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Update

Organellomic gradients in the fourth dimension

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Abstract

Organelles function as hubs of cellular metabolism and elements of cellular architecture. In addition to 3 spatial dimensions that describe the morphology and localization of each organelle, the time dimension describes complexity of the organelle life cycle, comprising formation, maturation, functioning, decay, and degradation. Thus, structurally identical organelles could be biochemically different. All organelles present in a biological system at a given moment of time constitute the organellome. The homeostasis of the organellome is maintained by complex feedback and feedforward interactions between cellular chemical reactions and by the energy demands. Synchronized changes of organelle structure, activity, and abundance in response to environmental cues generate the fourth dimension of plant polarity. Temporal variability of the organellome highlights the importance of organellomic parameters for understanding plant phenotypic plasticity and environmental resiliency. Organellomics involves experimental approaches for characterizing structural diversity and quantifying the abundance of organelles in individual cells, tissues, or organs. Expanding the arsenal of appropriate organellomics tools and determining parameters of the organellome complexity would complement existing -omics approaches in comprehending the phenomenon of plant polarity. To highlight the importance of the fourth dimension, this review provides examples of organellome plasticity during different developmental or environmental situations.

Introduction

The majority of molecules inside cells are grouped in morphologically and chemically distinct structures known as the organelles. Each organelle performs a set of specific functions. Historically, organelles were defined as compartments surrounded by at least 1 layer of membrane (endomembranes). There are 11 known membrane-bound organelles in plants, including plasmodesmata and organelle contact sites (Kang et al. 2022). The liquid-phase separation phenomenon contributes to the formation of membraneless organelles. Large complex structures, including cytoskeleton, ribosomes, and others, can also be considered as organelles due to their ability to maintain unique molecular composition and structural identity. Altogether, there could be, arguably, 33 different types of organelles in plants (Table 1).

Organelles can form de novo or through multiplication of existing organelles (Rafelski and Marshall 2008). Further, their size can change. It was proposed that both production of new organelles and their size are limited by the availability of critical building blocks (Chang and Marshall 2017). The stochastic nature of both the building block production and degradation of defunct organelles causes different organelle abundance in individual cells within the same population even under steady metabolic conditions (Mukherji and O'Shea 2014; Choubey et al. 2019). Consequently, at any given point of time each organelle population or organellome (Table 2) consists of forming, functioning, and aging individuals. Further, measuring the number of organelles as well as their life cycle stages in a limited number of cells may yield inaccurate estimates of the organelle abundance in an entire tissue or organ.

Developmental and environmental cues are known to alter the organellome. For example, quantitative ultrastructural analyses of cotton palisade mesophyll cells demonstrated that drought causes a higher number of chloroplasts per cell, enlargement of mitochondria, and reduction of

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Table 1. Plant organelles

Membranous	Nonmembranous
Autophagosomes	Ribonucleoprotein particle
Endoplasmic reticulum	Stress granules
Endosomes	Actin filaments
Exosomes	Microtubules
Golgi	Plasmodesmata
Trans-Golgi	Ribosome
Lipid bodies	
Mitochondria	
Multi-vesicular bodies	
Nucleus	
Peroxisome	
Plastids	
Amyloplst	
Elaioplast	
Etioplast	
Chloroplast	
Chromoplast	
Gerontoplst	
Iridoplast	
Leucoplast	
Proplastid	
Proteinoplast	
Phenyloplast	
Tannosome	
Intraplastidal organelles	
Stromule	
Thylakoids	
Plastoglobule	
Vacuole/tonoplast	

Table 2. Glossary or organellomic terms

Organelle	Cellular structure with unique molecular composition and functions
Organelle population	Diversity of organelles of the same type in a biological system at a given moment of time
Organellome	Diversity of all organelles present in a biological system at a given moment of time
Organellomics	Experimental approaches for characterizing molecular or structural diversity of organelles and quantifying organelle abundance
Organelle abundance	A value representing the number of organelles in a cell

endoplasmic reticulum (ER) area (Berlin et al. 1982). Abundance of peroxisomes and autophagosomes has been shown to change in response to stress (Lopez-Huertas et al. 2000; Mitsuya et al. 2010; Lai et al. 2011; Minina et al. 2018; Ustun et al. 2018; Hinojosa et al. 2019; Sanad et al. 2019). These examples imply that environmental cues introduce heterogeneity into the organellome (organellome gradients) in the time dimension by (1) synchronizing the life cycle of organelles; (2) changing the balance between organelle production and degradation; and (3) altering organelle structure and metabolic status. As such, the organellomics gradients are central for the interaction between the genotype and environment.

Advancing the understanding of organellomic gradients is limited by the availability of appropriate tools. Organelles could be counted directly by fluorescence microscopy using antibody, small fluorescent probes, fluorescent protein–based probes, and electron tomography (Mattiasson 2004; Kubínová et al. 2014). Flow cytometry can provide relative measurements of the organelle abundance (Mattiasson 2004). Organelle abundance also could be estimated by micro-dissection and extrapolating counts in the cells or tissues from analysis of thin sections (Kubínová et al. 2014). Information about organelles generated using the above methods is subject to several limitations. First, fast movement complicates counting numerous small organelles such as peroxisomes, mitochondria, and others. Second, counting organelles using microscopy can be time consuming, laborious, and expensive.

Small organelle-specific fluorescent probes can overcome these limitations. For example, fluorescence of Nitro-BODIPY (N-BODIPY) is activated inside peroxisomes of living cells and in total protein extracts (Landrum et al. 2010; Fahy et al. 2017). Peroxisome abundance in cells correlates with the fluorescence signal of N-BODIPY in the total extract (Fahy et al. 2017). As such, N-BODIPY fluorescence in total extracts measured by a spectrofluorometer informs on peroxisome abundance, hence bypassing expensive and laborious microscopy techniques. Libraries of small fluorescent probes (Alamudi and Chang 2018) open opportunities for identification of probes for each organelle and for exploiting organellomics data in basic plant biology as well as breeding. The main limitation of this approach is specificity: as the total protein extract averages billions of cells, resolving responses on the level of individual cells and tissues becomes challenging. Therefore, accurate information about organellome responses to environmental and developmental signals requires a combination of multiple approaches.

