Fission and Fusion of Plant Mitochondria, and Genome Maintenance[1][OPEN]

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In plant somatic cells, the number of mitochondria is usually larger than the copy number of their genome. The constant fission and fusion of mitochondria make it possible to share the internal materials between them (Arimura et al., 2004b). Therefore, the chondriome (the collective mitochondria in a cell) is thought to exist as a discontinuous whole (Logan, 2006). In this Update, I describe recent reports about mitochondrial dynamics during developmental stages, in specific organs, and in environmental responses, the molecular mechanisms underlying these dynamics, and the relationship to their genome maintenance. Several factors are involved in mitochondrial biogenesis, including gene expression in the nucleus and mitochondria and protein import from the cytosol to the mitochondria. These processes are covered in some excellent recent reviews (Millar et al., 2008; Carrie et al., 2013; Law et al., 2014; Czarna et al., 2016). Here, I focus on recent investigations of the fission and fusion of plant mitochondria and its relatedness to their genome maintenance.

Mitochondria have an endosymbiotic origin in which they are thought to be descendants of an α-proteobacteria. Mitochondria maintain themselves through growth and division but without de novo formation from other organelles. They differ from plastids and peroxisomes in how they control their numbers, shape, and volume. Plastids are generated by growth and division without de novo synthesis, and they rarely undergo fusion (Sakamoto et al., 2008; Osteryoung and Pyke, 2014). Peroxisomes also are generated by growth and division and rarely undergo fusion. However, they also are de novo synthesized from the endoplasmic reticulum (ER; Hu et al., 2012). Interestingly, peroxisomes share some division factors with mitochondria (Pan and Hu, 2011; Arimura and Tsutsumi, 2016).

The pleomorphy and dynamics of mitochondria were observed over 100 years ago (Lewis and Lewis, 1914) and have been further investigated more recently (Bereiter-Hahn, 1990; Logan and Leaver, 2000; Logan, 2006; Jaipargas et al., 2015). Fission and fusion can change the number and shape of mitochondria from a single network to hundreds of particles by shifting their balance without changing their total volume in a cell. Shifting the balance between fission and fusion of mitochondria can have many direct and indirect effects in plants (Logan, 2006, 2010) and in mammals (Liesa and Shirihai, 2013; Mishra and Chan, 2016; see Box 1).

MITOCHONDRIAL FISSION PROTEINS IN YEAST, ANIMALS, AND A RED ALGA

Dnm1, a dynamin-related protein in the yeast *Saccharomyces cerevisiae*, is the first mitochondrial fission protein to be identified and studied (Bleazard et al., 1999; Sesaki and Jensen, 1999; for review, see Bui and Shaw, 2013; Table I). Dnm1 polymerizes into a helical ring-like structure that wraps around and constricts the site of dividing mitochondria by their GTPase activity. Dnm1 is recruited from the cytosol through interaction with the adaptor protein Mdv1 (and its paralog Caf4), which interact with Dnm1 and Fis1. Fis1 is a small, mitochondrial outer membrane tail-anchored protein. Animal mitochondrial fissions also are implemented by

ADVANCES

- Mitochondrial fission in Arabidopsis and in liverwort requires a eukaryotic conserved dynamin, DRP3, and a plant-specific protein ELM1. FIS1 in yeast is essential for mitochondrial division, but FIS1 homologues in animals and plants do not appear to have similar roles.
- Plant mitochondria undergo constant fission and fusion. Fusion-dominant elongated mitochondria appear during germination and regeneration, and in shoot apical meristems, all of which involve rapid organellar DNA synthesis.
- Plant mitochondrial genomes appear to have circularly permutated sequences, giving the appearance of circular structures, but they exist mainly as linear molecules. Individual mitochondria have only portions of the genome.

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Table I. *Homologous relationships of mitochondrial fission and fusion factors in selected eukaryotes*

The table is reproduced and modified from Arimura and Tsutsumi (2016) with permission. IM, Inner membrane; OM, outer membrane. Dashes indicate that homologs are not present or not reported.

