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Lipid droplets in onion epidermal cells: interactions with the nucleus

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Abstract

Lipid droplets are the smallest organelles of eukaryotic cells, presumably with storage, metabolic and regulatory functions. To understand the role of lipid droplets in organelle coordination, in this work we analyzed the morphology and distribution of these oil bodies in epidermal cells in fresh preparations of white and red onions using differential interference contrast (DIC) microscopy. Cytological observations unveiled large extensions of membrane-bound cytoplasmic compartments that interact with the nuclear envelope, and peripheral tubular structures that transport lipid droplets. The lipid content of epidermal cell vesicles was confirmed by BODIPY493/503 staining and confocal microscopy, while Lugol staining enabled observation of the nuclear/organelle extensions that reach the whole cell. The functional relevance of such inter-organellar movement of lipid droplets appears to be the delivery of lipids for membrane construction as well as nuclear proteins.

Keywords: Dynamic organelles, vesicular trafficking, nuclear shape, onion epidermal cells, lipid droplets.

Introduction

Intracellular communication through organelles is vital for a variety of functions and depends on the movement promoted by cytoplasmic currents, the configuration of the endoplasmic reticulum (ER), and the cytoskeleton (Tikhomirova *et al.,* 2022). The ER, whose functions range from the synthesis of proteins and lipids to the production of other organelles and different types of vesicles was first described in the 1890s, later on with the use of electron microscopy its presence was demonstrated in both animal and plant cells (Hu *et al.,* 2011; Chen *et al.,* 2012; Kriechbaumer and Brandizzi, 2020). Understanding how the spatial and temporal distribution of organelles is orchestrated to perform their functions is a great challenge in systems biology.

Lipid droplets are the smallest known organelles, surrounded by a single membrane and containing neutral lipids and proteins with different functions. The droplets originate from specific domains within the endoplasmic reticulum (Wright *et al.,* 2025) and act both as energetic cell components or to deliver specific proteins to organelles (Stephenson *et al.,* 2021; Hamade *et al.,* 2025). Studies of subcellular structure in different plant species, including oat and barley coleoptyls, *Elodea* leaves, and onion bulb epidermis, allowed the identification of a dynamic, filamentous membrane network that was associated with rapid movements of lipid droplets (Allen, 1981). In onion epidermal cells, these movements are unidirectional and in parallel with actin fibers that assist cytoplasmic currents, which cease rapidly after application of cytochalasine B, a mycotoxin that inhibits the formation of contractile microfilaments (Allen and Brown, 1988) or by exposure to ultraviolet light (Quader and Schnepf, 1986).

Treatment with inhibitors stablished an important role for microtubules and the actomyosin system for lipid droplet movement. Long-term treatments (hours) with colchicine, an inhibitor of microtubule polymerization, caused the aggregation of organelles and ended lipid droplet movement (Allen and Brown, 1988). More recently, the movement of lipid droplets in the *Arabidopsis* pollen tube was found to be dependent on the actomyosin system (Yang *et al.,* 2023), while interactions among five different organelles (endoplasmic reticulum, Golgi

apparatus, lysosome, peroxisome, mitochondria) and lipid droplets were described as changeable over time (Valm *et al.,* 2017; Tikhomirova *et al.,* 2022).

The bulb epidermal cells of the onion constitute a single layer that acts as a protective skin, and effectively separates the thick and juicy scaly leaves. For decades, it has been used for cytological studies, mutagenesis and chromosomal analysis due to their simple and transparent structure, which has contributed to knowledge about the general anatomy of plant cells and the arrangement of organelles (Melo *et al.,* 2024). The use of onion epidermis to characterize the dynamics of lipid droplets and for their purification dates back to the classic works of Yatsu *et al.* (1971), Allen (1981) and Allen and Brown (1988). These reports sought to know the cellular nature of lipid droplets and their relationship with cytoplasmic currents and cytoskeletal dynamics.