This review highlights studies on organellomic gradients in which changes of organelle abundance, morphology, or functions were quantified in the context of developmental or stress responses (Table 3). Our goal is to emphasize the importance of organellomic gradients for plant biology and highlight limitations in our knowledge on this subject. We identify quantifiable parameters that could be used for assessing changes of each organelle. Description of structure and functions of individual organelles is covered in multiple published reviews and was not included here. Also, the impact of mutations on organelle abundance or structure as well as the transcriptional responses and corresponding changes in the organelles is beyond the scope of this review. We apologize to all authors whose important work on organelle biology was not discussed due to scope and space limitations.

Autophagosomes

Autophagy is a major pathway for removal and recycling of redundant or defunct cellular components in eukaryotes (Nakatogawa et al. 2009). Individual molecules, molecular complexes, and organelles undergo sequestration in the double-membrane compartment, autophagosome, with subsequent delivery and degradation inside the vacuole. The autophagic

Table 3. Changes of organelle abundance in response to developmental and environmental cues

Organelle	Response	Cue	Model system	Reference
Autophagosomes	Proliferation	Salinity, drought	Arabidopsis	Liu et al. 2009
	Proliferation	Drought	Tomato	Wang et al. 2015a
	Proliferation	Oxidative stress	Arabidopsis	Xiong et al. 2007
	Proliferation	Heat	Arabidopsis	Yang et al. 2016
	Proliferation	Heat	Tomato	Zhou et al. 2014
Cytoskeleton				
Actin filaments	Depolymerization	Salt	Arabidopsis	Wang et al. 2010
	Depolymerization	Cold	Tobacco BY-2 cells	Pokorna et al. 2004
	Depolymerization	Heat	Arabidopsis	Muller et al. 2007
Microtubules	Depolymerization	Cold	Rye	Kerr and Carter 1990
	Depolymerization	Cold	Spinach	Bartolo and Carter 1991b
	Depolymerization	Osmotic stress	Wheat	Wang and Nick 2001
	Depolymerization	Cold	Grapevine	Wang and Nick 2017
	Depolymerization	Heat	Tobacco	Smertenko et al. 1997
	Depolymerization	Heat	Arabidopsis	Muller et al. 2007
	Depolymerization	Salt	Arabidopsis	Shoji et al. 2006
	Depolymerization	Salt	Arabidopsis	Wang et al. 2007
Endoplasmic reticulum	Size reduction	Drought, field trial	Cotton	Berlin et al. 1982
Endosomes	Size, movement speed, mobility patterns	Control root hair cells	Arabidopsis	von Wangenheim et al. 2016
Lipid bodies	Proliferation	Cold, heat, darkness	Arabidopsis	Gidda et al. 2016
	Proliferation	*Colletotrichum higginsianum*	Arabidopsis	Shimada et al. 2014
	Proliferation	Embryo differentiation	Oilseed plants	Wanner et al. 1981
Mitochondria	Proliferation	Drought	*Bermuda grass*	Utrillas and Alegre 1997
	Proliferation	Heat	Wheat	Grigorova et al. 2012
	Elongation	Hypoxia	Arabidopsis Tobacco	Ramonell et al. 2001; Van Gestel and Verbelen 2002
	Degradation	Senescence	Wheat Arabidopsis	Ruberti et al. 2014 Keech et al. 2007
Multi-vesicular bodies	Proliferation	Heat, salt	Arabidopsis	Wang et al. 2015b
Peroxisome	Proliferation	Light	Arabidopsis	Desai and Hu 2008; Schrader et al. 2012
	Proliferation	Seed germination	Arabidopsis	Mansfield and Briarty 1996
	Proliferation	Ozone	Aspen and birch	Oksanen et al. 2004
	Proliferation	Salt		Fahy et al. 2017; Mitsuya et al. 2010
	Proliferation	Jasmonic Acid and wounding	Arabidopsis	Castillo et al. 2008
	Proliferation		Arabidopsis	Ulloa et al. 2002
	Proliferation	Heavy metals	Potato	McCarthy et al. 2001
	Proliferation	Pathogen, H_2O_2, or wounding	Pea Arabidopsis	Lopez-Huertas et al. 2000
	Proliferation	Drought	Wheat	Sanad et al. 2019
	Proliferation	Heat and drought	Quinoa	Hinojosa et al. 2019
Plastids				
Amyloplst	Differentiation	Columella cells	Oat	Hinchman and Gordon 1974
Elaioplast	Differentaition	Pericarp development	Citrus	Zhu et al. 2018
Chloroplast	Proliferation	Drought and heat	Wheat	Grigorova et al. 2012
	Degradation	Starvation	Wheat	Wardley et al. 1984
Chromoplast	Differentiation	Endocarp development	Citrus	Zhu et al. 2018
Iridoplast	Differentiation	Low light	Begonia	Pao et al. 2018 Jacobs et al. 2016
Leucoplast	Differentiation	Trichome development	*Stachys lanata*	Cheniclet and Carde 1988
Phenyloplast	Differentiation	Development	Vanilla	Brillouet et al. 2014
Tannosome	Formation from thylakoids	Development	Multiple species	Brillouet et al. 2013
Stromule	Formation	Pathogen attack Abiotic stress Diurnal cycle Strigolactone	Multiple species	Hanson and Hines 2018
Thylakoids	Degradation	Drought	Wheat	Grigorova et al. 2012

(continued)

Table 3. (continued)

