Novel functions for the plant nucleolus?

J.W.S. Brown, D. Lewandowska, S.H. Kim, T. Canto & S. Macfarlane

Gene expression is regulated at different levels including transcription; processing and degradation of messenger RNAs (mRNAs); and translation and turnover of proteins. Transcription and processing are functions of the nucleus and it is now clear that the nucleus is a highly structured organelle with functionally distinct compartments or regions. Major domains are chromatin and heterochromatin regions containing chromosomes and the inter-chromatin spaces. The latter contains nucleoplasm and a number of nuclear bodies with a range of functions. In animal cells, the nucleolus, Cajal bodies, splicing speckles, gems and paraspeckles etc. have been identified. Their functions are currently under intense investigation but it is clear that they are an integral part of the dynamics of nuclear processes involved in gene expression.

The most prominent nuclear body is the nucleolus. Classically, the nucleolus is involved in ribosomal RNA (rRNA) transcription and processing, and the assembly of ribosomal subunits, which following export to the cytoplasm form ribosomes for translation of mRNAs into proteins. In addition, the nucleolus is involved in processing and export of other RNAs, assembly of some RNA-protein complexes, the cell cycle and aging. More recently, in human, the nucleolus has been suggested to have an important role as a sensor of cell stress where external and internal factors compromise nucleolar integrity and trigger cell division arrest and even cell death. The multifunctionality of the nucleolus in terms of RNA metabolism and more general cellular functions is intriguing, particularly in terms of how cells respond to changing environmental conditions.

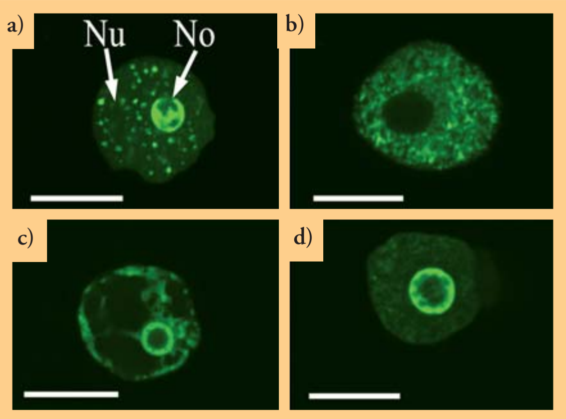

Figure 1 Nuclear and sub-nuclear localisation of the four *Arabidopsis* ALY proteins of the exon junction complex in *Nicotiana benthamiana* cells. **a)** ALY1, **b)** ALY2, **c)** ALY3, **d)** ALY4. Nu – nucleoplasm; No – nucleoli.

To understand the range of different functions in which the nucleolus is involved, the protein composition (proteome) of the plant nucleolus has been examined. This analysis was carried out in the model plant, *Arabidopsis*, due to the availability of the genome sequence providing a peptide database for protein identification[1] in collaboration with Prof. Peter Shaw (John Innes Centre), Prof. Angus Lamond (University of Dundee) and Prof. Matthias Mann (University of Southern Denmark). The 217 identified proteins have been directly compared to a proteomic analysis of human nucleoli. Comparison of the two proteomes showed that almost 70% of the *Arabidopsis* proteins have homologous proteins in the human dataset. Sixty-eight of the plant proteins did not have homologues in the human nucleolar proteome. Of these, 26 (12%) were plant-specific and 39 (18%) had homologues in human, but the proteins were present only in the plant nucleolar proteome but not in that of human suggesting differential localisation.

The value of such comparative proteomic analyses between widely divergent species is demonstrated by the presence of proteins involved in the exon junction complex (EJC) in the plant nucleolar proteome. This protein complex is involved in the export of mRNAs from the nucleus to the cytoplasm, in mRNA decay and in mRNA movement within the cell. The association of these proteins with the nucleolus was unexpected as they are thought to be excluded from the nucleolus in animal cells. The localisation of different EJC components was examined by expressing GFP fusion proteins in both *Arabidopsis* and *Nicotiana benthamiana*, which confirmed their nucleolar association (Fig. 1). These results suggest novel roles for the plant nucleolus in mRNA export or mRNA decay, in addition to its potential function in some virus infections[2]. Current biochemical, molecular and cell biological research is aimed at producing a complete proteomic analysis of the plant nucleolus and elucidating these novel nucleolar functions and their importance to plant gene expression.

References

[1] Brown, J.W.S., Clark, G.P. & Lewandowska, D. (2004) *Scottish Crop Research Institute Annual Report* 2002/2003, 93.

[2] Taliansky, M., Kim, S.H., Ryabov, E.V., Reavy, B. & Robinson, D.J. (2004) *Scottish Crop Research Institute Annual Report* 2002/2003, 94.