them into the siRNA pathway [111]. Also in Arabidopsis, the induced expression of ncRNAs of the IPS1/At4 family during phosphate starvation responses results in the accumulation of the PHO2 mRNA, a target of miR399 (micro – RNA 399). Franco – Zorrilla *et al*. [72] showed that a conserved motif of 23 nt in this ncRNA family is complementary to miR399 but has critical mismatches at positions 10 – 11, required for miRNA guided cleavage [72]. Therefore, IPS1/At4 RNAs are not cleaved by miR399 but instead sequester miR399 to inhibit its effect on PHO2 mRNA, in a mechanism known as target mimicry. PHO2 RNA encodes an E2 ubiquitin conjugase – related protein that negatively affects shoot phosphate content and remobilization in an unknown mechanism [120]. In *Cucumis sativus*, a lncRNA named CsM10 was isolated using differential display reverse transcription PCR, which showed differential expression patterns in different tissues, seedling developmental stages and photoperiods [74]. CsM10 harbors a 179 bp sequence with high sequence homology to a family of abiotic stress – associated ncRNAs known as the CR20 – GUT15 – Related (CGR) family, suggesting a role in the regulation of gene expression. More studies are required to elucidate its exact function.

In maize, a putative lncRNA, Zm401, is expressed specifically in pollen. Forward and reverse genetic studies deduced a function for Zm401 in regulating the expression of critical genes necessary for pollen development including ZmMADS2, MZm3 – 3 and ZmC5 [152 and 71]. MZm3 – 3 was upregulated in Zm401 mutants while ZmMADS2 and ZmC5 were both downregulated [71].

Overexpression of Zm401 severely affects pollen development due to abnormal tassels and degenerate anthers [152]. How this lncRNA can mediate the downregulation of certain genes but the upregulation of others is intriguing and remains to be elucidated. One possible mechanism may involve the association of specific domains of the transcript with different members of transcriptional protein complexes. lncRNA – mediated subcellular localization of proteins has also been described in plants. The lncRNA Enod40 directs the re – localization of MtRBP1 (Medicago truncatula RNA Binding Protein 1) from the nucleus to cytoplasmic granules during specific stages of legume (*Medicago truncatula*) root nodule organogenesis [4].

V. OTHER FUNCTION OF NON – CODING RNAS

In this paper non – coding RNAs and their functions were preferred in plants at first for studing. But non – coding RNAs have other functions that are general and common in living things and we can simply say they were studied in animal and human cells more. For example:

5.1 lncRNAs function as molecular cargos to target protein subcellular localization

The activity of many proteins required for cell cycle progression and gene transcription can be modulated by limiting their subcellular localization. This mechanism of control has been demonstrated and can be regulated by lncRNAs. In the fission yeast, *Mei2p*, an RNA – binding protein required for pre – meiotic DNA synthesis and meiosis I is transported from the cytoplasm to the nucleus via association with its RNA intermediate, the *MeiRNA*[17]. Mutated Mei2p with lower ability to bind to *MeiRNA* remained cytoplasmic. In the absence of *MeiRNA*, Mei2p transgene product containing an added nuclear localization signal is able to translocate to the nucleus and promote meiosis I, suggesting that the role of *MeiRNA* is to act a chaperon to guide Mei2p nuclear import [104]. The authors suggest that this mechanism of subcellular localization provides

an explanation for the puzzling finding that ongoing transcription is required for accumulation of certain proteins in the nucleus [104]. Indeed, such an explanation is logical but may not be applicable to germ cells that display little or no transcriptional activity such as those in mammalian species [82; 83; 124]. Conversely, cytoplasmic localization of proteins regulated by lncRNA has also been observed. Transcription of *5S ribosomal* RNA relies on TFIIA (Transcription Factor A). Following transcription, the *5S ribosomal RNA* binds to TFIIA and is escorted to the cytoplasm. The binding of *5S ribosomal* RNA masks the nuclear localization signal on the TFIIA protein, resulting in cytoplasmic retention during oocyte development in the Xenopus [39]. The subcellular localization of a transcription factor, NFAT (nuclear factor of activated T cells), important for T cell – mediated immune response, [115] is regulated by the lncRNA *NRON* (*Non – coding Repressor of NFAT*). *NRON*, expressed in a number of mouse and human tissues, binds to members of the nucleocytoplasmic trafficking machinery by inhibiting NFAT nuclear accumulation. This specifically represses NFAT activity and prevents the expression of genes mediated by NFAT [15].