Process	Organisms					Features, Functions, and Localization (Estimated)
	Yeast *S. cerevisiae*	Mammal *Homo sapiens*	Seed Plant Arabidopsis	Liverwort *M. polymorpha*	Red alga *C. merolae*	
Fission	Dnm1	Drp1	DRP3A, DRP3B	DRP3	Dnm1	Cytosolic, forming ring, GTPase
	Fis1	Fis1	AtFIS1A, AtFIS1B	FIS1	CMQ197C	OM, for localization of DRPs? (through Mdv1 in yeast)
	Mdv1, Caf4	–	–	–	Mda1	OM outer surface, interact with DRP and Fis1 (in yeast)
	–	Mff	–	–	–	OM, for localization of DRP to fission sites
	–	MiD49 and MiD51	–	–	–	OM, for localization of DRP to fission sites
	–	–	ELM1, At5g06180	ELM1	–	OM outer surface, interact with DRP3
	–	–	PMD1, PMD2	–	–	OM, independent of DRP3, Rosidae specific
	–	–	–	–	FtsZ1	Matrix, GTPase, polymerizes into ftsZ ring
	–	–	–	–	ZED	Matrix, bacterial cell division ZapA homolog, forms ring
Fusion	Fzo1	Mfn1, Mfn2	–	–	–	OM, for OM fusion, GTPase
	Mgm1	Opa1	–	–	–	IM and intermembrane space, for IM fusion, GTPase
	Ugo1	–	–	–	–	OM, for OM fusion, interacts with Fzo1 and Mgm1, OM
	Clu1	Clu	FMT	FMT	–	Cytosol and OM, deficiency causes clusters of mitochondria

Dnm1 orthologs, Drp1s. Sequences homologous to Fis1 also are found and well conserved in many eukaryote genomes. Orthologs of Mdv1/Caf4, the adaptors between Dnm1 and Fis1, are present in yeast but are rare or absent in other eukaryote genomes. In animals, Fis1 homologs had originally been thought to be required for the localization of Drp1 to the fission sites, as is the case with Fis1 in yeast. However, instead of Fis1, two other mitochondrial outer-membrane proteins (Mff and MiD49/51) were later found to have some redundant but major roles in the relocalization of Drp1 from the cytosol to mitochondrial fission sites (Otera et al., 2010; Palmer et al., 2011, 2013; Zhao et al., 2011).

The unicellular red alga *Cyanidioschyzon merolae* is an excellent experimental model for mitochondrial division because each cell has a single mitochondrion, whose divisions are linked to the host cell division cycle. For studies of mitochondrial division, the cell cycle in *C. merolae* cells can be synchronized. The proteins that form mitochondrial division rings have been purified and identified (Yoshida et al., 2006; Nishida et al., 2007). *C. merolae* has two mitochondrial division proteins, an FtsZ homolog (CmFtsZ1) and a ZapA-like protein (ZED), that are similar to bacterial cell division proteins (Takahara et al., 2000; Yoshida et al., 2009). The genes for both of these proteins have been lost in the genomes of yeast, animals, and green plants. ZED and FtsZ1 make rings in the matrix beneath the inner membrane. Then, another protein (Mda1) and a mitochondrial dividing ring, a structure that is observed by electron microscopy, localize to the outer surface and start to constrict the mitochondrion. In the last step, CmDnm1, which is a dynamin-related protein, forms a ring around the constricted site, and the CmDnm1 ring with the mitochondrial dividing ring cuts the mitochondrion into two pieces (Nishida et al., 2003; for review, see Kuroiwa et al., 2008; Kuroiwa, 2010).

MITOCHONDRIAL FISSION PROTEINS IN ARABIDOPSIS AND THE LIVERWORT *MARCHANTIA POLYMORPHA*

Arabidopsis (*Arabidopsis thaliana*) has well-conserved Dnm1/Drp1 orthologs, DRP3A and DRP3B (formerly known as ADL2A/2B), that are involved in mitochondrial fission (Arimura and Tsutsumi, 2002; Arimura et al., 2004a; Logan et al., 2004; Fujimoto et al., 2009). They localized to the prefission and postfission sites of mitochondria (Fig. 1A). Disruption of these genes causes a decrease in mitochondrial number and the formation of elongated, network-shaped mitochondria. Two homologs of the outer-membrane anchored protein Fis1, AtFis1a (Bigyin) and AtFis1b, also were found, and disruption of their gene expression in Arabidopsis caused the mitochondria to become larger (Scott et al., 2006; Zhang and Hu, 2009). Another factor in mitochondrial fission was identified from forward genetic screening and mapping of Arabidopsis mutants with elongate mitochondria (Arimura et al., 2008).