Oparka *et al.* (1990) conducted dehydration experiments by applying mannitol to onion epidermis and impermeable dyes, which fail to cross the cell membrane unless there is a hypertonic medium. Interestingly, osmotic stress induced endocytosis of vesicles loaded with dyes and rehydration re-established cytoplasmic currents. Then, the flow of dye-containing vesicles through extensions of the endoplasmic reticulum to the nuclear membrane was observed along with intracellular lipid droplets. These results indicate that osmotic stress is an important factor for the endocytic and exocytic processes that occur in plant cells and directly relate them to membrane flow among organelles and probably, to lipid droplet intracellular distribution.

In this work, the distribution and dynamics of lipid droplets in epidermal tissue of white onion and red onion bulbs were studied to understand their possible functions in plant cells. We found that the lipid droplets move inside membrane extensions, which target the nuclear membrane. BODIPY493/503 and Lugol staining allowed visualization of a wide membrane network that extends throughout the cell and distributes lipid droplets to the nucleus.

Materials and methods

Preparation of onion epidermal cell samples

In order to study the subcellular dynamics, epidermal samples of the onion (*Allium cepa*) bulb were used. White and red onion bulbs were purchased in a local market taking care that the material came from a recent harvest, which is evidenced by the turgor of the leaves that accompany the bulb and the presence of roots. The bulbs were superficially washed with sterilized distilled water, until any soil residue or dirt is removed, the rest of the procedure is conducted in a laminar flow hood. With assistance of a sterile scalpel, squared sheets of epidermis of 1 cm x 1 cm were carefully obtained from the inner surface of the bulb scales and placed with the smooth (superficial) side down on a cleaned slide disinfected with 96% ethanol. 100 µl of distilled water was applied to the sample to maintain adequate humidity, and a coverslip was carefully placed over the preparation with the help of fine-tipped tweezers and sealed with nail varnish. The preparations were analyzed by differential interference contrast (Nomarski) optics in a Leica DM500B microscope equipped with a digital camera.

For Lugol´s Staining, the square sheets of epidermis were placed for 30 s in a Lugol´s solution (1:2 w/w, iodine:potassium iodide) and rinsed twice with distilled water. Next, the epidermis preparations were mounted in water on coverslip and analyzed by Nomarski optics in a Leica DM500B microscope equipped with a digital camera.

Confocal microscopy

For analysis of onion cells stained with BODIPY493/503, squared sheets of epidermis were placed in the staining solution (10 µM BODIPY493/503) for 5 minutes, then the samples were rinsed twice with water and mounted on a coverslip with water. The fluorescence signal was analyzed in an Olympus FV1000 confocal microscope equipped with objective UPLFLN 40X and a digital camera at 488 wavelengths of excitation and the emission detected at SP 500-550 nm. Representative Z pictures were processed and obtained by the ImageJ2 software.

Results

Interaction of lipid droplets with the nuclear membrane in cells of the epidermis of the bulb of *Allium cepa* L

The nucleus harbors a double membrane, which contains nuclear pores that acts as gateways of macromolecular exchange between the nucleoplasm and cytoplasm and is by far the most prominent organelle in onion epidermal cells (Meier *et al.,* 2017). We analyzed the intracellular distribution of lipid droplets and its organellar distribution using fresh preparations of white onion and red onion by differential interference contrast (DIC) microscopy. **Figure 1** shows observations of white onion under different tissue magnification. In **Figure 1a** the different rows of cells that make up the epidermis can

be seen, with the nucleus as the most visible organelle and the cell walls that delimit the rows. **In Figure 1b-d** there are gradual magnifications of the nucleus area, denoting the presence of a membrane network that extends throughout the cytoplasm and carries mobile lipid droplets. **Figures 1c**, **d** distinguish the membrane connections between the outer part of the nucleus and finger-shaped connections carrying the moving vesicles, we were able to corroborate that the vesicles enter and leave the nucleus through a very dynamic flow through real-time videos (data not shown).