Organelle	Response	Cue	Model system	Reference
Plastoglobule	Formation	Oxidative stress Senescence	Arabidopsis Tobacco	Austin et al. 2006
Stress granules	Proliferation	Heat, low light	Arabidopsis	Kosmacz et al. 2019
	Proliferation	Drought	Arabidopsis	Marondedze et al. 2020
	Proliferation	Hypoxia	Arabidopsis	Sorenson and Bailey-Serres 2014
Vacuole/tonoplast	Volume/size changes	Stomata opening/closing	Arabidopsis	Andrés et al. 2014, Gao et al. 2005

pathway is controlled by a group of autophagy-related proteins (Klionsky et al. 2012). Autophagosomes can be imaged in cells using fusion of a fluorescent protein with the key autophagy-related protein ATG8 (Yoshimoto et al. 2004; Thompson et al. 2005). Quantification of autophagy using this and other approaches highlights the essential role of autophagy in plant development and stress response (Michaeli et al. 2016).

Live-cell imaging demonstrated that induction of unfolded protein response in ER using tunicamycin or DTT causes higher autophagosome abundance (Liu et al. 2012). Furthermore, higher abundance of autophagosomes was observed in response to nutrient starvation, salinity, and drought stresses (Fig. 1; Yoshimoto et al. 2004; Thompson et al. 2005; Liu et al. 2009). Tomato plants showed an over 4-fold increase in the autophagosome number after 6 days of drought (Wang et al. 2015a). Heat stress in Arabidopsis and tomato caused 2- to 6-fold higher autophagosome abundance per cell, respectively (Zhou et al. 2014; Yang et al. 2016). Formation of autophagosomes was also promoted by oxidative stress induced with hydrogen peroxide or methyl viologen (Xiong et al. 2007). Such a remarkable responsiveness to abiotic stresses and relative ease of quantification makes autophagosome abundance a very useful proxy of plant health.

Cytoskeleton

Components of plant cytoskeleton, microtubules and microfilaments, can grow, shrink, or sustain a given length. The balance between these processes determines the abundance and length of the cytoskeletal filaments. As both parameters can be quantified for microtubule networks, there is detailed information about the microtubule response to many different cues. The most common response is a reduction of the microtubule network density. For example, complete or partial loss of microtubules could be observed as early as 25 minutes of exposure to cold stress (Kerr and Carter 1990; Bartolo and Carter 1991b; Wang and Nick 2001; Wang and Nick 2017), heat stress (Smertenko et al. 1997; Muller et al. 2007), salt stress (Shoji et al. 2006; Wang et al. 2007), or osmotic stress (Bartolo and Carter 1991b). Microtubules under salt and cold stress subsequently recover (Abdrakhamanova et al. 2003; Wang et al. 2007). This recovery is attributed to adaptation responses. Depolymerization of microtubules appears to play an essential role in plant resilience as treatments with the inhibitor of microtubule depolymerization taxol prior to cold or salt stress compromised plant survival (Kerr and Carter 1990; Bartolo and Carter 1991a; Wang et al. 2007).

Although it was proposed that microtubules contribute to activating the tolerance responses by sensing stress-induced changes of the plasma membrane tension (Nick 2013), how depolymerization of microtubules contributes to the resiliency remains unknown. One hypothesis is by increasing membrane fluidity (Bartolo and Carter 1991a). Alternatively, considering that many proteins bind microtubules, microtubule depolymerization could increase the abundance or mobility of these proteins, leading to activation of adaptive mechanisms.

Quantification of microfilaments is complicated by the fact that most microfilaments form thick bundles or cables where the ends of individual filaments are masked. The loss of actin filaments in response to salt (Wang et al. 2010), cold (Pokorna et al. 2004), or heat stress (Muller et al. 2007) suggests that depolymerization of actin filaments is a common reaction to stress. Destabilization of actin filaments reduces plant survival under salt stress, whereas stabilization of microfilaments promotes resilience (Wang et al. 2010). It remains unknown whether depolymerization of actin filaments is a component of stress signaling or a stress-induced damage. Dynamicity of cytoskeletal responses above suggests that changes of cellular architecture and disruption of microtubule- and microfilament-dependent traffic are important components of environmental plasticity.

Endoplasmic reticulum

The ER is a dynamic network of interconnected tubules and flattened sheets or cisternae that together constitute the largest membranous surface area in the cell (Fig. 1; Stefano and Brandizzi 2018). ER tubules are on average 30 to 50 nm wide and able to fuse homotypically (Pain et al. 2019). About 5% of the ER is persistent and forms the anchor site on which movement of ER tubules occurs (Sparkes et al. 2009). ER forms contacts with other organelles, including Golgi apparatus (Brandizzi et al. 2002), vacuole (Shimada et al. 2018), chloroplasts (Hurlock et al. 2014), and the plasma membrane (Wang et al. 2017). ER forms a desmotubule that passes through the plasmodesmata connecting the neighboring cells (Knox et al. 2015). ER also connects to the nuclear

