Biochimica et Biophysica Acta 1819 (2012) 149–153

Contents lists available at ScienceDirect

Biochimica et Biophysica Acta

journal homepage: www.elsevier.com/locate/bbagrm

RNA regulation in plant abiotic stress responses ☆

Kentaro Nakaminami [a], Akihiro Matsui [a], Kazuo Shinozaki [b], Motoaki Seki [a,c,*]

[a] Plant Genomic Network Research Team, RIKEN Plant Science Center, Japan
[b] Gene Discovery Research Group, RIKEN Plant Science Center, Japan
[c] Kihara Institute for Biological Research, Yokohama City University, Japan

ARTICLE INFO

Article history:
Received 15 June 2011
Received in revised form 27 July 2011
Accepted 29 July 2011
Available online 5 August 2011

Keywords:
RNA regulation
Abiotic stress response
Non-coding RNA
Alternative splicing
Post-transcriptional regulation
RNA-binding proteins

ABSTRACT

RNA regulatory processes such as transcription, degradation and stabilization control are the major mechanisms that determine the levels of mRNAs in plants. Transcriptional and post-transcriptional regulations of RNAs are drastically altered during plant stress responses. As a result of these molecular processes, plants are capable of adjusting to changing environmental conditions. Understanding the role of these mechanisms in plant stress responses is important and necessary for the engineering of stress-tolerant plants. Recent studies in the area of RNA regulation have increased our understanding of how plants respond to environmental stresses. This review highlights recent progress in RNA regulatory processes that are involved in plant stress responses, such as small RNAs, alternative splicing, RNA granules and RNA-binding proteins. This article is part of a Special Issue entitled: Plant gene regulation in response to abiotic stress.

1. Introduction

Environmental stresses such as drought, heat, salinity and low temperature are major limiting factors for plant geographical distribution and productivity. These stresses are expected to increase in the future due to drastic changes in climate, much of which are driven by global warming. Agriculture will be affected greatly by these changes. Plants can acquire tolerance to these environmental stresses through advanced molecular breeding techniques and genetic engineering, therefore it is important to understand the molecular mechanisms of these responses.

In natural conditions, plants are exposed to a variety of environmental stresses. In order to understand the molecular mechanisms of tolerance and adaptation, many stress-inducible genes have been identified and characterized. Recently, various types of RNA regulatory factors and processes such as small RNAs, antisense RNAs, alternative splicing, RNA decay, RNA stability control and RNA-binding proteins have emerged as new research areas involved in plant stress responses (Fig. 1). In this review, we summarize the recent findings on RNA regulation of plant stress responses.

2. Non-coding RNAs

Recently, transcriptome analyses using high-density microarrays and high throughput sequencing technologies have revealed a vast number of non-coding RNAs (ncRNAs) that are expressed from unannotated genomic regions. These ncRNAs include small RNAs, such as micro RNAs (miRNAs) and small interfering RNAs (siRNAs), as well as long non-coding RNAs such as natural antisense RNAs. These ncRNAs are expected to be involved in transcriptional and post-transcriptional regulation of gene expression and modulation of RNA stability and translation.

2.1. Small RNAs

Small RNAs, such as miRNAs and siRNAs, are short 20 to 24-nucleotide single-stranded RNAs. Small RNAs regulate the expression of their complementary genes by affecting mRNA levels, chromatin remodeling and DNA methylation. Several stress-responsive small RNAs have been identified in plants [1,2] and their roles in the detoxification of reactive oxygen species (ROS) have been demonstrated [3]. Functional roles of the small RNAs in stress signaling networks are summarized in recent reviews [4–6].

2.2. Antisense RNAs

Whole transcriptome studies under abiotic stresses using *Arabidopsis* tiling arrays have revealed that about 7000 novel transcriptional units, including those that are stress-responsive map to antisense strands of protein-coding genes [7]. Most of these transcripts are longer than 500 nt

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* Corresponding author at: Plant Genomic Network Research Team, RIKEN Plant Science Center (PSC), RIKEN Yokohama Institute, 1-7-22 Suehiro-cho, Tsurumi-ku, Yokohama 230-0045, Japan. Tel.: +81 45 503 9587; fax: +81 45 503 9584.
E-mail address: mseki@psc.riken.jp (M. Seki).

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doi:10.1016/j.bbagrm.2011.07.015