Cytological observations of lipid droplets in red onion epidermal cells

There are several varieties of onions, each with unique properties and characteristics that influence its flavor, texture, and size (Theshika *et al.,* 2019; Hao *et al.,* 2023). The red onion owes its color to the presence of anthocyanins, water-soluble pigments found in the cytoplasm. It was of interest to analyze if the interactions of lipid droplets with nuclei observed in white onion could be also present in red onion. Thus, fresh preparations of red onion epidermis were made and analyzed by DIC microscopy to detect the presence of lipid droplets. In **Figure 2a-c** micrographs are presented at different magnifications, the remarkable contrast presented by the purple color in the preparations allowed us to observe interactions among the nucleus, the plasma membrane and plasmodesmata and the presence of lipid droplets within the neighboring cells. Again, it can be seen that these lipid vesicles are not isolated but distributed along membranous extensions that approach the plasma membrane (**Figure 2c** inset).

Close up of nuclei in both onion varieties (**Figure 3**), clearly shows the distribution of lipid droplets in the periphery of the nuclear membrane.

Detection of lipid droplets in white onion epidermis by BODIPY493/503

BODIPY493/503 (4,4-difluoro-1,3,5,7,8-pentamethyl-4-bora-3a,4a-diaza-s-indacene) is a dye commonly used for cytological studies to visualize lipid droplets in both animal and plant cells. Thanks to its nonpolar structure, fluorescence and long-wavelength absorption, this dye allows the detection of nonpolar lipids and oils by confocal microscopy (Qiu and Simon, 2016).

Sections of white onion epidermis were obtained, and treated with BODIPY493/503 prior to observation by confocal microscopy. With this procedure, it was possible to identify the lipidic nature of a large number of vesicles with green fluorescence associated with membranous