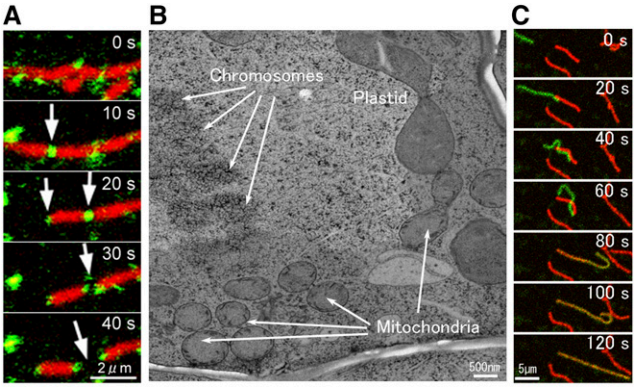

Figure 1. Plant mitochondrial fission and fusion. A, Mitochondrial fission (arrows) with a dynamin-related protein, DRP3A (in green; GFP-DRP3A), which localizes to predividing and postdividing sites of mitochondria (in red; stained by MitoTracker) in a tobacco cultured BY-2 cell. Images were made by Dr. Masaru Fujimoto. B, Cell cycle-dependent divisions of organelles. The image shows aligned chromosomes, a dividing plastid, three pairs of divided mitochondria, and a dividing mitochondrion in a part of a dividing Arabidopsis root cell in metaphase. The electron micrograph was made by Dr. Mayuko Sato, Mayumi Wakazaki, and Dr. Kiminori Toyooka. The scale bar is approximate. C, Mitochondrial fusion in an onion (*Allium cepa*) epidermal cell in which mitochondrial fission was disrupted by coexpression of a dominant-negative type of DRP3B(K56A). Mitochondria matrices were labeled with a photoconvertible fluorescent protein, Kaede, causing some mitochondria to be green and others to be red. Fusion results in a yellow color.

These mutants, called *elm1* (*elongate mitochondria*) mutants, were defective in a gene that we called *ELM1*. The ELM1 protein is a plant-specific factor that localizes on the surface of the mitochondrial outer membrane, where it is required for the localization of DRP3A (Arimura et al., 2008). In a review (Logan, 2010), *elm1* was suggested to be allelic to a previously screened mutant, *nmt* (*network mitochondria*; Logan et al., 2003), although the sequence of the responsible gene in *nmt* was not determined and the two mutants were not tested for allelism.

DRP3A, *FIS1a*, and *ELM1* have additional homologs (*DRP3B*, *AtFIS1b*, and *At5g06180*, respectively) in the Arabidopsis genome, which complicate their analysis. We recently used another model plant, the liverwort *M. polymorpha*, whose genome has single copies of *DRP3*, *ELM1*, and *FIS1* (Nagaoka et al., 2017). Liverworts are considered as one of the earliest diverging distant land plant lineages (Wickett et al., 2014). Therefore, an examination of the characteristics of mitochondria in liverworts could help us to understand the commonalities and differences of mitochondrial fission factors among land plants. *M. polymorpha drp3* and *elm1* knockout mutants have highly elongated, networked mitochondria, and their growth is severely retarded (Nagaoka et al., 2017). The authors suggested that DRP3 and ELM1 were used for mitochondrial fission before the diversification of these two plants. However, the *M. polymorpha fis1* knockout mutant grew almost as well as the wild type, and its mitochondria show little or no elongation. Therefore, *FIS1* may have little or no involvement in mitochondrial fission in *M. polymorpha* epidermal cells, as is the case in mammals (Otera et al., 2010; Palmer et al., 2011, 2013; Zhao et al., 2011). Although Arabidopsis *fis1* mutants are reported to have larger mitochondria (Scott et al., 2006; Zhang and Hu, 2009), their phenotypes seemed to be less obvious than those in *drp3* and *elm1* mutants. The conservation of *FIS1* in animals, yeast, and plants raises the possibility that these proteins have other common roles not directly linked to mitochondrial fission with dynamins.

Two other mitochondrial outer-membrane proteins (peroxisomal and mitochondrial division factor1 [PMD1] and PMD2) were shown to be involved in the proliferation of mitochondria (Aung and Hu, 2011). PMD1 has a coiled-coil motif and a C-terminal transmembrane domain. PMD2 localizes specifically to mitochondria. PMD1 and PMD2 act in a nonredundant manner and in a manner independent of DRP3 and FIS1.

