

Preface

In recent years, nuclear pre-mRNA processing, especially alternative splicing, has been taking center-stage as an important regulator of gene expression and ultimately plant growth and development. Bioinformatic analyses using the sequences of completed plant genomes and available cDNAs/ESTs have revealed that alternative splicing of pre-mRNAs contributes greatly to transcriptome and proteome complexity in eukaryotes. During the last few years, considerable progress has been made in understanding various aspects of pre-mRNA processing including alternative splicing and its importance in plant growth and development as well as in plant responses to hormones and stresses. This volume of CTMI, entitled *Nuclear pre-mRNA Processing in Plants*, with 16 chapters from leading scientists in this area, summarizes recent advances in nuclear pre-mRNA processing and its role in plant growth and development. It provides researchers in the field, as well as those in related areas, with an up-to-date and comprehensive, yet concise, overview of the current status and future potential of this research in understanding plant biology.

The first four chapters focus on spliceosome composition, genome-wide alternative splicing, and splice site requirements for U1 and U2 introns using computational and empirical approaches. Analysis of sequenced plant genomes has revealed that 80% of all protein-coding nuclear genes contain one or more introns. The lack of an *in vitro* plant splicing system has made it difficult to identify general and plant-specific components of splicing machinery in plants. Plant spliceosomes have not been isolated so far. However, computational analysis of the sequenced plant genomes as reviewed here by Y. Ru, B.-B. Wang, and V. Brendel identified many of the known snRNAs and proteins components found in two types (major and minor) of non-plant spliceosomes. Although many of the core snRNA and protein components of the spliceosome are conserved between plants and animals, plants do contain some distinct proteins. Alternative splicing of pre-mRNAs provides a means to produce structurally and functionally different proteins from the same gene. Despite several reports of alternative splicing of specific genes in plants, the extent of alternative splicing in plants was not known until recently. However, the genomic era and development of advanced bioinformatics tools have changed this dramatically. The chapter by B.J. Haas reviews the computational approaches used for genome-wide identification of alternatively spliced genes in plants and summarizes the recent findings from such analyses. These recent studies revealed that at

least 30% of plant genes undergo alternative splicing, suggesting that it considerably increases the transcriptome and likely proteome complexity in plants. The following chapter by M.A. Schuler describes different types of splice sites, splice site requirements, unique features of plant introns, and their functional significance. As there is no plant *in vitro* splicing system, many *in vivo* studies using various mutants were performed to identify the importance of nucleotides in splice sites, intron length, and nucleotide composition in splice site selection. The outcome of these studies is also summarized in this chapter. Intron sequences in nuclear pre-mRNAs are excised using either the major U2 snRNA-dependent spliceosomal pathway or minor U12 snRNA-dependent spliceosomal pathway. The next chapter by C.G. Simpson and J.W.S. Brown focuses on properties and splicing signals of plant U12 introns, the minor spliceosome that splices these rare introns, as well as known cis-elements and trans-factors that regulate the splicing of these introns.

The next three chapters focus on serine/arginine-rich (SR) proteins, a family of highly conserved proteins, which are known to play key roles in constitutive and regulated splicing of pre-mRNA and other aspects of RNA metabolism in metazoans. These proteins engage both in RNA binding and protein–protein interactions and function as splicing regulators at multiple stages of spliceosome assembly. This family of proteins has expanded considerably in plants with several plant-specific SR proteins. The chapter by A. Barta, M. Kalyna, and Z. Lorković provides an overview of complex interactions among SR proteins and between SR and other spliceosomal proteins, alternative splicing of pre-mRNAs of SR proteins, and evolutionary conservation of some of these splicing events. *In vivo* functions of plant SR proteins in regulating splicing and several aspects of plant growth and development are also presented in this chapter. Several recent studies have used fluorescence microscopy techniques to study *in vivo* localization and dynamics of spliceosomal proteins, especially SR proteins. The chapter by G.S. Ali and A.S.N. Reddy reviews the experimental approaches used to study localization, dynamics, and regulation of mobility of spliceosomal proteins. Differences in the regulation of mobility of plant and animal SR proteins suggest that not all SR proteins exhibit similar dynamics and that such differences are likely to have important implications in pre-mRNA splicing. Protein phosphorylation and dephosphorylation have been shown to play an important role in spliceosome assembly, splice site choice and localization, and mobility of splicing factors. The next chapter by R. Fluhr summarizes different mechanisms by which protein phosphorylation can influence pre-mRNA splicing. The role of protein kinases, especially LAMMER-type and SRPKs, in modulating alternative splicing and cellular partitioning of SR proteins is also discussed.