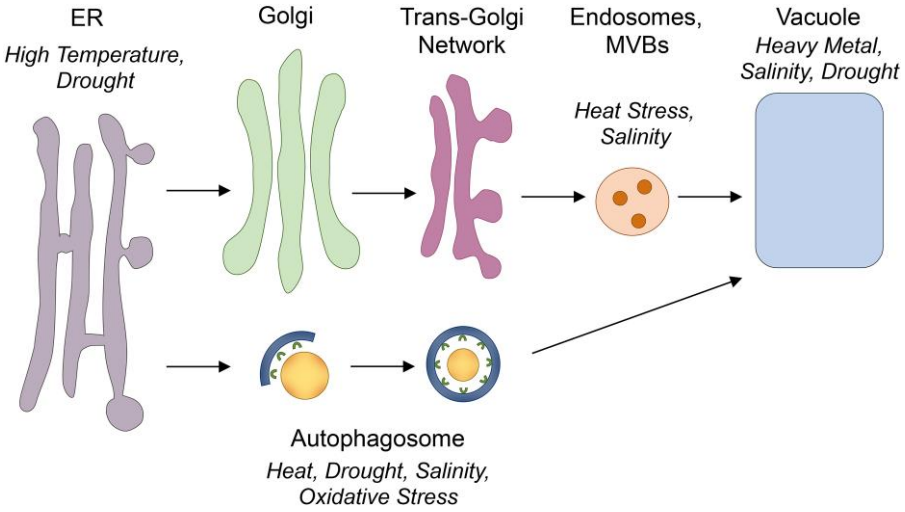

Figure 1. The abundance and morphology of the membrane trafficking organelles can cange in response to environmental cues. The ER is affected by high temperatures and drought stress. MVBs are affected by heat stress and salinity. The vacuole plays a role in heavy metal, salinity, and drought stresses. Autophagosomes are affected by heat, drought, salinity, and oxidative stresses. The abundance of Golgi and TGN have not been studied in the context of stress response.

envelope through nuclear envelope gates. An estimated 30 to 50 nuclear envelope gates have been described in pea root tip cells (Craig and Staehelin 1988).

Drought stress leads to reduction of ER surface area in cotton palisade cells (Berlin et al. 1982). Quantification of ER dynamics demonstrated that both heat shock and inhibitor of actin polymerization Latrunculin B affected movement of the ER with no discernible impact on the cisterna morphology (Pain et al. 2019). Changes of the ER morphology in response to high temperature could be associated with protein misfolding that triggers the unfolded protein response (Srivastava et al. 2014). It remains to be determined whether changes of ER morphology constitute a component of stress resilience or a consequence of stress-induced damages.

Endosome and multivesicular bodies (MVBs)

Endosomes are vesicles involved in sorting, signaling, trafficking, and selective degrading of proteins and lipids within the endomembrane system (Fig. 1). Early endosomes (EE) emerge from the trans-Golgi network (TGN), where secretory and endocytic pathways converge (Contento and Bassham 2012). Detecting EE and tracking their behavior can be achieved using fluorescent protein markers such as GFP–RABA1b (Asaoka et al. 2013). Another marker, AtECA4:sGFP, localizes to EE and AtECA4:sGFP fluorescence signal increases in response to drought stress induced by treatment with mannitol and PEG (Nguyen et al. 2018). Analysis of dynamic properties of endosomes in Arabidopsis root hair tip with specific markers YFP-VTI12 and GFP-RabA1 using time lapse–structured illumination microscopy and multitracking software demonstrated the average size of endosomes is 197 nm and movement speed is 6.5 to 8.7 μm/s (von Wangenheim et al. 2016).

Late endosomes mature into MVBs (Fig. 1) and deliver cargo for the degradation or storage in vacuoles (Cui et al. 2018). MVB maturation from endosome is defined by the formation of intraluminal vesicles with the help of endosomal complex required for transport (ESCRT) proteins. ESCRT-SNF7 was successfully used for MVB observation in developing barley grain (Roustan et al. 2020). Another component of ESCRT-Lyst-Interacting Protein5 (LIP5) was used to quantify MVB dynamics under heat and salt stress in Arabidopsis (Wang et al. 2015b). Lines expressing LIP5-GFP showed doubling of MVB puncta under heat stress and over 80% increase in number of MVB under salt stress. Vacuolar sorting receptors (VSR) facilitate cargo targeting for transport between TGN and vacuole via MVB. MVB dynamics can be tracked using YFP-VSR (BP-80; Tse et al. 2004). Although parameters for endosome and MVB organellome are still being developed, these data would inform on impact of environmental cues on the endocytosis.

Golgi and TGN

The Golgi apparatus comprises membrane cisternae, the TGN, and matrix proteins (Fig. 1). The number of cisternae per Golgi apparatus ranges between 3 and 10, of which cis-cisternae makes 1 or, with rare exceptions, 2 counts (Zheng and Staehelin 2011). Under normal conditions each plant cell contains on average 35 Golgi, and duplication of the Golgi apparatus occurs in a cell cycle–dependent manner (Segul-Simarro and Staehelin 2006). The TGN originates from the Golgi and functions as a distinct organelle (Fig. 1). There are 2 types of TGN: Golgi-associated (GA-) TGN and free TGN (Kang et al. 2011). The GA-TGN is formed through cisternal peeling process that causes approximately 30% reduction in surface area compared with the trans-cisternae (Staehelin and Kang 2008). The free TGN gets further

reduced to 50% to 20% of the trans-cisternae through vesicle budding. Only about 50% of Golgi have GA-TGN (Zhang and Staehelin 2011). The main difference between GA-TGN and free TGN is the ratio of secretory vesicles and clathrin-coated vesicles. The secretory vesicles on the free TGN are 52 to 88 nm in diameter, whereas secretory vesicles on the GA-TGN are 83 to 107 nm in diameter (Kang et al. 2011). Each TGN forms about 30 secretory vesicles and clathrin-coated vesicles. Our knowledge of the impact of cell differentiation and stress on abundance and morphology of Golgi and TGN remains scant. However, considering the dynamicity of Golgi and TGN structure and their importance in biosynthetic pathways and vesicle trafficking, the number of Golgi and TGN per cell as well as the number of cisternae and secretory vesicles per each structure are likely to be responsible to the external cues.

Lipid bodies

Lipid bodies or lipid droplets consist of mostly neutral lipids (triacylglycerols and steryl/wax ester) surrounded by a monolayer of phospholipids and a coat of structural proteins oleosins. Other types of proteins found in the lipid droplets are enzymes caleosin, dioxygenase, and steroleosin; and proteins with diverse functions (Huang 2018). Lipid droplets originate from the ER, and their number in cells increases during embryo differentiating in oilseed plants (Wanner et al. 1981), in response to heat, cold stress, or at the end of the night (Gidda et al. 2016). Lipid droplets also contribute to the pathogen response. It has been shown that proliferation of lipid droplets in Arabidopsis could be induced by pathogenic fungus *Colletotrichum higginsianum* (Shimada et al. 2014). Two lipid droplets components, dioxygenase and caleosin, are responsible for the synthesis of 2-hydroxy-octadecatrienoic acid, which has antifungal properties (Shimada et al. 2014). Organellomics of lipid droplets offer insights into changes of pathways for the energy production in response to developmental or stress signals.