Mitochondrial fission is thought to be required for the inheritance and maintenance of mitochondria during the host cell division. Figure 1B shows four synchronized mitochondrial divisions that probably occur in a dividing Arabidopsis root cell in metaphase. In tobacco (*Nicotiana tabacum*) BY2 suspension cells, AtDRP3A/3B is activated by phosphorylation at metaphase and DRP3A/3B is partially degraded by ubiquitination at interphase (Wang et al., 2012). Overexpression of an outer-membrane-anchored ubiquitin protease, UBP27, changed mitochondrial morphology and reduced the mitochondrial association of DRP3 (Pan et al., 2014b), although it remains unclear whether UBP27 interacts directly with and deubiquitinates DRP3.

OTHER FACTORS, STRUCTURES, AND PHENOMENA RELATED TO MITOCHONDRIAL FISSION

Cardiolipins are phospholipids that are found mainly in the mitochondrial inner membrane. Cardiolipins are required for the localization or function of fission and fusion proteins in yeast and mammalian cells (for review, see Frohman, 2015). In an Arabidopsis cardiolipin synthase mutant, the mitochondria were enlarged and DRP3A/3B did not localize properly to mitochondria (Pan et al., 2014a).

In yeast and mammalian cells, the ER also appears to have a role in mitochondrial fission (Friedman et al., 2011). Mitochondrial fission occurs at the sites where ER tubules contact mitochondria and mediate constriction before the localization of dynamin-related proteins. Recent double-labeling studies of mitochondria and ER in plants have led to speculation that similar processes may occur in Arabidopsis (Jaipargas et al., 2015) and *Physcomitrella patens* (Mueller and Reski, 2015).

BOX 1. Effects of a Shift in the Balance between Fission and Fusion of Plant Mitochondria

The balance could be affected by either the up-regulation of one process or the down-regulation of the other.

When fission is dominant:

- Mitochondrial size change: increase of number and decrease of each size, which results in altered mobility and cellular distribution.
- Secured mitochondrial transmission during host cell division.
- Division of labor (e.g. genetic vault and labor; Logan, 2006).
- Secured mitochondrial autophagy: selective elimination of degenerative mitochondria via autophagic digestion.
- Secured respiratory activity: higher energy supply in cells that demand ATP.

When fusion is dominant:

- Decrease of number and increase of each size.
- Sharing internal molecules.
- For recombination and starting replication of DNA molecules?
- Contribution to the horizontal gene transfer?
- In cells with higher energy demands?

In the *adl2a* (*drp3a*) Arabidopsis mutant, matrix-localized fluorescent proteins revealed the presence of thin tubules called matrixules protruding from mitochondria (Logan et al., 2004). Similar tubules called stromules were observed to protrude from plastids (Köhler et al., 1997). We found similar structures in Arabidopsis by double labeling the mitochondrial outer membrane and the matrix (Yamashita et al., 2016b). These structures, which we named mitochondrial outer-membrane protrusions (MOPs), extended several micrometers from the main bodies of mitochondria (Yamashita et al., 2016b). MOPSs, as the name implies, tend to be composed more of the mitochondrial outer membrane than the matrix, whereas matrixules are extensions of the matrix. However, some MOPs have a limited amount of matrix. MOPs also were observed to bridge mitochondria (Yamashita et al., 2016a). The tips of some of the MOPs were pinched off to form smaller pieces that resembled mitochondria-derived vesicles in mammalian cells (for review, see Sugiura et al., 2014). MOPs and mitochondria-derived vesicle-like structures also were seen in the *drp3a/3b* double mutant (Yamashita et al., 2016b), suggesting that DRP3-dependent mitochondrial division is not required for their formation. These structures were more frequently observed in senescent leaves, suggesting that they were related to the degradation of mitochondria (Yamashita et al., 2016b). During leaf senescence in individually darkened leaves in Arabidopsis, the number of mitochondria decreases (Keech et al., 2007), probably by autophagy (Li et al., 2014, Li and Vierstra, 2014). The remaining mitochondria retain their motility and respiration activity until the last step of leaf senescence (Keech et al., 2007; Keech, 2011; Ruberti et al., 2014; Chrobok et al., 2016). These mitochondria are thought to provide energy and metabolites for degrading the cell components and relocating them to other younger parts of the plant (Keech et al., 2007; Keech, 2011; Ruberti et al., 2014; Chrobok et al., 2016).

