PREFACE

This volume was conceived to bring together reviews describing recent advances in knowledge and understanding of plant nuclear structures and functions, including that of the nuclear envelope. The book is particularly timely in that recent progress has been rapid in key areas including description and characterization of proteins of the nuclear envelope and nuclear pore complex, novel insights into nucleoskeletal structures, as well as developments related to chromatin organization, function and gene expression. Together these advances provide a framework for comparative understanding of nuclear envelope structure and function in a range of organisms and for understanding its evolution.

Current knowledge of the dynamic structure of plant DNA and chromatin is discussed by Sanchez-Moran in Chapter 5. Despite intensive study of histones and other chromosome-associated proteins, interactions to achieve the complex structures required both in interphase and during cell division remain poorly understood. The structures require several levels of organization, the first being the nucleosomal fibre comprising DNA wrapped around a core of histones. This is a dynamic structure and mechanisms for its remodelling are described. The nucleosomal fibre is then wound into a structure termed the chromatin fibre, which is arranged in loops associated with a multi-protein chromosome scaffold, the third level of structure. This interphase structure undergoes rapid dynamic change in mitosis with further condensation for replication and division. The importance of the structural organization of chromatin for processes such as transcription, replication, repair, recombination, condensation and segregation is also discussed. As in metazoans, plant chromatin is organized into regions of hetero- and euchromatin with heterochromatin adjacent to the NE.

Recent advances in understanding heterochromatin structure are presented in Chapter 6 by Vanrobays *et al.* Heterochromatin, originally thought to be condensed, gene-poor and 'silent', is now known often to be preferentially localized to the nuclear envelope and nucleolus and its significance is becoming clear as an epigenetic state required for many functions of the genome, including gene regulation, segregation of chromosomes and maintaining stability of the genome. Despite limited knowledge of it, in most species heterochromatin is the main form of chromatin and key questions remain to be answered. How is spatial organization of heterochromatin maintained through the cell cycle as DNA is replicated, chromatin condensed, and the nuclear envelope disrupted and reformed? Interactions between nuclear envelope, nucleoskeleton and chromatin are likely to be very significant and are discussed together with other theories for heterochromatin positioning.

Plant genomes vary greatly in size but in all cases the genome is contained within a very small compartment and it is clear that complex three-dimensional organization is needed in order for the many processes required for function. This three-dimensional structure requires interactions between chromatin, the envelope, the nuclear pores and the rest of the cell. In Chapter 4, Goldberg discusses from an ultrastructural and biochemical perspective the presence of an equivalent of the highly ordered lamina and nucleoskeleton described in metazoans. Such a structure appears to be required for nuclear function, but until recently its protein composition has eluded plant scientists. Plant cells have no proteins homologous to the lamins or other intermediate filament protein. Recent electron microscope studies in Goldberg's laboratory of the inner face of the plant nuclear envelope reveal a filamentous structure interconnecting the NPCs. This appears to be organized similarly to the lamina of *Xenopus* oocytes. Protein candidates for a plant nucleoskeleton have recently been suggested from a number of approaches; these long coiled-coil nuclear-localized proteins show some similarities to nucleoskeletal proteins of the metazoans and Goldberg presents the growing, but as yet incomplete, evidence for their role. The likely (direct or indirect) interactions of these proteins with the proteins of the nuclear envelope via a 'Linker of Nucleoskeleton and Cytoskeleton' complex is also considered in Chapter 2 by Graumann and Evans. Therein, the authors describe that, in common with metazoans, plants have one key family of proteins that in other kingdoms constitutes the inner nuclear envelope component of this bridging complex, namely the Sad1/Unc84 (SUN)-domain protein family. Absence of a variety of other inner nuclear envelope components involved in nuclear envelope-chromatin interactions in other kingdoms suggests that the SUN- domain proteins play a particularly significant and broader role in plants. In many respects however, the higher plant SUN-domain proteins show remarkable conservation in structure to those of other organisms. They are smaller than their metazoan counterparts, being closest in size to the yeast homologue Sad1. In addition, the authors discuss first evidence of proteins interacting with SUN-domain proteins in plants that show similarity in structure and mechanism to the Klarsicht/Anc-1/Syne Homology (KASH)-domain proteins of other kingdoms, which complete the nucleo-cytoskeletal bridging complexes. Chapter 2 also focuses on other protein components of the plant nuclear envelope as well as its lipid composition and highlights many of the cellular and nuclear processes in which the plant nuclear envelope plays key roles.

Structure and position of chromosomes must be achieved both for successful mitosis and meiosis. Evidence for SUN- domain protein involvement in the breakdown and reformation of the nuclear envelope in plant mitosis is presented in Chapter 2 together with suggestions of conserved mechanisms between kingdoms. Meiosis, while more complex, has received considerable attention and the role of telomeres is presented by Roberts *et al.* in Chapter 7, who reveal emerging evidence for their role in early events in the movement and synapsis of homologous chromosomes. Studies in Arabidopsis suggest that paired telomeres loosely cluster at the nuclear periphery in meiotic prophase 1; it is suggested that this facilitates chromosome alignment and synapsis. The proteins involved in the attachment of telomeres to the nuclear envelope remain elusive; however, in common with the yeast and metazoans, a role for SUN-domain proteins is suggested. Exploration of the structural protein interactions in meiosis is being vigorously pursued.