Mitochondria

The number of mitochondria in cells is determined by the balance between fusion and fission. This balance, in turn, is governed by the energy demand with the fission favoring an increase in energy supply (Arimura 2018). Direct quantification of mitochondria abundance using microscopy has significant challenges as mitochondria move rapidly and undergo frequent fusion and fission (Arimura et al. 2004). An alternative approach relies on measuring the mitochondrial genome copy number (Moraes 2001). However, variability of the genome copy number compromises the accuracy of this approach. For example, in somatic cells, the average number of mitochondria per cell could be greater than the average number of genome copies (Logan 2006). Previous attempts to quantify abundance of mitochondria generated highly variable values. For example, Arabidopsis leaf cells have between 40 and 200 mitochondria (Keech et al. 2007), and protoplasts from tobacco leaf can have up to 2,000 mitochondria (Sheahan et al. 2004). Mitochondria abundance and shape can change during development: fusion-dominated elongated mitochondria appear during seed germination and in the shoot apical meristem (Arimura 2018), whereas the number of mitochondria per mesophyll and stomata cells decreases during leaf senescence in Arabidopsis and grapevine (Keech et al. 2007; Ruberti et al. 2014).

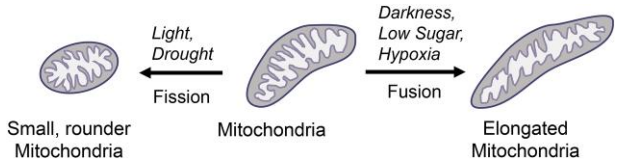

Figure 2. Responses of mitochondria to environmental cues. Mitochondria abundance and morphology is goverend by the balance between fusion and fission events. Light and drought promote proliferation through fission and form smaller, rounder mitochondria. Darkness, low cellular sugar, and hypoxia favor fusion events resulting in larger elongated mitochondria.

Cues that alter the energy balance cause mitochondria to fuse or undergo fission. Light promotes fission causing small mitochondria (Fig. 2), whereas darkness and low sugar levels favor fusion creating elongated mitochondria (Jaipargas et al. 2015). Elongated and giant mitochondria have been reported in response to hypoxia (Ramonell et al. 2001; Van Gestel and Verbelen 2002). Drought stress was shown to promote mitochondrial proliferation in mesophyll and bundle sheath cells of Bermuda grass (Utrillas and Alegre 1997). Thus, distinct morphological and functional parameters of mitochondria correlate with changes of energy production in the cell, though quantification of these parameters still remains technically challenging due the rapid movements and changes of shape.

Peroxisome

The peroxisome is a highly metabolically-active, single-membrane organelle. Peroxisomes can form de novo through budding from the ER or can proliferate through fission (Fig. 3). In spinach and sunflower, peroxisomes represent 1% to 1.5% of total leaf extract volume (Tolbert and Yamazaki 1969). Arabidopsis Columbia (Col-0) cells reportedly have on average 30 to 40 peroxisomes (Zhang and Hu 2008, 2009). Mesophyll cells in 4-week-old Arabidopsis Col-0 contain 100 to 120 peroxisomes, and the majority of them (approximately 90%) are 50 to 350 nm long (Orth et al. 2007).

Peroxisome abundance varies significantly under different environmental conditions. The number of peroxisomes in Arabidopsis leaf cells increased by 47% after 4 h of transition from dark to light conditions (Desai and Hu 2008; Schrader et al 2012) and by 2-fold during seed germination (Mansfield and Briarty 1996). Peroxisome abundance also increases in response to ozone (Oksanen et al. 2004), salt (Mitsuya et al. 2010; Fahy et al. 2017), jasmonic acid (Ulloa

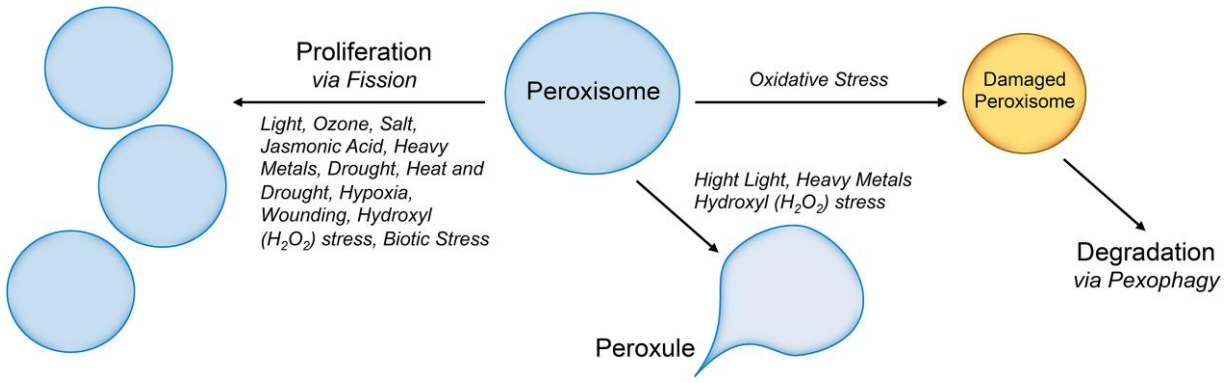

Figure 3. Impact of environmental cues on peroxisomes. Light, ozone, salt stress, jasmonic acid, heavy metals, drought, heat, hypoxia, wounding, hydroxyl (H_2O_2) stress, and biotic stress stimulate peroxisomes proliferation via fission. ROS scavenging reactions inside peroxisomes make them vulnerable to oxidative damages. Damaged peroxisomes are degraded through an autophagy process called pexophagy. Peroxisomes can form extension called peroxule under high light intensity, heavy metals, and hydroxyl stress.

et al. 2002; Castillo et al. 2008), heavy metals (McCarthy et al. 2001), drought (Sanad et al. 2019), heat and drought (Hinojosa et al. 2019), hypoxia (Li and Hu 2015), wounding, and H_2O_2 (Lopez-Huertas et al. 2000). Lower peroxisome abundance correlates with higher yield under drought in wheat and under drought, heat, and combination of drought and heat stress in quinoa (Hinojosa et al. 2019; Sanad et al. 2019).