5.2 lncRNAs as molecular chaperons to confer protein conformational activity

The folding structure of proteins deduced by post – translational modifications including phosphorylation can affect their active or inactive states. The discovery that lncRNAs are also capable of changing the conformational activity of many critical protein factors has added another level of complexity to our understanding of protein regulation. Wang *et al*.[150] showed that under DNA damage signalling conditions, ncRNAs transcribed from the 5' regulatory regions of the CCND1 (Cyclin D1) gene in human cell lines function to allosterically modify the structure of an RNA – binding protein named TLS (Translocated in LipoSarcoma) by releasing it from its inactive conformation. TLS is not only modified by the ncRNA but is also guided to the promoter region of the CCND1 gene to inhibit the histone acetyltransferase activities of CREB – binding protein and p300, resulting in repression of CCND1 expression [150]. This is consistent with the role of CDND1 as a cell cycle regulator known to be repressed by DNA damage signals. Similarly in human cells, Lanz *et al*. [121] showed that a lncRNA known as *steroid receptor RNA activator* (*SRA*) is required to confer functional specificity of a ribonucleoprotein complex known as SRC – 1 (Steroid Receptor Coactivator 1),[121] a nuclear receptor coactivator [126]. However, unlike the previous study which resulted in gene repression, *SRA* association with the SRC – 1 results in the activation of hormone related nuclear receptors which then functions to direct the assembly and stabilization of a preinitiation complex for transcriptional activation at the promoter of targeted genes associated with hormonal changes [99]. This mechanism appears to be tissue – specific as *SRA* is only expressed in several tissues, particularly in the brain [121]. Expression analysis in muscle cells and RNA interference showed that *SRA* is a coactivator of MyoD transcription factor during skeletal muscle differentiation [42]. A coding *SRA* has also been described; this RNA differs from the non – coding *SRA* by an extended exon – 1 containing methionine codons necessary for translation [34]. The SRA protein (SRAP) also functions as a coactivator of hormone related nuclear receptors and many other transcription factors including transcription factor IIB [110; 49; 139]. The role of SRA and SRAP in the activation of nuclear receptors has been implicated in prostate cancer [49 and 139]. It is unknown whether *SRA* can associate and regulate its protein form. lncRNAs also have the ability to affect the transcriptional machinery as a whole by binding to RNA polymerase II (RNA Pol II), causing global gene repression. The *Alu* RNA and *B2* RNA are transcribed from short interspersed elements (SINE) during heat shock in human and mouse cells, respectively [134; 22; 114]. These RNA molecules, although not evolutionarily related and share no sequence homology, are both able to bind to RNA Pol II causing general repression of transcriptional activity, suggesting that ncRNAs with diverse sequences can possess conserved functions. Therefore, information from the primary sequence of these ncRNAs is insufficient to allow prediction of function. Interestingly, *scAlu* and *B1* RNA, which are the short form of *Alu* and a homologue of *B2*, respectively, are able to bind to RNA Pol II but cannot induce transcriptional repression [114]. This suggests that neither sequence specificity nor the binding to the RNA Pol II itself is sufficient to inhibit gene transcription. The repressive component (the regulatory domain) lies in two separate regions in the *Alu* RNA which are different to the regions required for binding (the binding domain) to RNA Pol II [114]. The authors suggest that it is the structural conformation of those two regulatory domains and not the sequence that confers transcriptional repression. SINE transcripts also increase during other cellular stresses and during viral infection [146 and 85], suggesting that they may also modulate transcription in a variety of other biological responses. Heat shock induced transcriptional repression appears to also exist in many other eukaryotic species including Drosophila [122 and 141] and plants [52 and 29]. Paradoxically, some genes including those that encode heat shock proteins are transcriptionally activated during heat shock, suggesting that an underlying mechanism must exist to overcome SINE RNA mediated gene repression at those specific gene loci. Shamovsky *et al*. [56] demonstrated that the activation of heat shock proteins in mammalian cells rely on the trimerization of a heat shock transcription factor (HSF) with a ncRNA named *HSR1* (*Heat Shock RNA 1*) and translation elongation factor eEF1A in a ribonucleoprotein complex [56]. This association renders the transcription factor active in DNA – binding activity. In *C. elegans*, a starvation induced

lncRNA, *Rncs – 1* (*RNA non – coding, starvation upregulated*), affects the processing of siRNAs by inhibiting the activity of the RNase III catalytic enzyme, Dicer [128]. This impaired activity is due to the branched structures present in its 300 nt double – stranded RNA structure that presumably allows its association with the RDE – 4/Dicer complex but prevents Dicer cleavage; thus inhibiting Dicer processing of other double – stranded RNA to siRNAs necessary for target messenger RNA downregulation.

VI. CONCLUSION

In recent years, many lncRNA transcripts have been identified. lncRNA studies have become one of the new hotspots in current molecular biology. Broadly, lncRNAs can be considered as a large and diverse collection of polyadenylated or nonpolyadenylated transcripts with low protein – coding potential. lncRNAs are often cell type specific, and the functions of individual lncRNAs can be diverse. Also lncRNAs reported in plant species are limited to only a few model angiosperm plants such as Arabidopsis, rice, maize, wheat, foxtail millet, and soybean. lncRNAs have many functions in the regulation and developmental processes. such as proliferation, through the expression of independent lncRNA transcripts and also gene – associated RNAs, such as promoter – associated RNAs that regulate cell cycle genes. A large proportion of functions mediated by these lncRNAs appear to involve the regulation of proteins involved in transcription, particularly transcription factors, whether it is the mRNA form or the protein form, including those that play critical roles in the maintenance of hormonal balance to induce cellular survival such as nuclear receptor transcription factors.

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