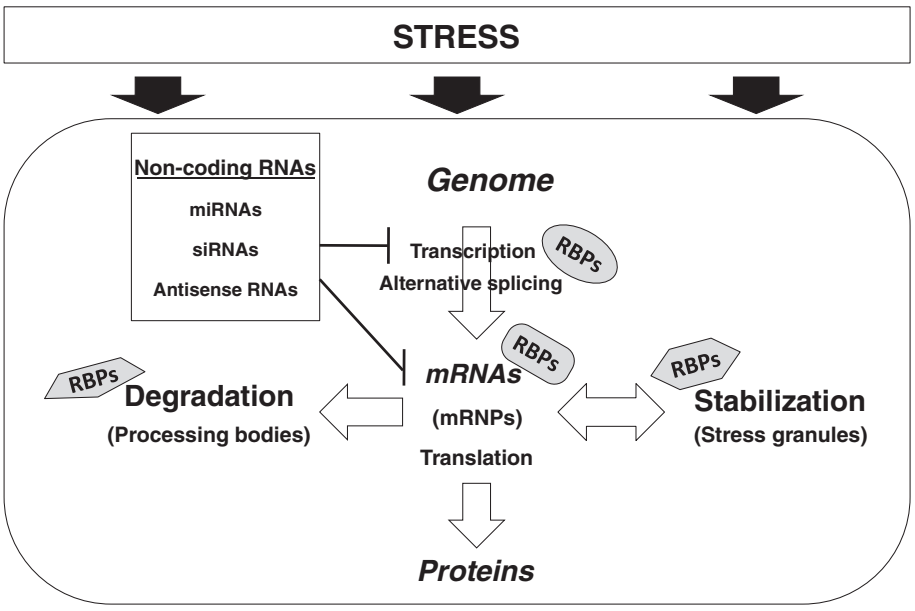

Fig. 1. Various types of RNA regulations function in plant stress responses. Non-coding RNAs are involved in the regulation of transcription, alterative splicing and mRNA degradation. mRNAs are degraded in processing bodies and stored in stress granules. RNA-binding proteins (RBPs) are involved in all aspects of RNA regulations.

and do not have sequence similarity with protein-coding genes, suggesting the existence of long non-protein coding antisense RNAs. Most of them belong to pairs of the fully overlapping sense–antisense transcripts (fSATs). Interestingly, a significant linear correlation between the expression ratios (treated/untreated) of the sense transcripts and the ratios of the antisense RNAs was observed in the fSATs. The sequences of *RD29A* and *CYP707A1* antisense RNAs that are drought- and ABA-inducible, were complementary to that of the sense mRNAs, indicating that expression of the antisense RNAs depends on that of the sense mRNAs [7]. Deep sequencing analysis has revealed that mutations of *ABH1* and *EIN5* (*XRN4*), which are involved in mRNA processing and mRNA degradation, respectively, affect the level of small RNAs mapped on the antisense strand of endogenous protein-coding genes [8]. As the siRNAs are generated from double-stranded RNAs, these results also indicate that a certain type of antisense RNA is synthesized from mRNA templates. On the other hand, expression of the *FLOWERING LOCUS C (FLC)* antisense RNA, COOLAIR (cold induced long antisense intergenic RNA), was controlled by a cold-inducible promoter which exists downstream of the *FLC* gene [9]. A tiling array analysis of circadian regulation showed that the majority of the rhythmic antisense transcripts overlapped with circadian-regulated sense transcripts with a similar phase of expression and that the distribution of the antisense RNAs was enriched toward morning [10]. These data indicate that antisense RNAs are synthesized through various mechanisms.

Biological functions of the antisense RNAs remain unclear in most cases. Abiotic stress can induce expression of sense and antisense transcripts from several transposons, retrotransposons and pseudogenes, which are a source of siRNAs [11,12]. Sense and antisense transcript pairs have the potential to produce endogenous siRNAs. After heat stress, a *copia*-type retorotransposon named *ONSEN* became transcriptionally active and synthesized extrachromosomal DNA copies. Heat-induced expression and transgenerational retrotransposition of *ONSEN* were suppressed by siRNA-mediated silencing [13]. The cold-induced *FLC* antisense transcript, COOLAIR, has a role in the epigenetic silencing of *FLC*, that acts transiently in response to cold stress [9,14]. Two long intronic non-coding RNAs, COLDAIR (cold assisted intronic non-coding RNA), that exists in the sense direction relative to *FLC* mRNA, and COOLAIR, are required for establishing tri-methylated histone H3 Lys27 at the *FLC* locus through the interaction of COLDAIR with the polycomb repressive complex 2 (PRC2) [15]. COOLAIR and COLDAIR have specific mechanisms of chromatin modification mediated gene silencing other than RdDM (RNA-dependent DNA methylation). Previous studies have also shown that antisense RNAs participate in a broad range of regulation such as gene silencing, RNA stability, RNA editing and translational inhibition [16–19].

3. Alternative splicing

Alternative splicing significantly increases protein diversity in higher eukaryotes [20]. In plants, it is known that alternative splicing is frequently associated with environmental conditions, such as abiotic stress [21,22]. Genome-wide studies by RNA-seq using an Illumina high throughput sequencer indicated that alternative splicing events occur in at least 42% of genes in *Arabidopsis*. It was also found that the relative abundance of unproductive isoforms with premature termination codons (PTC) of some essential regulatory genes can be regulated by the nonsense mediated mRNA decay (NMD) surveillance machinery under abiotic stress [22].

Several splicing and splicing-related factors function in the abiotic stress response. SR proteins are a family of RNA-binding proteins which contain a serine/arginine-rich region in their C-termini and function as essential factors for alternative splicing [23]. Alternative splicing of pre-mRNAs encoding several *Arabidopsis* SR proteins are controlled by heat and cold stress. [24]. In response to heat stress, a splicing factor, IRE1b (inositol-requiring transmembrane receptor protein kinase/endoribonuclease-1b), that functions in endoplasmic reticulum (ER) stress responses, splices the mRNA-encoding bZIP60, a basic leucine-zipper domain transcription factor, that is required for the up-regulation of binding protein 3 (BIP3) [25]. The floral initiator Shk1 kinase binding protein (SKB)1/protein arginine methyltransferase (PRMT)5, which is a type II arginine methyltransferase, mediates the salt stress response by regulating transcription and pre-mRNA splicing. This is accomplished through alterations of the methylation status of histone4 arginine3 (H4R3) symmetric dimethylation (H4R3sme2) and LSM4, a small nuclear ribonucleoprotein Sm-like4 [26]. Two subunits of the nuclear cap-binding complex (CBP), CBP20 and CBP80 also affect alternative splicing of stress-related genes [27].

Arabidopsis homologs of polypyrimidine tract-binding proteins (PTBs), which are key splicing factors, are localized in processing