Peroxisome abundance also changes in response to pathogens. Proliferation of peroxisomes was reported in the first 8 days after nematode infection followed by a decline after day 12 (Dinh et al. 2014). Infection with wheat streak mosaic virus was also shown to induce peroxisome proliferation (Mishchenko et al. 2021). In addition to changes in abundance, peroxisome morphology is very dynamic. Peroxisome size increases 6-fold in cotyledons of Arabidopsis during the first 60 h of seed germination (Mansfield and Briarty 1996). Peroxisomal membrane can form an extension called peroxule. Formation of peroxules is promoted by high light intensity (Jaipargas et al. 2015), heavy metals (Rodríguez-Serrano et al. 2016), and hydrogen peroxide (Sinclair et al. 2009). Organellomics of peroxisomes demonstrates both the importance of temporal gradients in responses to environmental cues and the value of these data for identification of stress-resilient genotypes in germplasm collections.

Plasmodesmata

Plasmodesmata are membrane-lined pores in the cell wall that link cytoplasm of neighboring cells and facilitate intercellular signaling and transport (Brunkard et al. 2013). Plasmodesmata consists of a 20- to 40-nm plasma membrane opening and ER membrane–bound desmotubule forming a cytosolic sleeve between them (Nicolas et al. 2017). Plasmodesmata permeability can be modulated by developmental and stress cues (Vu et al. 2020). Primary plasmodesmata with a simple linear structure form during cytokinesis, whereas secondary plasmodesmata that form during cell differentiation usually have a branched complex structure. High-throughput imaging platform for quantitative analysis of complex plasmodesmata was developed in Arabidopsis (Fitzgibbon et al. 2013). Spinning disc confocal microscopy and an image analysis algorithm PDQUANT were used with movement protein (MP17-GFP), which targets complex plasmodesmata and PLASMODESMATA LOCALIZED PROTEIN1, which targets all plasmodesmata. Authors estimated 10 to 35 complex plasmodesmata per cell in leaves under normal developing conditions. Treatments with mannitol or salicylic acid increased numbers of complex plasmodesmata up to 2-fold, whereas hydrogen peroxide did not induce significant change (Fitzgibbon et al. 2013). Thus, organellomics of plasmodesmata can be useful for assessing capacity of inter-cellular communication system in response to different environmental cues.

Plastids

Plastids constitute the largest group of organelles with highly diverse structure and functions (Fig. 4; Table 1). The most common plastid, chloroplast, differentiates from etioplast in response to light (Solymosi and Schoefs 2010). Mature leaf cells maintain steady chloroplast abundance, though their number appears to be genotype specific. For example, mesophyll cells of Arabidopsis ecotypes Landsberg erecta, Wassilewskija, and Col-0 contain 120, 80 to 90, and 100 chloroplasts, respectively (Aldridge et al. 2005). Drought and heat stress cause 20% to 40% more chloroplasts per cell in wheat (Grigorova et al. 2012) and 17% more (from 88 to 118) in cotton cells (Berlin et al. 1982). On the contrary, starvation caused reduction of chloroplasts from 185 to 140 per mesophyll cell in wheat (Wardley et al. 1984). In finger millet, the number of chloroplasts in mesophyll cells and bundle sheath cells almost doubles in response to mycorrhizal infection (Krishna et al. 1981).

Chloroplasts can differentiate into iridoplasts or lamelloplasts in the epidermal cells of shade-dwelling *Begonia* (Pao et al. 2018). Iridoplasts form in shade-adapted plants and

