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Review

Nuclear movement and positioning in plant cells

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ABSTRACT

Plant cells connected to adjacent cells with rigid cell wall cannot change their position, so that appropriate nuclear positioning according to nuclear movement is indispensable for cellular development involving unequal cell division. Sessile plants are severely affected by fluctuating environmental conditions, so that movement of organelles including nucleus is fundamental to accomplish physiological functions. The mechanisms of nuclear movement and their purposes studied recently with *Arabidopsis thaliana*, the model plants for genetics and molecular biology, and the nuclear behavior in fern gametophytes, an apical growing protonemal cell and a two-dimensional prothallus of *Adiantum capillus-veneris*, the model plants for cell biology and photobiology are described in this review.

Contents

1. Introduction

Unlike animal cells, plant cells are surrounded by a rigid cell wall. Therefore, the direction and position of cell division are very important for plant development. Once established, the position of cells in a tissue and relative to other cells cannot change. Consequently, ensuring the nuclei are positioned correctly before cells divide is crucial in plants. Additionally, nuclear positioning in plant cells is physiologically indispensable, especially nuclear movement in growing apical cells and light-induced nuclear movement [1–4].

The first nuclear positioning category involves movement to an appropriate position for cell division. Fully expanded mature cells contain a large vacuole, which usually pushes the nucleus toward the cell wall. Before cells divide, nuclei migrate to a position that is appropriate for cell division [5,6]. In a parenchyma cell, the nucleus usually moves to the center of the vacuolated cell. Nuclei also migrate to an appropriate cellular location when an unequal cell division is needed (e.g., stoma differentiation) [3].

The second nuclear positioning category refers to the migration that occurs during apical cell growth. When fern, moss, and liverwort protonemata or rhizoids (root hair-like cells for water absorption) and root hairs as well as vascular plant pollen tubes grow at their cell apex, the nucleus in these cells migrate toward the cell tip, while usually maintaining a constant distance from the tip

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[1,7,8]. Regarding the fern protonemata, apical cell growth and cell division are regulated by light. Nuclear movements during apical cell growth, before and after cell division, and during the formation of new branches have been well analyzed [9,10]. Several components necessary for nuclear migration in an apically growing cell have been recently identified in *Arabidopsis thaliana*. In root hair cells, the nuclear migration rate decreases in mutant lines with defective myosin XI-i and WPP domain-interacting tail-anchored proteins (WIT1 and WIT2), which are localized at the outer nuclear membrane [11]. The WPP domain-interacting proteins and their binding partners (i.e., WITs) are essential for the delivery of a vegetative nucleus and two sperm cells in a pollen tube to ovules [12].

The third nuclear positioning category is related to the movement induced by environmental conditions, especially by light that was described by Gustav Senn in 1908 [13]. This phenomenon was recently observed in two model plants, the fern *Adiantum capillus-veneris* [14] and in *A. thaliana* [15]. When we observed this nuclear response in *A. capillus-veneris* prothallial cells, we thought we had uncovered a new phenomenon. However, Senn wrote in his book that the phenomenon was first reported in 1881 by Frank, who was studying a *Sagittaria* species, which is a flowering plant native to wetlands. Senn also observed this phenomenon in the moss *Funaria hygrometrica*. The mechanisms underlying the movement have recently been investigated in detail [15–18]. Additionally, the possible physiological effects of the movement on the protection of DNA from photodamage have been proposed [18]. Biotic influence on nuclear movement is another interesting issue [19], although it is not discussed in this review.

The first nuclear positioning category is well known, although the associated mechanisms have not been fully characterized [6,20]. Thus, in this review, the light-regulated nuclear movement mainly in *A. thaliana* and the nuclear behavior during *A. capillus-veneris* protonemal growth will be thoroughly discussed.

The reason why *A. capillus-veneris* was used in these studies besides *A. thaliana* is that *A. capillus-veneris* gametophytes are linear (protonemata) or two-dimensional (prothalli) and single cell-layer when they are young, and not surrounded with any tissue, so that the developmental processes, e.g., cell growth, cell division, tropic response, could easily be observed microscopically and are controlled step-by-step as different light responses. Moreover, various cell biological techniques, such as partial cell irradiation with a microbeam, cell centrifugation, and even cell ligation in long protonemal cells are available [9,10].