Several serendipitous discoveries made using forward genetics are indicating that RNA metabolism (alternative splicing, alternative polyadenylation, mRNA transport) plays an important role in many aspects of plant growth and development and in plant responses to biotic and abiotic stresses. The next seven chapters focus on these aspects of RNA metabolism.

The plant hormone abscisic acid (ABA) regulates a number of physiological processes during plant growth and development. The chapter by J.M. Kuhn, V. Hugouvieux, and J.I. Schroeder summarizes the role of mRNA cap-binding proteins and other proteins involved in mRNA processing in ABA signaling.

Messenger RNA 3' end formation is an important step in producing mature mRNA. A.G. Hunt's chapter provides an overview of plant polyadenylation signals and alternative polyadenylation of plant pre-mRNAs and its influence on flowering. Further, the author discusses the current status of our understanding of the functioning and regulation of plant polyadenylation factor subunits. The chapter by D.A. Belostotsky summarizes the recent findings pertinent to plant mRNA turnover, which is important for the maintenance of cellular and organismal homeostasis. This chapter covers different pathways of mRNA decay and describes the high-throughput approaches that could be used to study mRNA decay globally. Flowering time in plants is controlled by internal (hormones) and external (light and temperature) cues. Analysis of many flowering mutants revealed a link between mRNA metabolism and flowering. The chapter by L.C. Terzi and G.G. Simpson discusses the involvement of alternative 3' end formation, splicing, RNA export, and miRNA biogenesis in flowering. The authors discuss novel plant-specific RNA-binding proteins involved in flowering and present the network of control pathways.

The activation of plant resistance (R) proteins is a part of plant immunity, which is tightly regulated at multiple levels. The chapter by W. Gassmann discusses the role of alternative splicing of R genes in plant defense. Possible mechanisms by which R gene splicing is regulated and how different splice forms fit into the current view of R protein-mediated defense responses are presented. The chapter by G.S. Ali and A.S.N. Reddy discusses stress-induced changes in alternative splicing with emphasis on abiotic stresses. Global and focused studies suggest that stresses significantly change splicing patterns of many pre-mRNA including those of SR proteins. The transcript variants generated by stresses are likely to play a role in stress adaptation. The chapter by V. Chinnusamy, Z. Gong, and J.-K. Zhu reviews the mRNA export pathway in plants. Genetic studies indicate a central role for mRNA export in hormonal and stress responses in plants.

A.B. Rose discusses the ways introns affect gene expression both positively and negatively in plants. The mechanisms, where known (e.g., enhancer elements or alternative promoters), are presented. A model for intron-mediated enhancement is also presented in this chapter. The final chapter by J.W.S. Brown and P.J. Shaw discusses the role of the nucleolus in pre-mRNA processing. Based on proteomic and RNomic analysis, the authors summarize emerging evidence for novel roles for this compartment in mRNA export, transcriptional silencing, and nonsense-mediated decay in plants.

Despite recent findings that alternative splicing contributes significantly to transcriptome and likely proteome complexity in plants, surprisingly little is known about the mechanisms that control alternative splicing and the functions of alternatively spliced isoforms. This will be the next frontier of research in gene regulation. The availability of high-throughput global approaches to study gene expression, alternative splicing, and mRNA decay and to identify targets of RNA binding proteins and emerging computational tools are likely to significantly further our understanding of the regulatory role of nuclear pre-mRNA processing in plant growth and development and stress responses.

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