Recent characterization of proteins of the plant nuclear pore complex (NPC) has revealed that the structure more closely resembles those of vertebrates than yeast or fungi. In Chapter 3, Zhou *et al.* describe the significant progress made recently in identifying 30 constituent proteins of the plant NPC as well as characterizing plant NPC structure. While the overall architecture of NPCs is conserved in eukaryotes, the plant NPC are set apart by several unique features and absence of a number of vertebrate nucleoporins. Significantly, the anchorage of RanGAP, involved in the generation of the RanGTP/GDP gradient required for nuclear import and export (a mechanism conserved between kingdoms) has been shown to differ significantly between plants and other organisms. In mammals, for instance, RanGAP is anchored to the pore complex by sumoylation. In plants, this function is taken over by interaction with proteins associated with the nuclear pore complex termed the WPP (tryptophan proline proline) interacting proteins (WIPs) and WPP interacting tail-anchored proteins (WITs). Apart from structural differences, the authors also discuss plant-specific functions and non-trafficking processes that plant nucleoporins are involved in, including mitotic functions, plant development, hormone and abiotic stress responses and plant-microbe interactions. The latter topic is the primary focus of Chapter 8 by Binder and Parniske. Using *Lotus japonicus* as a model system, loss of function mutants of several nucleoporins result in impaired mycorrhizal association as well as root-nodule symbiosis linked to failure of nuclear calcium signalling. In *Arabidopsis thaliana*, nucleoporins have been shown to be required for the two major forms of response to fungal pathogens, namely pathogen-associated molecular pattern (PAMP)-triggered and disease resistance (R) gene-mediated defence signalling. This is presented in the context of expanding knowledge of the nuclear pore complex and other proteins of the nuclear envelope and suggests important targets for attention in relation to the introduction of nitrogen fixation into cereals and in the development of crops showing enhanced resistance to fungi. The authors also focus on the challenges of correlating specific functions with individual nucleoporins due to the complexity of interactions and functions of NPC components and functional redundancies.

It is evident that exploration of plant nuclear structure, genome architecture and gene regulation has widespread implications for crop improvement and food security. Movement of the nucleus occurring as stress and developmental responses are presented in Chapter 2 by Graumann and Evans and include movement in intense light, due to touch and viral and fungal infection. Such movements are likely to be significant in plant tolerance to stress and infection and to involve nucleo-cytoskeletal bridging complexes at the nuclear envelope. The positional effects of chromatin structure and the structure of the nucleus on gene expression, discussed in Chapter 6 by Vanrobays *et al.*, suggest an area with considerable potential for exploration as tools to study gene targeting to subnuclear localizations become available. It has yet to be established whether localization to the nuclear periphery, pore complex or other regions of the nucleus induces a repressive or activation effect in respect to gene expression. Such effects, if reproducible, have considerable potential for development. Perhaps the most comprehensively studied role for the plant nuclear structures with widespread significance concerns the role of the nuclear pore complex in fungal pathogenesis and symbiosis.

There is a very clear need to expand knowledge of protein interaction networks at the nuclear envelope involving cytoskeleton, nucleoskeleton and chromatin components. Study of the nuclear envelope proteome has been held back by a combination of limited interest by researchers and the technical difficulties of isolating and analysing it. Recent advances – the identification of SUN domain proteins and first evidence for a linker of nucleoskeleton and cytoskeleton complex, the characterization of more than 30 nucleoporins and increasing functional evidence and the tentative characterization of a plant lamina – all provide a framework for rapid advances coupled with increased understanding of chromatin structure and function. Given the outstanding importance of the nucleus and of epigenetic factors, we anticipate that the study of plant nuclear structure, genome architecture and gene regulation will play a very significant role in the near future.

As knowledge and understanding of the structure and properties of the nucleus and nuclear envelope expand, we come tantalizingly closer to understanding the origins of the structures of the eukaryotic cell. John Bryant (Chapter 1) uses the information presented together with knowledge of replication of nuclear DNA and the import of the replication proteins to present and develop current theories of the origins of the nucleus and its envelope. The early presence of the nucleus and nucleoskeleton, predating the arrival of chloroplasts and mitochondria in the proto-eukaryotic cell and the probable formation of the nuclear envelope from invaginations of the plasma membrane are discussed in the light of the development of key features of the higher plant nucleus. Just as we hope that presenting advances in understanding the structure and function of the plant nucleus will stimulate research in this field, it is equally our hope these advances will result in better appreciation of their origins not only in plants but across the orders of living things.