2. Nuclear photo-relocation movement

When we studied chloroplast photorelocation movement using two-dimensional *A. capillus-veneris* gametophyte (prothallus) cells, we observed that nuclei and chloroplasts behaved similarly under different light conditions (Fig. 1A) [14,21]. Under weak white light (e.g., 5 Wm^{-2}), prothalli growing on the surface of an agar medium spread perpendicular to the incident light, while the nuclei stayed at the center of the prothallial cells (Fig. 1A, middle panel). However, the nuclear positions were not determined because the nuclei remained under the chloroplasts that gathered at the cell surface (periclinal wall). When prothalli were fixed with formaldehyde and then stained with 4′,6-diamidino-2-phenylindole (DAPI), round nuclei were clearly observed under a fluorescence microscope. When a prothallus grown under weak light was transferred to darkness, nuclei and chloroplasts at the periclinal wall moved to the cell walls between adjacent cells (anticlinal wall), especially on the centripetal side of cells (the side toward the prothallial base) (Fig. 1A, left panel). Therefore, nuclei and chloroplasts were not detected along the periphery of prothallial cells [14]. When a prothallus was transferred from weak to strong light conditions, nuclei moved to

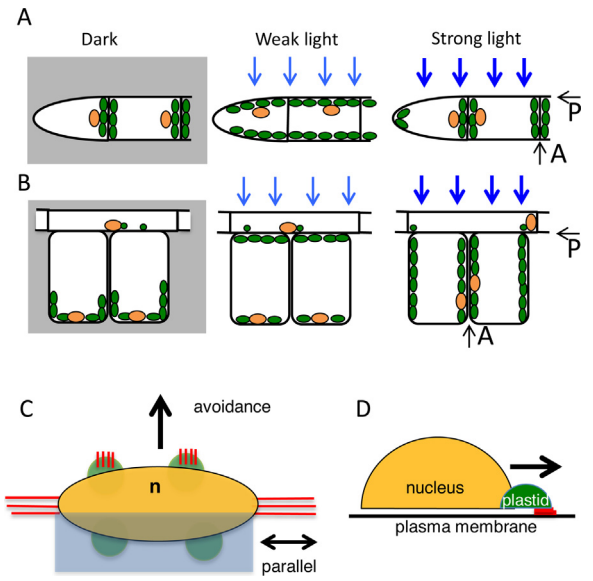

Fig. 1. Schematic illustration of nuclear position under the darkness, weak and strong light conditions. A,B. Cross section of two-dimensional single cell-layered prothallus of *Adiantum capillus-veneris* (A) and epidermal pavement cell and palisade cells of *Arabidopsis thaliana* leaf (B) are shown. green: chloroplast, yellow: nucleus. Arrow with P shows periclinal wall, arrow with A shows anticlinal wall. Blue arrows indicate light irradiation from the top of the cells. C. Nuclear movement model. When part of the nucleus was exposed to strong blue light (blue rectangle), the nucleus moved to avoid the blue light being pulled by a plastid (green) with cp-actin filaments (short red lines) or migrated parallel to the actin bundle (red lines). D. Side view of nuclear avoidance movement pulled by a plastid with cp-actin filaments attached to the plasma membrane. Panel C is reproduced from [16] with permission from the National Academy of Science, USA.

either side of the anticlinal cell walls (Fig. 1A, right panel) [22], probably to the closest side. Nuclei on the anticlinal wall during the dark positioning [14] and avoidance movement were spindle-shaped [22]. These results indicate that nuclei are not spherical, but are flat like a convex lens, even though they look round on the periclinal wall under weak light condition.

Nuclei move slower than chloroplasts. When prothalli were transferred from light to darkness, the nuclei started to move from the periclinal wall to the anticlinal wall, and 50% of the nuclei had reached the anticlinal wall by 30 h after the transfer. In contrast, when prothalli maintained in darkness for 2 days were transferred to white light (5.5 Wm^{-2}), 50% of the nuclei reached the periclinal wall within 3.5 h [14]. Nuclei at the periclinal wall of fern prothalli migrate to the anticlinal wall under strong light (800 $\mu mol\ m^{-2}\ s^{-1}$) [22]. A recent study involving *A. thaliana* revealed that this nuclear migration likely protects DNA from photodamage [18]. The speed of the nuclear avoidance response (0.2 $\mu m\ min^{-1}$) was similar to that of the chloroplast avoidance response (approximately 0.3 $\mu m\ min^{-1}$) [22]. Unfortunately, there are no available data regarding the time needed for 50% of the chloroplasts to migrate from the periclinal wall to the anticlinal wall. The nuclear avoidance movement is probably faster than the nuclear accumulation response, as is the case for chloroplast movements [23].

Nuclear accumulation responses are induced by polarized red and blue lights *in A. capillus-veneris* [14]. When dark-adapted prothalli on an agar medium surface were irradiated from the horizontal direction with horizontally vibrating polarized light, the nuclei moved from the anticlinal walls to the periclinal walls. Conversely, when the light-adapted prothalli were irradiated from the horizontal direction with vertically vibrating polarized light, the nuclei migrated from the periclinal walls to the anticlinal walls. In the former case, it took 3 h for 50% of the nuclei to migrate to the

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