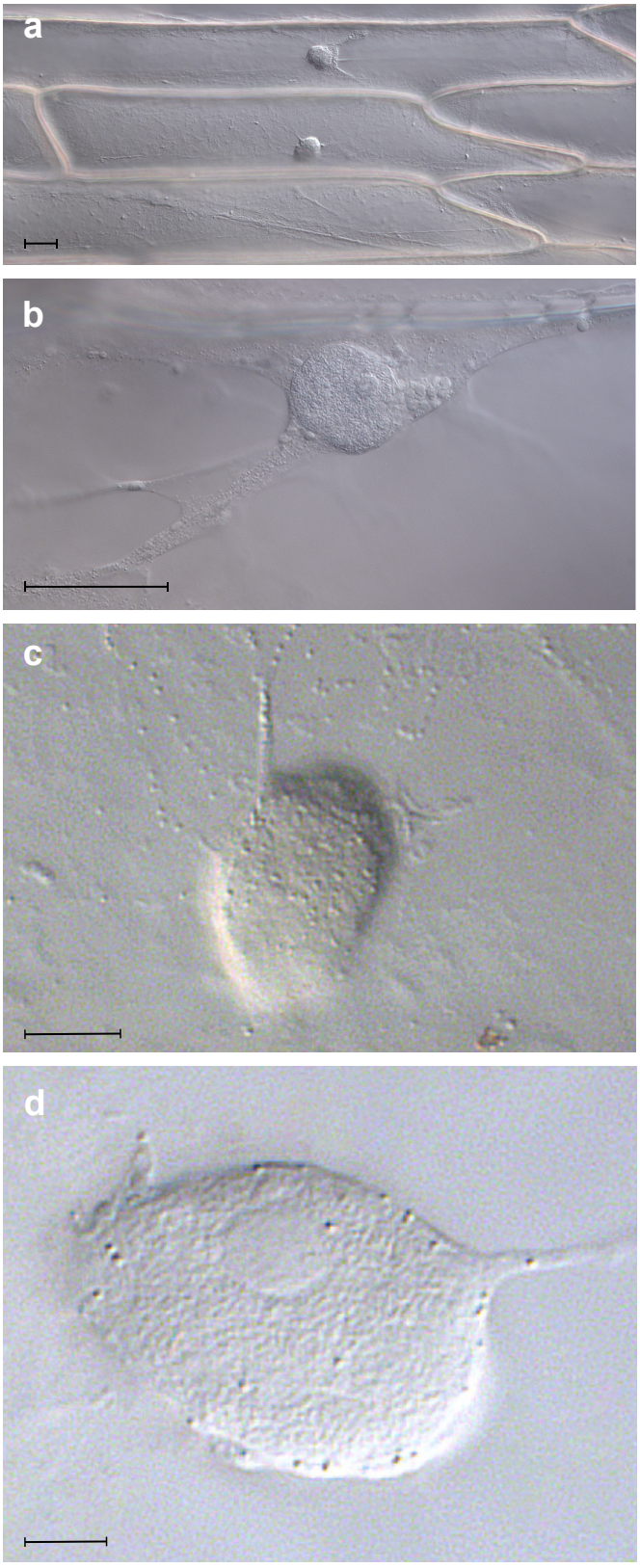

Figure 1. Lipid droplets in white onion bulb epidermal cells. The images were taken at different magnifications and the membrane extensions that carry lipid droplets to the nuclear membrane are observed. Scale bars: 50 µm (**a**, **b**), 25 µm (**c**), and 10 µm (**d**). Images were taken with a Leica DM5000B microscope under Nomarski optics.

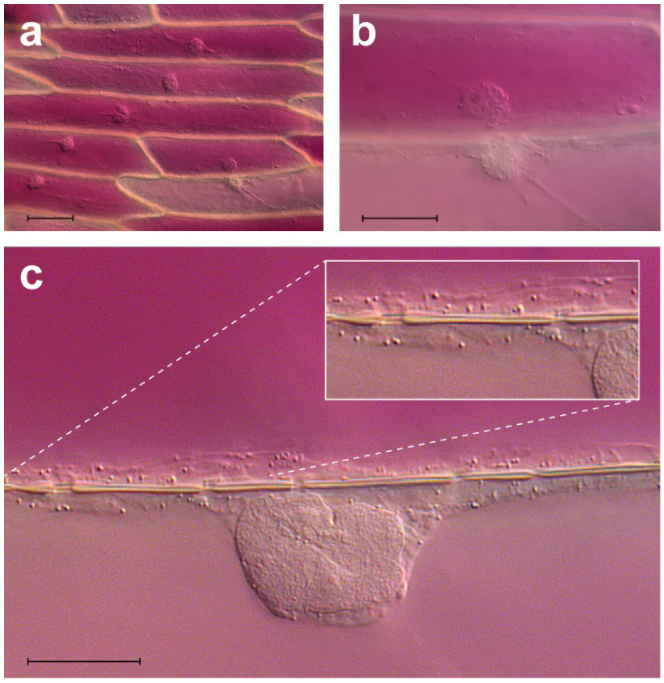

Figure 2. Lipid droplets in epidermal cells of red onion bulb. The images were taken at different magnifications and the extensions of the nucleus positioned at the edge of the cell are observed, which carry lipid droplets. Plasmodesmata are also observed in panel **c** inset. Scale bars: 100 µm (**a**), 50 µm (**b**), and 25 µm (**c**). Images were taken with a Leica DM5000B microscope under Nomarski optics.

structures, mainly the nucleus and the surrounding cell membranes (**Figure 4a**). In our analyses, the lipid vesicles were detected in tight connection with the nuclei (**Figure 4b**). This information underscores the relevance that these small organelles may have for proper nucleus functioning.

Lugol staining of onion bulb epidermal cells

Lugol is a dye based on potassium iodide used as an indicator of the presence of animal glycogen or plant starch that stains the nucleus and reserve substances of cells and makes these structures more visible (Martín-Sánchez *et al.,* 2013). Based on these properties, we stained segments of onion bulb epidermis with Lugol and made observations by DIC microscopy at different magnifications. The micrographs show the extensive network of membrane connections that exist between the nucleus and the rest of the cell, which occupy most of the cell volume (**Figure 5a**). The most observable structure is the nucleus (**Figure 5b**) and its faraway membrane extensions that contain the lipid droplets (**Figure 5c**). These results show the tight connection between the membranes of different organelles within the plant cell.