Mitochondrial fission could serve not only to divide mitochondria but also to diversify them. Mitochondrial divisions without equal distribution of nucleoids were reported in tobacco cultured cells (Arimura et al., 2004b). Unequal division of mitochondria with different (lower and higher) membrane potentials was observed in mammalian cells (Twig et al., 2008). Mitochondria with low membrane potential (i.e. depolarized mitochondria) would not be able to fuse, resulting in their isolation from the healthy mitochondria that are continually undergoing fission and fusion. The isolated (nonfunctional) mitochondria are thought to be degraded specifically by bulk autophagy or mitophagy (mitochondria-specific autophagy; Twig et al., 2008). The mammalian *Parkin* and *Pink1* genes, the causal genes for familial Parkinson's diseases, were shown to have a role in mitophagy of degraded mitochondria (Narendra et al., 2008). Because plants have fission-fusion cycles of mitochondria and undergo autophagy, they may have a similar mechanism for mitochondrial quality control.

Different types of mitochondria coexist in germinating seeds (Dai et al., 1998; Logan et al., 2001) and individual senescence-induced leaves (Keech et al., 2007). On shorter time scales (e.g. seconds), individual mitochondria are depolarized spontaneously by an influx of calcium ions and then are immediately repolarized in several seconds (Schwarzländer et al., 2012). These changes, called pulsing, are observed much more frequently under stress conditions (Schwarzländer et al., 2012). At every time point, the mitochondria in each cell seem to have different physiological statuses and components.

MITOCHONDRIAL FUSION

Mitochondrial fusion in animals and yeast is carried out by two kinds of GTPases, Mfn/Fzo1 and Opa1/Mgm1, both of which are distantly related to dynamins (Chan, 2012; Mishra and Chan, 2016; for review, see Willems et al., 2015). Mfn1/Fzo1 and Opa1/Mgm1 are anchored in the outer and inner membranes, respectively, and contribute to the fusions of their respective membranes to those of another mitochondrion. Although mitochondrial fusion clearly occurs in plants

(Fig. 1C; Arimura et al., 2004b; Sheahan et al., 2005), functional orthologs of dynamin-related proteins or other proteins involved in mitochondrial fusion have not been found so far in any plant. Arabidopsis has homologs of Mfn1/Fzo1 and Opa1/Mgm1, but the homologs most similar to these dynamin-related proteins are DRP3A/3B, which are apparently mitochondrial division-type dynamins. Another factor structurally similar to Mfn1/Fzo1, named FZL (for FZO-Like), is unrelated to mitochondrial fusion but was shown to localize in chloroplasts and contribute to the organization of thylakoids (Gao et al., 2006). Thus, the factors and molecular mechanisms directly involved in mitochondrial fusion in plants seem to be very different from those in animals and fungi. Forward genetic screenings for mutants of mitochondrial fusion (Logan et al., 2003; Feng et al., 2004) were unsuccessful, possibly because fusion mutants are more lethal than fission mutants, as is the case in yeast (Bleazard et al., 1999; Sesaki and Jensen, 1999). In Arabidopsis, the *fmt* (*friendly mitochondria*) mutant has aggregations of portions of mitochondria in each cell (Logan et al., 2003). FMT protein has been proposed to mediate the intermitochondrial association before fusion (El Zawily et al., 2014).

The evidence for mitochondrial fusion in plants was reported indirectly over 30 years ago (Belliard et al., 1979). In cybrids (cytoplasmic hybrids), which are plants regenerated from the fusion of cells of two species, the mitochondrial genomes were found to have new restriction enzyme fragment patterns, suggesting that recombination occurred between the parental mitochondrial genomes (Belliard et al., 1979). On the other hand, genetic recombination was not observed in plastids (i.e. only one of the parental genomes was observed). The mitochondrial genome of a cybrid between two plants in the nightshade family (tobacco and henbane [*Hyoscyamus niger*]) had more than 35 regions of recombination between homologous sequences, ranging from 100 to 9,000 bp (Sanchez-Puerta et al., 2015). Recombination and coexistence of the mitochondrial genes from different species also were observed in (1) plants generated from the junction of grafted tissues (Fuentes et al., 2014; Gurdon et al., 2016), (2) parasitic plants whose mitochondrial genomes contained some host plant fragments (Davis and Wurdack, 2004; Sanchez-Puerta et al., 2017), and even (3) host plants, in which fragments of parasitic plant mitochondrial genomes were observed in the host mitochondrial genomes (Mower et al., 2004). Furthermore, horizontal gene transfer between nonrelated plants is more frequently observed in mitochondrial genomes than in nuclear and plastid genomes (Bergthorsson et al., 2003). The mitochondrial genome of the flowering shrub *Amborella trichopoda* includes the entire mitochondrial genome of a moss (Rice et al., 2013; Taylor et al., 2015). At least in some cases, mitochondrial fusion might have contributed to horizontal gene transfer between plant mitochondrial genomes (Rice et al., 2013).

