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EDITORIAL

Plant cell compartments

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The formation of different intracellular compartments is necessary for the physical separation of various biochemical reactions, their products as well as different ions by barriers made up by membranes. This kind of compartmentalization of different metabolic activities into organelles played a crucial role during the evolution of life on earth (*e.g.* Matsumura et al. 2016) and also during the subsequent tremendous diversification of prokaryotic and eukaryotic organisms (Diekmann and Pereira-Leal 2013). Spatial separation of toxic metabolites or protein degradation pathways is of vital importance for the normal functioning of the cells. Because membranes are mostly nonpermeable to water and ions, they host several structural and functional proteins, including water channels (*e.g.* Beebo et al. 2013) and ion transporters (*e.g.* Marchand et al. 2018). Similarly, the possibility to build up a proton motive force across membranes separating two aqueous phases drives the ATP synthesis in bioenergetic processes and thus provides energy for all living organisms (Lane and Martin 2012).

Three major types of organelles are in general distinguished, i.e. membrane-based, protein-based or endosymbiotic compartments (Diekmann and Pereira-Leal 2013). Recent literature data showed that examples for such compartments can be found in both prokaryotes and eukaryotes, but are more complex in eukaryotes which have several lineage- or even tissue- or cell-specific organelles (Diekmann and Pereira-Leal 2013). Several compartments and biochemical pathways are unique to photosynthetic eukaryotes (Schoefs 2008). The evolution of the incredible diversity of plant secondary metabolites is thought to be related to the sessile lifestyle of plants which forced them to develop chemical weapons against herbivores and unfavourable environmental conditions (Knudsen et al. 2018).

Such examples include the strictly controlled and compartmentalized production of some specific toxic intermediates or endproducts as well as compounds antagonist to other reactions (reviewed by Gabaldón and Pittis 2015) like for example condensed tannins (Brillouet et al. 2013), essential oils (Dong et al. 2016) or some apocarotenoid glycosides (Demurtas et al. 2018). In general, the formation of highly complex organic compounds necessitates the precisely regulated cooperation and communication between different organelles (for instance through the generation of reactive oxygen species or retrograde and anterograde signals – *e.g.* Lemoine and Schoefs 2010; Solymosi and Schoefs 2010) as well as various intra- or extracellular transport processes (*e.g.* Lindquist, Solymosi, and Aronsson 2016). The biosynthetic pathway leading to red crocins, the well-known apocarotenoid glycosides of saffron (*Crocus sativus*), the most expensive spice in the world, starts with zeaxanthin in the chloroplast, but the endoplasmic reticulum and cytoplasm function as transit centers for its transport along the cytoskeleton towards the vacuole (Demurtas et al. 2018). Similarly, the highly toxic and protein denaturing condensed tannins are formed from their monomeric building blocks synthesized in the endoplasmic reticulum inside the recently described, strictly membrane surrounded thylakoid-derived plastid organelles, the tannosomes, which are then encapsulated into tannosome shuttles which transport them from the plastid through the cytoplasm towards their final storage site, the vacuole (Brillouet et al. 2013).

Since the pioneering observations of Antonie van Leeuwenhoek during the 17th century, the progress made in microscopic and (micro)analytical methods has been tremendous, providing novel insights into cellular processes, including the observations of novel cellular compartments or activities related to them. Recently, new suborganellar functional units termed microcompartments have been described also in plants which are protein assemblies formed by protein–protein interactions and are involved in several intracellular processes including redox signaling (Zachgo, Hanke, and Scheibe 2013).

A better understanding of the functioning of plant cell compartments, their regulation, and the interactions of the various organelles with each-other and their environment both under non-stressed and stressed conditions is important for plant productivity, thus agriculture, food industry, medicine, but also from the ecological point of view. In addition, a deeper knowledge about the organization of the cells opens avenues for synthetic biology, a developing field in which compartmentalized protocells or artificial cells are promising for the production of interesting

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molecules, including energy-rich ones, under more and more controlled conditions (Xu et al. 2017; Yewdall, Mason, and van Hest 2018) or also for the genetic engineering of complex plant-specific biosynthetic pathways with valuable final products (*e.g.* monoterpene essential oils) into *Escherichia coli* or yeast cells (Zebec et al. 2016).