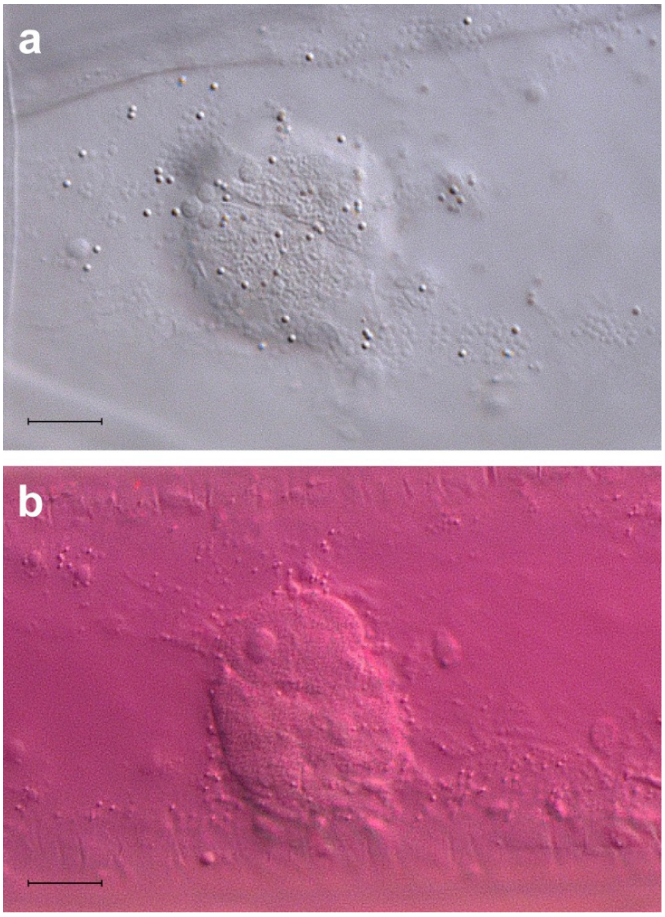

Figure 3. Lipid droplets around nuclei in white and purple onion epidermal cells. Representative images of white onion (**a**) and red onion (**b**) cells taken in a Leica DM5000B microscope under Nomarski optics. Scale bar: 10 µm.

Discussion

Lipid droplets have been identified in organisms of all kingdoms, including bacteria, yeasts, plants, animals, and humans (Olzmann and Carvalho 2019; Guzha et al. 2023; Fujimoto, 2024). In eukaryotic cells, their lipid content is delimited by membrane containing specific proteins, responsible for at least three fundamental functions: 1) The use of lipids contained in the vesicles as energy reserves, 2) membrane recovery from injury, and 3) communication between organelles to deliver specific proteins and lipids.

In angiosperms, an essential function of the reserves present in the seed is to provide energy to the embryo for post-germinative growth until the seedling can start photosynthesis. These stores consist of proteins, carbohydrates, and storage lipids (Li *et al.,* 2006; Quettier and Eastmond, 2009). Onion bulb cells are primarily a specialized type of storage cells, and we can argue that the function of lipid droplets within it is to act as energetic reserves, but we cannot exclude

