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Small RNAs: Driver Seat in Plant Stress Responses

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SUMMARY

Non-coding RNAs (ncRNAs) have emerged as critical components of gene regulatory networks across a plethora of plant species. In particular, the 20–30 nucleotide small ncRNAs (sRNAs) play important roles in mediating both developmental processes and responses to biotic stresses. Small RNAs play myriad important roles in plant gene regulation through targeted degradation and/or translational silencing of mRNAs at the post-transcriptional level, collectively termed RNA interference (RNAi). Several desirable traits have been improved in the crop varieties through RNAi, which include crop protection against biotic and abiotic stresses.

INTRODUCTION

Plants being sessile are exposed to various environmental stresses (both biotic and abiotic stresses), which severely affect the growing crop plants leading to yield loss and quality of production. Consequently, to feed the ever-increasing world population it is highly important to find solutions to increase global food production by developing stress-tolerant crop plants. Plants have developed various physiological and molecular mechanisms to deal with abiotic stresses such as drought, salinity, heat, cold, and dehydration by minimizing water loss and photosynthesis rates, etc. RNA interference (RNAi) is a naturally occurring biological process that regulates plant growth and development, defense against pathogens, and environmental stresses. Biotic stresses account for up to 30% of crop loss worldwide. To deal with these devastating pathogens and pests, plants have specialized defense mechanisms, which get induced when there is stress. Recently discovered small RNAs such as small interfering RNAs (siRNAs) and micro RNAs (miRNAs), present in the plants, are reported to regulate various developmental pathways and are also involved in abiotic and biotic stress responses (Chen 2009). The miRNA biogenesis pathway is well conserved and hence researchers have used a strategy to manipulate the miRNA sequences, popularly known as artificial miRNA (amiRNA) technology, which is an emerging as a potential tool for gene silencing studies in plants (Ossowski et al. 2008). The review will be discussed on the role of small RNAs during various biotic stress reactions in plants and how this understanding can be exploited for the management of these stresses.

Role of RNA

RNA interference (RNAi) is a naturally occurring biological process that regulates plant growth and development, defense against pathogens, and environmental stresses. It is a sequence-specific homology-based silencing mechanism in which the function of a gene is interfered with or suppressed. Small interfering RNAs (siRNAs) and microRNAs (miRNAs) are produced inside the plant cell through the activation of RNAi machinery, which downregulates the expression of the target genes at transcriptional and translational levels. Post-transcriptional modifications are found extensively in stable and structured RNAs (tRNA and rRNA, mRNAs, and an expanding catalog of small and large noncoding RNAs).RNA modifications are also observed in small RNAs to perform various cellular functions that include development in plants, metabolic study, maintenance of genome integrity, immunity against pathogens, and abiotic stress responses. Eukaryotic organisms possess 20–40-nucleotide-long noncoding RNA molecules called small RNAs and depending on their biogenesis and precursor structure, small RNAs are placed in two discrete groups: microRNAs (miRNAs) and small interfering RNAs (siRNAs)