This issue entitled *Plant Cell Compartments* gathers together contributions on various fields of cell biology in photosynthetic organisms. Due to space and other limitations, this compilation is of course not covering all aspects of compartments but discusses only few selected topics. Our major focus was on specific key compartments of plant cells such as the cell wall, vacuole and plastids, as well as on the specific features of plant peroxisomes.

The neighboring cells of plant tissues are separated by their cell walls but are indeed in connection with each other thanks to cytoplasmic channels called plasmodesmata through which various molecules and molecular signals (*e.g.* hormones) can be transported and exchanged between cells (Sager and Lee 2014, 2018). Plasmodesmata thus represent an important cell-to-cell communication pathway in plants (and recently it has been shown that also in animals and bacteria) that facilitate processes related to the perception of environmental stimuli, stress signaling and response at the organ- and even the whole organism level (Lee 2014). In this context, it is clear that compartmentalization is not only restricted to intracellular separation of various processes but is at the extracellular level also important for the strict spatial separation of specific cells from surrounding tissues during certain phases of their development when they need to be fully isolated from their environment. Such a situation is the meiotic division, prior to which some reproductive cells (i.e. microspore and macrospore mother cells) of angiosperms produce a callose layer in their cell wall, which is isolating them from somatic cells during meiosis, but is later degraded or dynamically changed in order to control traffic at the cell periphery during the development of the reproductive cells (Tucker and Koltunow 2014). However, it is still not very well understood whether callose deposition is present in apomictic (*e.g.* diplosporic, asexually reproducing) species during the development of the gametophyte or not. The research paper by Musiał and Kościńska-Pająk (2019) published in this Special Issue presents clear evidence on the temporary presence of callose in the cell walls of *Chondrilla brevirostris* (Asteraceae) during meiotic diplospory. This example further outlines another important role of the cell wall compartment in the regulation of reproduction and signal transduction in plants.

The cell wall is often considered as an important molecular barrier both for ion and water transport and also during pathogen attack, but cellular integrity is more importantly determined by the plasma membrane. This membrane that limits the cell is a key structure regulating nutrient and signal exchange with the cell exterior. These roles are ensured by a myriad of structural and functional proteins that are able to receive and transmit environmental signals such as the presence of pathogens. In this sense, they are key players in the development of adaptive responses to a continuously fluctuating environment. Plasma membrane lipidomics allowed the complete and detailed characterization of the main classes of lipids present in the plant plasma membrane (phospholipids, phosphoinositides, sphingolipids and sterols) (Wenk 2010; Yu et al. 2018). The three-dimensional structure of most plasma membrane lipids favors their spontaneous organization into lamellar phase in the presence of water (Mamode Cassim et al. 2019). However, perturbations of their arrangement or membrane composition may result in the formation of nonlamellar membrane organization such as cubic phase (Almsherqi, Landh, and Kohlwein 2009). These latter consist of a three-dimensional network of membrane tubules and were observed in various cell compartments (e.g. endoplasmic reticulum, perinuclear space, mitochondria and plastids) and organisms (amoeba, animal, human and plant cells) (Almsherqi, Landh, and Kohlwein 2009; Solymosi and Schoefs 2010). In this issue, Absolonova, Foissner, and Sommer (2019) reported cubic phase organization of certain regions of the plasma membranes of *Chara* internodal cells termed charasomes.

Charasomes are enriched in H^+-ATPases involved in the acidification of the immediate environment of the charasome (Schmölzer, Höftberger, and Foissner 2011; Absolonova, Foissner, and Sommer 2019). The exact role of this local acidification is still not completely clear but may be related to carbon import processes for photosynthesis. Actually, the acidification is thought to shift the carbon dioxide – carbonic acid equilibrium toward CO_2, the most diffusive carbon form.

Peculiar organization of the plasma membranes analogous to charasomes (Absolonova, Foissner, and Sommer 2019) can be also observed in angiosperm plant cells for instance during the formation of the so-called plasmalemmasomes (Keresztes and Bóka 2019). These structures are omega-shaped small engulfings of the plasma membrane first into the cytoplasm and finally into the vacuolar compartment. In this Special Issue, the research paper by Keresztes and Bóka (2019) presents evidence for plasmalemmasome formation and discusses the factors inducing this process as well as the potential role of these organelles in facilitating water transport between the apoplast and the vacuole.