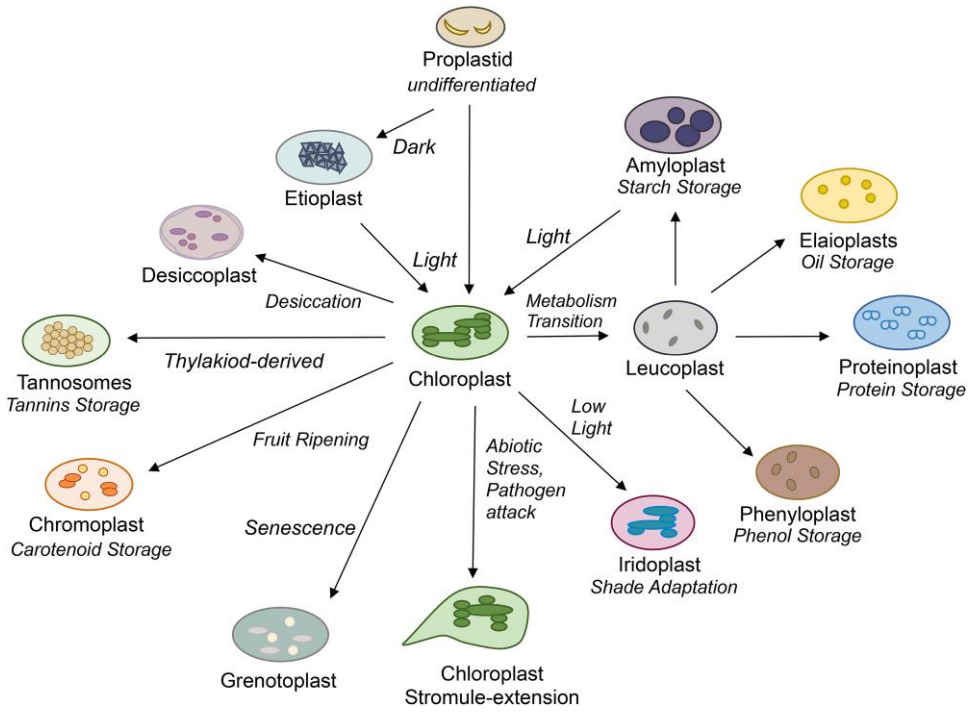

Figure 4. Plastid diversity and differentiation. Proplastids are undifferentiated meristematic plastids. Etioplasts originate from proplastids in the dark. Upon light exposure, proplastids and etioplasts differentiate into chloroplasts. Chloroplasts contain thylakoid membranes, where light harvesting reactions take place. Under pathogen attack and abiotic stress, chloroplasts increase its surface area through a stroma-filled tubule called stromule. During senescence, chloroplasts dismantle into grenotoplasts. Specialized plastids, primarily found in nonphotosynthetic tissues, are called leucoplasts, which can further differentiate into amyloplasts, elaioplasts, proteinoplast, and phenyloplast. Elaioplasts specialize in oil storage, proteinoplasts store proteins, and phenyloplasts stores phenolic compounds. Amyoplasts store starch and upon light can transition into chloroplasts. Chromoplasts develop during fruit ripening and store carotenoids. Tannosomes are tannin-containing organelle that forms from thylakoid membranes. Iridoplastids are a shade-adapted type of chloroplast that increases light absorption. Desiccoplasts are desiccated chloroplasts found in desiccation tolerant plants and can transition back to chloroplast upon rehydration.

absorb light more efficiently than chloroplasts (Jacobs et al. 2016). Desiccoplasts are specialized plastids that can be interconverted between chloroplasts and proplastids in desiccation tolerant plants (Solymosi et al. 2013).

Some plastids specialize in metabolic pathways. For example, leucoplast functions in monoterpene synthesis (Cheniclet and Carde 1988). Leucoplast can differentiate into amyloplast, elaioplast, or proteinoplast. Elaioplasts store oil in the oil-seeds species and in the epidermal cells of some monocots, whereas proteinoplast (also known as proteoplasts) store proteins in the endosperm (Lopez-Juez and Pyke 2005). Amyloplasts store starch and can also function as statolith during gravity perception in columella cells. As much as 30 to 65 amyloplasts per columella cell were reported in oat (Hinchman and Gordon 1974) and 23 amyloplasts in corn (Moore et al. 1986). Microgravity does not affect the number of amyloplasts per cell but causes reduction of their size and the size of starch granules (Moore et al. 1986). Another type of plastids, chromoplasts, accumulate carotenoids (Lopez-Juez and Pyke 2005). Abundance of both elaioplasts and chromoplasts increases during fruit development. Elaioplasts are typical for the pericarp of citrus fruits, whereas chromoplasts form in the endocarp (Zhu et al. 2018). A chloroplast-derived organelle phenyloplast stores phenolic secondary metabolites in *Vanilla planifolia* fruit (Brillouet et al. 2014).

Plastids contain structures, such as thylakoids, plastoglobuli, and stromules, that can be considered as chloroplast organelles (Fig. 4). The abundance of these organelles also changes. For example, *T. aestivum* chloroplast has an average of 10 to 15 thylakoids per granum, whereas under drought stress this number decreases to between 4 and 8 (Grigorova et al. 2012). The loss of thylakoids occurs during senescence-induced differentiation of chloroplast into gerontoplast (Biswal et al. 2003). An additional organelle, tannosome, forms through pearling off the thylakoids into 30-nm spheres that are then trafficked and stored in the vacuole (Brillouet et al. 2013). The tannosome stores condensed tannins. Another structure in plastids is the plastoglobule, a multifunctional lipoprotein particle (Austin et al. 2006; Bréhélin and Kessler 2008). The abundance of plastoglobuli increases in gerontoplast (Wardley et al. 1984; Biswal et al. 2003) and in response to oxidative stress (Vidi et al. 2006; Bréhélin et al. 2007; Rottet et al. 2015). Finally, the stromule is a stroma-filled tubule that increases the plastid surface area and establishes connection with other plastids (Waters et al. 2004) or nuclei (Erickson et al. 2017). Abundance of stromules

increases in response to pathogen attack, abiotic stresses, diurnal cycle, and hormone strigolactone (Hanson and Hines 2018). In summary, plastids exemplify both morphological and structural changes of an organelle in response to developmental and environmental cues. Parameters of plastid organellome inform on both differentiation of specific organs and on stress adaptation.

Stress granules

Stress granules (SGs) are liquid-phase organelles consisting of mRNA and ribonucleoproteins that form under abiotic stresses and function in translation inhibition (Protter and Parker 2016). Despite lacking the membrane boundary, these organelles can maintain specific composition. Poly(A) mRNA, poly(A) binding protein, 40S ribosomal subunits, and eukaryotic initiation factors are the key components of SG (Gutiérrez-Beltrán et al. 2015). Plant SG markers were identified based on homology with yeast and animal proteins (Weber et al. 2008) and by SG isolation in Arabidopsis (Kosmacz et al. 2019). A GFP fusion of SG-assembly factor RNA-binding protein Rbp47b revealed formation of SG following exposure to heat and low light (Kosmacz et al. 2019). Formation of SG was also observed in response to hypoxia in leaf cells of Arabidopsis expressing GFP fusion of OLIGOURIDYLATE BINDING PROTEIN 1 (Sorenson and Bailey-Serres 2014). In another study, assessment of SG proteome in Arabidopsis during drought stress, using interactome capture followed by mass spectrometry, revealed higher abundance of 11 SG proteins (Marondedze et al. 2020). Formation of SGs under stress conditions makes them a useful proxy for stress, though organellomics tools for SGs are limited. Advancing such tools relies on development of informative molecular probes.