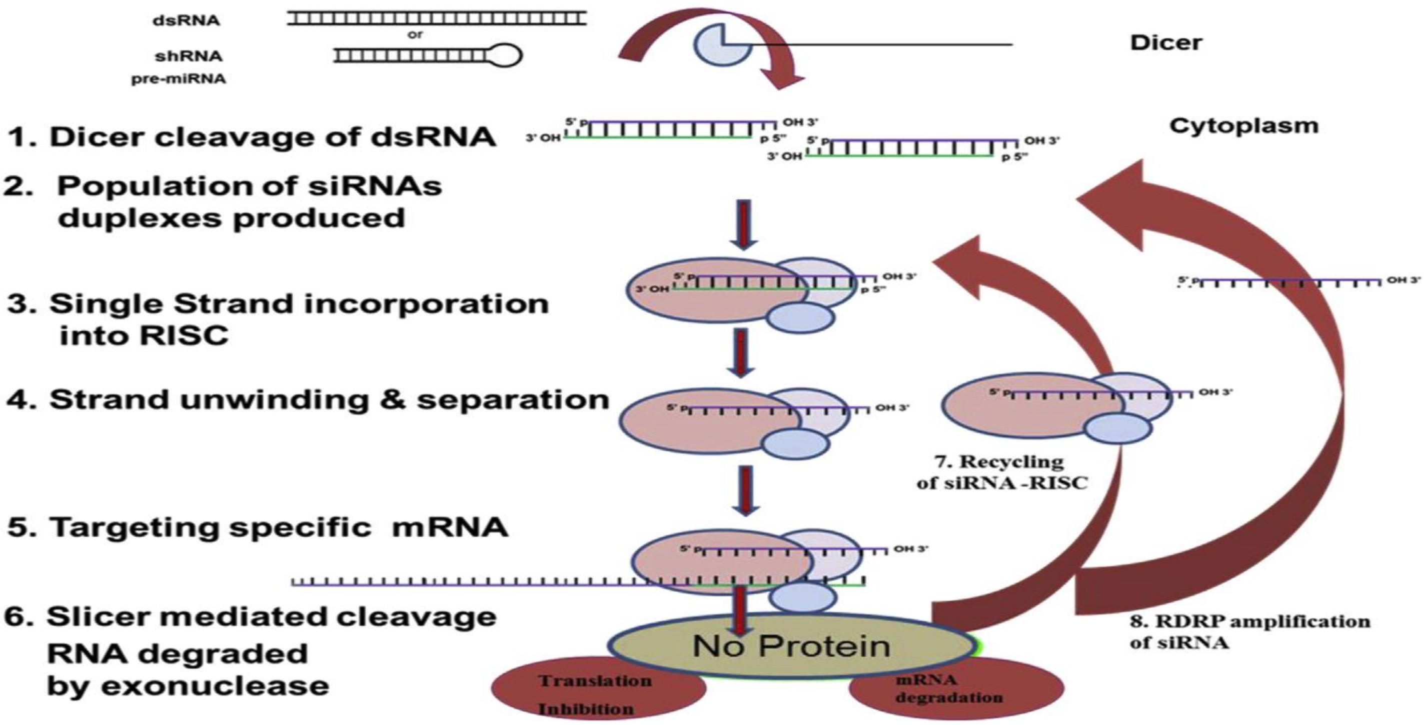
Non-Coding RNAs

Non-coding RNAs (ncRNAs) have emerged as critical components of gene regulatory networks across a plethora of plant species. In particular, the 20–30 nucleotide small ncRNAs (sRNAs) play important roles in mediating both developmental processes and responses to biotic stresses. Several different sRNA classes have been identified, and their specific functions have begun to be characterized.

RNA Silencing (RNAi)

RNA interference is a conserved, naturally occurring gene regulatory mechanism. It is evolved to protect the organisms against the invading foreign nucleic acids. Fire et al. (1998) coined the term RNAi for the unknown silencing mechanism observed upon exogenous supply of dsRNAs of sense and antisense transcripts in *Caenorhabditis elegans*.

Fig. 1. The RNAi Pathway. The diagram shows a generalized view of the RNAi pathway



Ref: Sherman et al (2015)

RNA interference (RNAi) is a gene silencing event that regulates sequence-specific gene and gets induced by double-stranded RNA (dsRNA). This results in the inhibition of translation or transcription. Gene regulation is initiated by sRNAs in hosts or pathogens by posttranscriptional gene silencing (PTGS) or transcriptional gene silencing (TGS). PTGS is induced by miRNAs and siRNAs through messenger RNA (mRNA) cleavage/degradation or translational inhibition with the help of an RNA-induced silencing complex (RISC). RNAi involves homology-based sequence-specific degradation of target gene transcripts. It is triggered by aberrant dsRNAs which can vary in length and origin. These aberrant or foreign dsRNAs are processed into small RNA duplexes of variable sizes ranging from 21 to 28 nucleotides (nt). Small RNA molecules are loaded on protein complex and then directed toward their cognate RNA where they cause cleavage of the target gene or suppression of translation. Plant sRNAs and RNA interference (RNAi) pathway components are major regulatory players in providing immunity to plants against viruses, bacteria, fungi, and pests.