Peroxisomes were one of the last major and ubiquitous eukaryotic organelles discovered (De Duve and Baudhuin 1966) and they still represent mysterious single membrane-bound compartments involved primarily in cellular lipid metabolism and in the regulation of the cellular redox balance. This way they play crucial roles

in cell metabolism and thus their malfunctioning is linked to several human metabolic disorders (Castro, Schuldiner, and Zalckvar 2018; Islinger et al. 2018; Schrader, Kamoshita, and Islinger 2019). They also play a major role in plant primary and secondary metabolism, development and stress responses (Hu et al. 2012; Corpas 2019). Their morphology and metabolism are highly versatile and dynamically changing (Hu et al. 2012; Corpas 2019) and peroxisomes are strongly interrelated with other subcellular compartments (Castro, Schuldiner, and Zalckvar 2018; Schrader, Kamoshita, and Islinger 2019; Corpas 2019). Their proteome and metabolic networks are very large and strictly regulated. An increased knowledge on them may allow us to engineer plants with higher biotic (e.g. pathogen) and abiotic stress tolerance or increased biomass and/or improved metabolism. The review by Corpas (2019) in this Special Issue provides a general overview of peroxisomes and is focused primarily on their tremendous metabolic diversity.

One of the key steps of evolution was the acquisition of the capacity for autotrophic energy production via photosynthesis by various prokaryotes including cyanobacteria (Martin, Bryant, and Beatty 2018). Mitochondriate eukaryotes acquired photosynthesis by engulfing ancient cyanobacteria and a subsequent co-habitation and co-evolution with their (primary) endosymbionts. During this process, the cyanobacterial endosymbiont gradually lost its genetic independence and became the strictly controlled "tiny green slave" of the host cell. Most genes of the original endosymbiont have been transferred to the host nucleus or were lost, only few of them remained encoded by the plastid DNA. In this Special Issue, De Marchis et al. (2019) provide a critical and comparative overview on the plastid translational machinery and its regulation in land plants and in the green alga *Chlamydomonas reinhardtii*. Their major conclusion is that the expression of the few genes that are still encoded by the chloroplast genome is in general regulated at the post-transcriptional or translational levels.

Through plastid translational regulation and also other processes, the host cell and its metabolism strictly control plastid differentiation and activity. This constitutes a crucial point during the diversification of plastid structure and function that accompanies the increased complexity of algal and plant life cycles and organization (Solymosi 2012; Solymosi and Keresztes 2012; Solymosi, Lethin, and Aronsson 2018). Chloroplasts are responsible for photosynthesis using the energy of sunlight. On the other hand, chloroplast differentiation is inhibited and so-called etioplasts develop in some algal cells or plant tissues when they are fully deprived of light (Solymosi and Schoefs 2010; Solymosi 2012; Solymosi and Keresztes 2012). Etioplasts contain low amounts of a chlorophyll precursor, protochlorophyllide and a peculiar, three-dimensional tubuloreticular membrane structure called prolamellar body (Solymosi and Schoefs 2010; Kowalewska, Bykowski, and Mostowska 2019). Several data indicate that prolamellar bodies serve as a membrane reservoir for the fast formation of the photosynthetic apparatus and play a key role in greening under low light or other specific conditions also in the nature (Solymosi and Schoefs 2010). Electron tomography is a promising tool to investigate cell organization, including the structure of the subcompartments. In this Special Issue, Kowalewska, Bykowski, and Mostowska (2019) provided an overview on its uses to elucidate the exact structure and structural alterations of prolamellar body membranes during greening and transformation into the normal thylakoid network of the chloroplasts.

The papers published in this Special Issue clearly demonstrate the fast evolution of plant cell biology. Despite all the progress made during the last decades, it is still an emerging field. In addition, the continuous methodological and technological progress that we are witnessing – including the fast development of various cryo-electron microscopic methods – will allow in the near future to unravel further molecular and structural details to better understand the organization and the functioning of plant cells as well as the interactions of the various compartments with each other, their response to external stimuli and the regulation of their metabolism.

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Author Contribution

KS and BS both wrote, corrected and approved this manuscript.

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