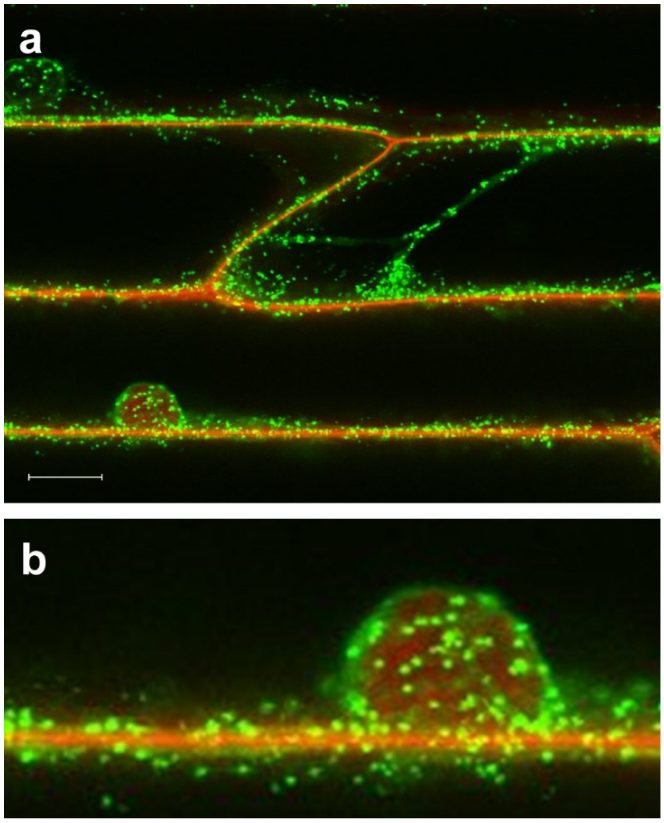

Figure 4. Detection of lipid droplets in cells of the epidermis of white onion by confocal microscopy using BODIPY493/503 stanning. Representative micrograph showing the lipid droplets emitting a green fluorescence in onion epidermal cells and are mainly associated with membranous structures (**a**). Close up of the cell with visible nucleus (**b**). Scale bar: 50 µm.

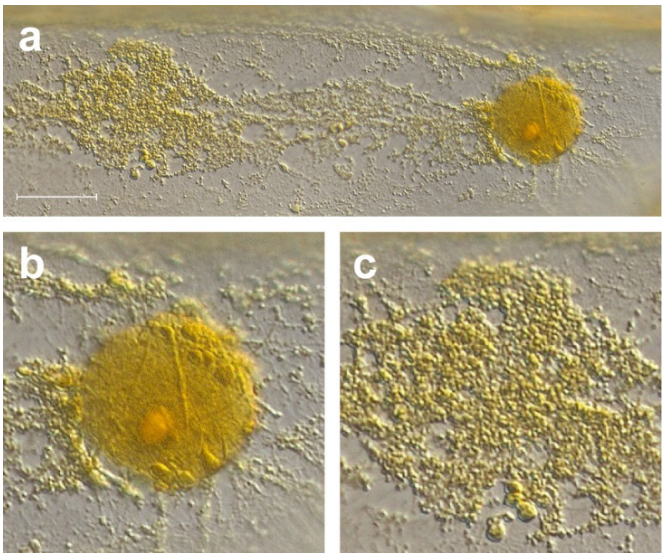

Figure 5. White onion cell staining with Lugol. Representative photograph showing the nucleus and their membranal connections (**a**). Close up images of the nucleus (**b**) and distal membranes with lipid droplets (**c**). Scale bar: 25 µm.

additional roles owing the very dynamic movements within membrane extensions along the cell.

The main storage lipids that accumulate in the lipid droplets are triacylglycerols (TAGs), which in the cotyledons of mature embryos of *Arabidopsis thaliana* occupy approximately 60% of the cell volume (Baud *et al.,* 2008). After germination, TAGs are hydrolyzed to release free fatty acids (FAs) and glycerol. Lipases have been purified from the seeds of different plant species and there is physiological evidence of their role in the mobilization of TAG, also known as lipolysis (Kawinsky *et al.,* 2021; Wleklik *et al.,* 2023). Eastmond (2006) conducted genetic analyses in *Arabidopsis* for the identification of mutants altered in TAG mobilization, which do not develop in the absence of an exogenous carbon source, and fail to grow normally without sucrose supply. The affected mutants were called *sugar dependent* (*sdp*) and define lipases necessary for the breakdown of storage lipids. Noteworthy, SDP1 lipase is located on the surface of the lipid droplets, being transported to the vesicles from the peroxisomes through extensions of their own membrane (Thazar-Poulot *et al.,* 2015). The phenotype of *sdp* mutants shows the important role of lipid metabolism and lipid droplet turnover for proper plant growth.

