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Regulation of nuclear shape and size in plants Iris Meier, Anna HN Griffis, Norman R Groves and Alecia Wagner



Nuclear shape and size changes have long been used by cytopathologists to diagnose, stage, and prognose cancer. However, the underlying causalities and molecular mechanisms are largely unknown. The current eukaryotic tree of life groups eukaryotes into five supergroups, with all organisms between humans and yeast falling into the supergroup Opisthokonta. The emergence of model organisms with strong molecular genetic methodology in the other supergroups has recently facilitated a broader evolutionary approach to pressing biological questions. Here, we review what is known about the control of nuclear shape and size in the Archaeplastidae, the supergroup containing the higher plants. We discuss common themes as well as differences toward a more generalized model of how eukaryotic organisms regulate nuclear morphology.

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Introduction

In animals, changes in nuclear shape and size are associated with cell differentiation, development, and disease (recently reviewed by [1]). Cancer cell nuclear morphology is often altered, but the cause is not well understood [2,3]. In addition, changes in nuclear morphology are associated with several laminopathies and nuclear envelopathies [4,5]. Thus, understanding the physiological relevance and mechanism of nuclear morphology regulation is a topic of fundamental cell biology with potentially high translational impact.

In animal model systems, nuclear size and shape are influenced by DNA ploidy, nuclear structural components, cytoplasmic factors, nucleocytoplasmic transport, the cytoskeleton, and the extracellular matrix [3]. It is becoming increasingly evident that mitotic events also influence nuclear morphology [1]. However, our understanding of how nuclear shape and size are regulated is rather poor and our knowledge of the role that nuclear shape plays in nuclear function is limited [6].

The Archaeplastidae and Opisthokonta separated roughly one billion years ago as single-celled organisms [7]. While the fairly late recognition of the vastness of separate evolution has hampered fundamental plant cell biology research for a couple of decades, recent discoveries about how plants 'solve' shared cellular problems in different ways promise to enlighten research in all model organisms by introducing a broader evolutionary perspective. Here, we review what is known about nuclear size and shape regulation in plants, discuss the first emerging molecular players, and compare and contrast them to their opisthokont counterparts.

Nuclear size and shape in plants

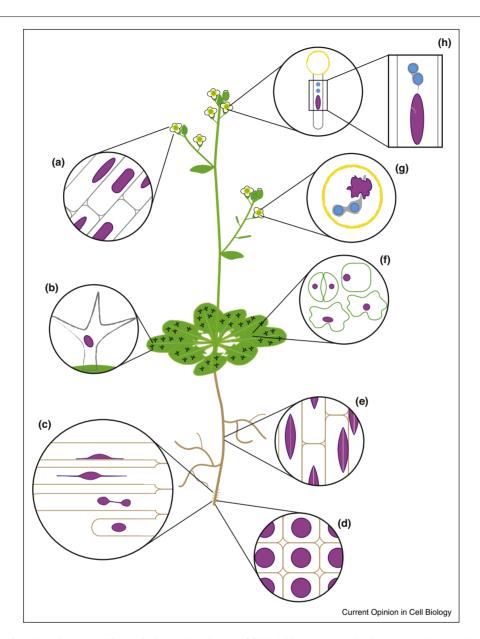
Embryonic and meristem nuclei in flowering plants are nearly spherical. During cell and tissue differentiation, however, nuclei adopt a variety of elongated and superelongated shapes and increase their size, correlated to endoreplication [8]. In *Arabidopsis thaliana*, nuclei range from spherical in meristems and guard cells to hyperelongated with extended membrane tails in root hairs $[9,10^{\bullet\bullet}]$. Some nuclei even divide into multiple subnuclear structures connected by thread-like projections (Figure 1) [11].

Elongated nuclei typically correlate with elongated cells. Nuclear size roughly correlates with cell size, with the smallest leaf nuclei in the diploid guard cells, bigger nuclei in epidermal cells, and the biggest nuclei in the large, highly polyploid unicellular trichomes [12].

The haploid pollen grain is the plant male gametophyte (Box 1). An Arabidopsis pollen grain contains three nuclei: the vegetative nucleus (VN) of the pollen cell and the two nuclei of the embedded germ cells (GCs). While the GC nuclei are small and spherical and contain highly condensed chromatin, the VN is larger and narrows during pollen tube growth, becoming oval to spindle-shaped, and has reduced chromatin compaction [13–16].

Nuclear size and volume decrease during seed maturation and increase again during imbibition and germination of Arabidopsis seeds. This correlates not with passive water uptake, but rather with heterochromatin distribution [17^{••}]. There is, however, no clear correlation between nuclear size changes and seed dormancy or desiccation tolerance. Several mutants with defects in seed dormancy





Graphical depictions of nuclear shapes in different Arabidopsis cell types. (a) Nuclei in petal vascular tissue are rod-shaped and oval-shaped [9]. (b) Trichome nuclei are large and oval-shaped [9]. (c) Root hair nuclei adopt a range of shapes during development and after differentiation. Nuclei in elongating root hairs tend to be oval (bottom). Nuclei in mature root hairs can adopt a range of shapes. From top to second from bottom: flattened, with tails [9]; spindle-shaped [9]; and multiple connected subnuclear structures [9]. (d) Root meristem nuclei are generally spherical. (e) Root epidermal nuclei are spindle-shaped. (f) Nuclear shape in leaf cells varies between cell types. Nuclei in guard cells and mesophyll cells tend to be spherical. Pavement (epidermal) cell nuclei can be either ellipsoid or spherical. (g) In mature pollen, the vegetative nucleus (purple) is highly invaginated, including a channel that facilitates attachment to the cytoplasmic projections (gray) of the sperm cells (their spherical nuclei shown in blue) are connected to each other and the vegetative nucleus (purple) by cytoplasmic projections (gray) [14,16,44]. The nucleus elongates during pollen germination, and is oblong in shape, with some invagination [14,16,45].

undergo wildtype (WT)-like nuclear size changes [17^{••}]. Also, a *crwn1 crwn2* mutant (see below) that has imbibition and germination-insensitive small nuclei has no germination or dormancy defects. This suggests that specific properties of nuclei are an adaptation to desiccation, but independent of dormancy. Several other studies have observed changes in seed nuclear size. *Phaseolus vulgaris* seed pith and plumule cell nuclei shrink when they approach the dormant phase [18]. *Phaseolus lunatis* and *Zea mays* have smaller nuclei in dormant pith, cortex, and vascular cells of the seed [19], and an Arabidopsis study suggests a correlation between

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