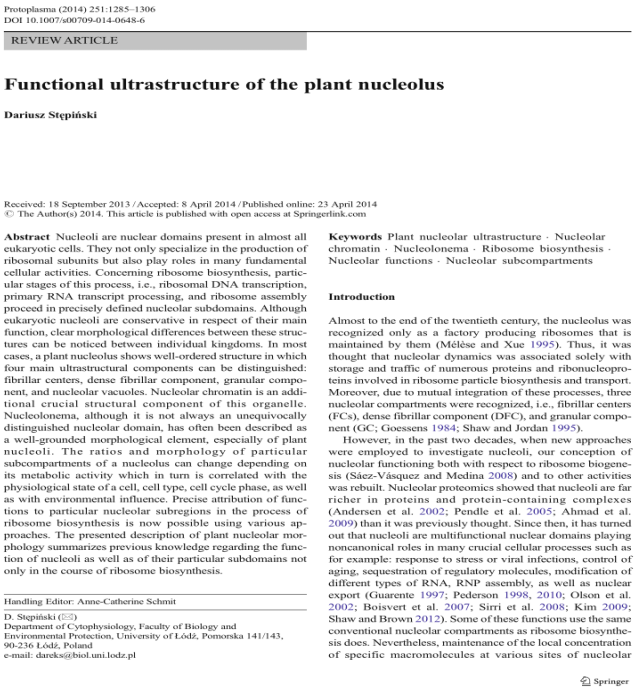
Dynamic Aspects Of Plant Ultrastructure



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REVIEW ARTICLE

Functional ultrastructure of the plant nucleolus

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Abstract Nucleoli are nuclear domains present in almost all eukaryotic cells. They not only specialize in the production of ribosomal subunits but also play roles in many fundamental cellular activities. Concerning ribosome biosynthesis, particular stages of this process, i.e., ribosomal DNA transcription, primary RNA transcript processing, and ribosome assembly proceed in precisely defined nucleolar subdomains. Although eukaryotic nucleoli are conservative in respect of their main function, clear morphological differences between these structures can be noticed between individual kingdoms. In most cases, a plant nucleolus shows well-ordered structure in which four main ultrastructural components can be distinguished: fibrillar centers, dense fibrillar component, granular component, and nucleolar vacuoles. Nucleolar chromatin is an additional crucial structural component of this organelle. Nucleolonema, although it is not always an unequivocally distinguished nucleolar domain, has often been described as a well-grounded morphological element, especially of plant nucleoli. The ratios and morphology of particular subcompartments of a nucleolus can change depending on its metabolic activity which in turn is correlated with the physiological state of a cell, cell type, cell cycle phase, as well as with environmental influence. Precise attribution of functions to particular nucleolar subregions in the process of ribosome biosynthesis is now possible using various approaches. The presented description of plant nucleolar morphology summarizes previous knowledge regarding the function of nucleoli as well as of their particular subdomains not only in the course of ribosome biosynthesis.

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Introduction

Almost to the end of the twentieth century, the nucleolus was recognized only as a factory producing ribosomes that is maintained by them (Mélèse and Xue 1995). Thus, it was thought that nucleolar dynamics was associated solely with storage and traffic of numerous proteins and ribonucleoproteins involved in ribosome particle biosynthesis and transport. Moreover, due to mutual integration of these processes, three nucleolar compartments were recognized, i.e., fibrillar centers (FCs), dense fibrillar component (DFC), and granular component (GC; Goessens 1984; Shaw and Jordan 1995).

However, in the past two decades, when new approaches were employed to investigate nucleoli, our conception of nucleolar functioning both with respect to ribosome biogenesis (Sáez-Vásquez and Medina 2008) and to other activities was rebuilt. Nucleolar proteomics showed that nucleoli are far richer in proteins and protein-containing complexes (Andersen et al. 2002; Pendle et al. 2005; Ahmad et al. 2009) than it was previously thought. Since then, it has turned out that nucleoli are multifunctional nuclear domains playing noncanonical roles in many crucial cellular processes such as for example: response to stress or viral infections, control of aging, sequestration of regulatory molecules, modification of different types of RNA, RNP assembly, as well as nuclear export (Guarente 1997; Pederson 1998, 2010; Olson et al. 2002; Boisvert et al. 2007; Sirri et al. 2008; Kim 2009; Shaw and Brown 2012). Some of these functions use the same conventional nucleolar compartments as ribosome biosynthesis does. Nevertheless, maintenance of the local concentration of specific macromolecules at various sites of nucleolar

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