The vacuoles

The vacuole is a single-membrane organelle that can occupy up to 90% of the cell volume. During embryo development in Arabidopsis, there is 1 large vacuole per cell in the torpedo stage, which is then remodeled into protein storage vacuoles during subsequent stages (Feeney et al. 2018; Shimada et al. 2018). In tobacco and Arabidopsis root cells, the protein storage vacuoles are transformed into lytic vacuoles as the cells mature (Zheng and Staehelin 2011; Cui et al. 2019). Using 3D electron tomography, Cui et al. (2019) tracked the remodeling of the vacuoles during differentiation of Arabidopsis root cells. In early cortical cells, small vacuoles (400–1,000 nm in diameter) derived from multi-vesicular bodies occupy <5% of the cell volume. As the cell matures, these vacuoles undergo fusion to form a large central vacuole (Fig. 5A; Cui et al. 2019). Vacuoles also undergo changes during cell cycle: in the M-phase of Arabidopsis shoot meristem cells, vacuole undergoes fragmentation accompanied by significant reduction of the surface area and volume (50% and 80% respectively; Segui-Simarro and Staehelin 2006).

Stomata closure and opening are regulated through changes in vacuole morphology (Fig. 5B). Gao et al. (2005) found that in *Vicia faba*, during stomata opening, the number of vacuoles decreases, whereas the average volume of individual vacuoles increases. The vacuole volume can change by more than 40% during the opening and closing of the stomata (Andrés et al. 2014). The above examples demonstrate the importance of information about vacuole organellome for understanding plant responses to developmental and environmental cues.

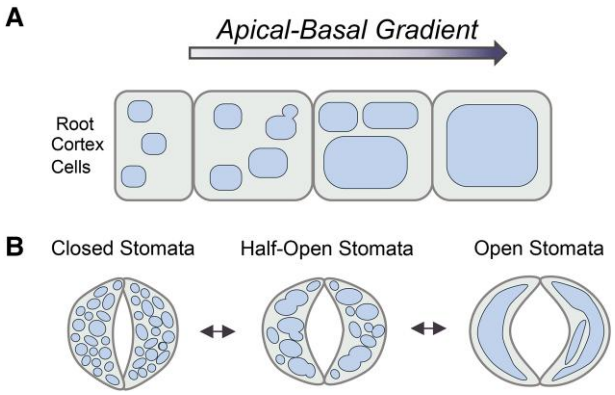

Figure 5. Changes of the vacuole morphology during cell differentiation and stoma opening. **A)** Differentiation of Arabidopsis root cortex cells is accompanied by reduction of vacuole number and increase of their volume. In differentiated cells the vacuole can occupy up to 90% of cell volume. **B)** During stoma opening the number of vacuoles decreases, whereas the average volume of individual vacuoles increases. The vacuole volume can change by more than 40% during the opening and closing of the stoma. As the stoma closes, the large vacuoles fragment into smaller vacuoles.

Concluding remarks and outstanding questions

Published data thus far illustrate the importance of information about polarization of organellome in the time dimension for deeper understanding of cellular responses to external cues. The diversity of plastids and biogenesis of vacuoles exemplifies the impact of tissue differentiation on the organelle morphology and functions. Changes of abundance of peroxisomes, autophagosomes, lipid bodies, and stress granules during stress treatments demonstrate contribution of organellomics data to untangling cellular mechanisms of stress resiliency and environmental plasticity. Our review reveals that information about responses of many organelles to external cues still remains limited, yet all organelles likely undergo changes during differentiation and stress responses. It has been shown that each organelle can be described with a set of quantifiable parameters. Measuring these parameters under different developmental or stress situations is essential for exploiting organellomics for dissecting cellular responses to each cue in the contexts of interactions between genotype and environment.

Further advancement of organellomics requires addressing the following knowledge gaps:

1) What governs the rate of organelle proliferation? If organelle abundance is controlled by production of the "limiting building blocks" (Marshall 2016), then identification of these blocks and determining what controls their production is an important task.
2) What determines the degradation rate of defunct or excessive organelles: the targeted degradation of the limiting building blocks or higher organelle turnover rate, for example, by activation of specific types of autophagy? If turnover is the mechanism, then what determines the selectivity of organelle degradation in the case of damage or redundancy?
3) How to determine the structural heterogeneity of an organelle population? Although transcriptomics, translatomics, and proteomics provide quantitative information on changes of the structural blocks for each organelle in response to a given cue, these data are not sufficient for determining the frequency of newly formed, fully functional, and defunct organelles.
4) How does structural heterogeneity of an organelle population and the organelle abundance correlate with their functionality? How can we measure the activity of metabolic pathways inside organelles? Considering that organelles have multiple functions, could there be a functional specialization of organelles within a population and how is this specialization affected by external cues?
5) How dynamic are the organellomic gradients, and is there a cross-talk between the gradients of different organelles? If yes, what makes these connections?

Addressing these questions requires the advancement of organellomics tools: (1) identification of molecular markers for different stages of the organelle life cycle; (2) development of probes for detecting and quantifying these markers; (3) development of probes for measuring distinct functionalities of each organelle; and (4) advancement of detection approaches for these probes. Application of such probes in combination with high-resolution light and electron microscopy techniques as well as with biochemical and other -omics approaches would take our understanding of cellular polarity to the next dimension.

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Data availability

This manuscript contains no online data.

Author contribution

K.H., T.N., and A.S. wrote the draft, K.H., T.N., and A.S. edited the draft. A.S. supervised the project and acquired funding.

Supplemental data

This manuscript contains no supplemental data.

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