microRNA

Llave et al. (2002) reported the first plant miRNA when they cloned a large set of miRNAs of predominantly 21- to 24-nt length from Arabidopsis. Plant miRNAs are transcribed from non-coding nuclear genes by RNA Pol II, which generates capped and polyadenylated long primary transcripts (pri-miRNAs), which are then processed into precursor miRNA (pre-miRNA) of about 80–200 nt in length, by an enzyme having RNaseIII activity called DICER-LIKE 1 (DCL1). The miRNA strand of the duplex, also known as the guide strand, is incorporated in the miRNA-programmed silencing complex, often referred to as RNA induced silencing complex (RISC), whereas the miRNA* strand or the passenger strand is degraded. miRNAs regulate the target gene expression either by mRNA cleavage or by translational repression. The miRNA cleaves the targets mRNA at the 10th or 11th nucleotide from the 5' end of the miRNA, which requires the 5' end of the miRNA to base pair with the target mRNA. Once incorporated into a cytoplasmic RISC, the miRNA will determine the mRNA cleavage if it base pairs with the target mRNA with high complementarity, else it will repress the mRNA translation in case of insufficient complementarity.

The siRNA

Small interfering RNAs (siRNAs) are formed from near-perfect complementarity long double-stranded RNAs (dsRNAs) and are generated either from antisense transcription or by the action of RNA-dependent RNA polymerases (RDRs).

The Application of sRNAs in Plant Protection

The pathogens (viruses, bacteria, and fungi), insect pests, and nematode parasites are the biotic factors, which hinder the growth and development of crop plants and affect their quality and yield. RNAi-mediated crop protection against biotic factors opened up a new era in this direction. RNA silencing-mediated pathogen-derived resistance Pests and pathogens are two major sources of biotic stress limiting plant growth and development. In the battle of survival, plants developed sRNAs to silence particular genes to protect themselves from pathogen attack. Scientists utilized the properties of RNA silencing and developed a strategy, to create plants with increased resistance against pathogen and insect herbivores. With the discovery of RNA silencing, transgenic plants that express exogenous RNAi targeting essential genes in pathogens and insect herbivores have been developed to protect plants from many pathogens and pests.

Small RNAs in Plant Defense:

sRNAs facilitate plant immunity against insect herbivores

More than one million insects obtain nutrients from plants. To defend against insect pest attack, plants have several physical barriers in place, such as trichomes, hairs, and wax. Plant hormone levels are also altered during insect herbivore attacks. In addition to plant hormones, increasing evidence suggests that plant RNAi machinery plays an essential role in plant immunity against insect herbivores. In defense against pathogens, RNAi mechanisms have been used as a useful tool in insect control. Many insect genes can be silenced by injection or oral administration of dsRNAs. Thus, transgenic plants expressing dsRNAs targeted essential insect genes were generated to be resistant against insect herbivore attack.

miRNAs and Plant Biotic stresses

Biotic stress has become a major concern due to the continuous and fast evolution of biotic agents such as viruses, bacteria, fungus, insects, and nematodes. In the genomics era, the whole genome, transcriptome, proteome, and interactome sequencing were done and has become used as a baseline for different areas of research. High throughput sequencing of tomato microRNAs in 2011 identified conserved and novel miRNAs expressed in tomato (Zuo et al. 2011), which regulates the expression of genes involved in biotic stresses. Hence, the small RNA sequencing of organisms identified putative and novel RNAs that might be involved in regulatory pathways.

CONCLUSION

Insect pests mostly damage the plants during reproductive stages. Insecticides offer a quick control for the eradication of insect pests, but excessive use of insecticides and its persistence in the environment and food crop makes it unsuitable for long use. RNAi-based technology has proven its potential in the development of crop varieties resistant to biotic and abiotic stresses. RNAi has been employed to remove carcinogenic, neurotoxin, and mycotoxin compounds from food crops. Most of the RNAi-based studies involve a single-gene silencing for the improvement of useful traits in crops. The applications of RNAi technology should move from lab to field and from model plant to crop plants. Shortly, RNAi- mediated crop improvement programs in combination with other technologies will change the food security parameter across the world and improve the way of life. Numerous miRNAs and siRNAs are present in plants, which play essential roles in plant growth, development, and immunity. In response to biotic and abiotic stress, sRNAs finetune the expression of plant hormones and resistance genes to achieve the balance between defense and growth. The basic research on sRNA has provided information for scientists to utilize the features of sRNA and generate transgenic plants with disease and insect herbivore resistance. Further study on sRNAs, as well as their function in transgenic plants, would provide a powerful tool to protect plants from pathogen and insect herbivore attack and also improve food production. Once the novel resistance performances are in line with these expectations, this technology will create a new era in plant disease management, and its application will be extended to the commercial product in agriculture crops.

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