Taking our data together, we provide a schematic model for lipid droplet delivery into the onion cell nucleus (**Figure 6**). It denotes the presence of lipid droplets moving within membrane extensions that connect the nuclear membrane, probably to deliver lipids to the nucleus for the maintenance of the wide membrane network that composes it and their neighbor organelles. An additional function could be the supply of nuclear proteins, such as histones, nuclear pore proteins, and components for the processing of genetic material, which has been reported for lipid droplets in animal cells (Cho *et al.,* 2007; Gao and Goodman, 2015; Kumanski *et al.,* 2021).

Application of the dye BODIPY493/503 to samples of onion epidermis allowed the visualization of the vesicles that emit a green fluorescence, which we were able to detect by confocal microscopy. The numerous lipid droplets were found inside membrane compartments interacting with nuclei. On the other hand, images of the cells stained with Lugol allowed us to observe a wide membrane network, through which such vesicles move through the different organelles. The formation of membranous systems and the communication among them is vital for various functions in eukaryotic cells. Integrity of membranous system depends on the inter-organellar movement of lipid droplets promoted by cytoplasmic currents, the configuration of the endoplasmic reticulum

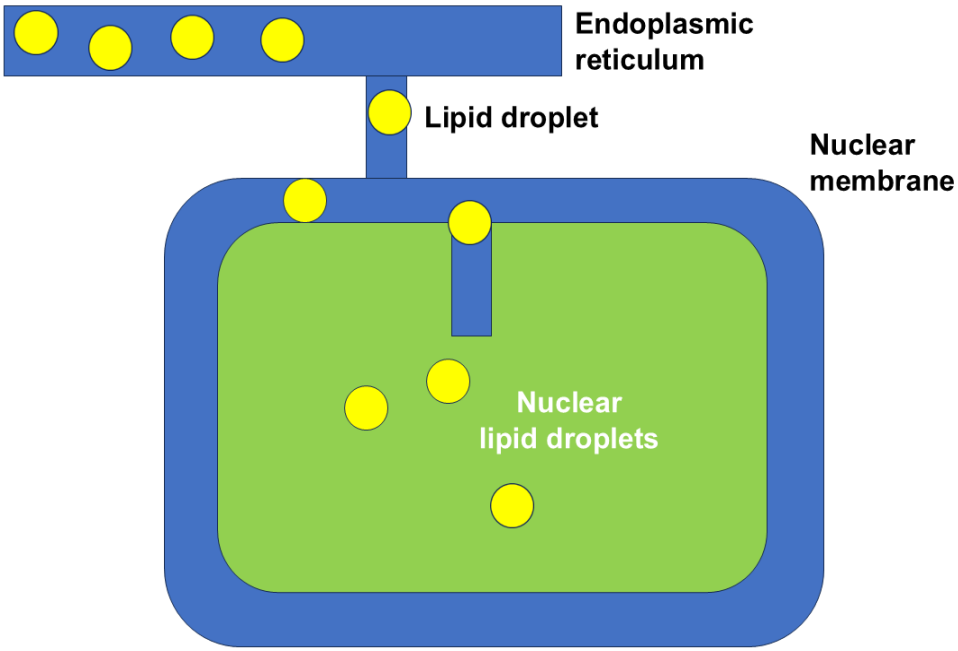

Figure 6. Transport of lipid droplets from the endoplasmic reticulum (ER) to the nucleus. The lipid droplets are produced within ER domains and can move over long distances inside membrane compartments that fuse with the nuclear membrane.

(ER) and the cytoskeleton (Tikhomirova *et al.,* 2022). Depending on developmental stage and physiological state of the plant, lipid droplets can be present either in seeds or vegetative tissues such as roots, leaves, dormant buds and pollen grains and an important function can be the protection of organelles to environmental injury such as heat, which induces the production of reactive oxygen species and membrane lipid peroxidation (Bouchnak *et al.,* 2023). Understanding the specific functions of lipid droplets in eukaryotic cells should consider organelle interactions and in particular, the nucleus. A major challenge is to understand how its movement and organelle interactions is influenced by age as well as biotic and abiotic stress, which disturb the microtubule network.

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