MITOCHONDRIAL DYNAMICS IN DIFFERENT ENVIRONMENTS AND ORGANS

When Arabidopsis plants were kept in the dark for 1 week without Suc, mitochondria in the mid cells of the hypocotyl became longer, but after the mid cells were exposed to light or Suc, their mitochondria fragmented (Jaipargas et al., 2015). Low oxygen also caused mitochondrial elongation and network formation in suspension-cultured tobacco cells (Van Gestel and Verbelen, 2002) and in Arabidopsis leaf mesophyll cells (Ramonell et al., 2001). Recently, transient fragmentation of mitochondria in Arabidopsis leaf epidermal cells was observed after cold treatment (Arimura et al., 2017). Such environmentally induced changes in mitochondria are probably due to changes in the balance between fission and fusion. In mammalian studies, cells with higher energy demand tend to have more elongated mitochondria, and on the other hand, cells with higher energy supply have more fragmented mitochondria (for review, see Liesa and Shirihai, 2013). The findings that plant mitochondria are longer in the dark without Suc (Jaipargas et al., 2015) or in low oxygen (Ramonell et al., 2001; Van Gestel and Verbelen, 2002) and fragmented in the light or with Suc (Jaipargas et al., 2015) seem to be consistent with such mammalian observations (i.e. mitochondrial fragmentation is associated with an increased energy supply).

Mitochondria have a characteristic cup shape or a long, stretched-rod shape, in the egg cells in *Pelargonium zonale* (Kuroiwa et al., 1996) and *Zea mays* (Diboll and Larson, 1966), but have relatively numerous small particle or peanut-like shapes in rice (*Oryza sativa*; Takanashi et al., 2010). Their DNA amounts in mitochondria in egg cells increase compared with those in pollen or leaf cells in species in which mitochondrial DNAs are maternally inherited (for review, see Nagata, 2010). During fertilization, mitochondria in the sperm cells in pollen were found to enter an egg cell and a central cell of a female gamete in Arabidopsis (Matsushima et al., 2008). However, mitochondrial DNA in pollen degraded before fertilization, suggesting that such DNA degradation apparently contributes to the maternal inheritance of mitochondrial genomes (Matsushima et al., 2008; Nagata, 2010; Wang et al., 2010). The DNA was reported to be degraded by an Mg^{2+}-dependent exonuclease, DPD1 (Matsushima et al., 2011). However, the pollen from *dpd1* mutants, in which organelle DNAs were clearly detected, could not cause paternal inheritance of mitochondrial DNA to the progeny, suggesting that some other mechanism suppresses the paternal inheritance of organelle DNA, independent of DPD1. Another protein for mitochondrial dynamics, a MIRO1 GTPase, is known to be essential for the proper mitochondrial morphology and distribution in pollen tube and in early embryogenesis, and the knockout of this gene causes lethality (Yamaoka and Leaver, 2008; Yamaoka et al., 2011).

Elongated or networked mitochondria also have been observed in some organs or developmental stages.

In germinating Arabidopsis seeds, even just after imbibition, mitochondria first develop an inner-membrane potential and respiration ability, gradually acquire mobility, and then undergo transient elongation and branching (Paszkiewicz et al., 2017). At this latter stage (i.e. at the elongation and branching stage), the percentage of mitochondria with DNA increased. Long and branched tentaculate mitochondria were observed to surround the nucleus in the shoot apical meristems (but not in the root meristems) of Arabidopsis (Seguí-Simarro et al., 2008) and cucurbit plants (watermelon [*Citrullis vulgaris*] and muskmelon [*Cucumis melo*]; Bendich and Gauriloff, 1984). In tobacco, Arabidopsis, and *Medicago* spp. protoplasts before the first cell division, mitochondria underwent a transient massive fusion, resulting in elongated mitochondria (Sheahan et al., 2005). None of these cells with elongate mitochondria (germinating cells, shoot apical meristems, and culture-starting protoplasts) could be considered as somatic cells. Rather, they are meristem-like cells that are the sites of organellar DNA replication just before massive cell proliferation (Rose and McCurdy, 2017). Plant organellar DNA synthesis amplifies DNA copy numbers by 2 or more orders of magnitude during the early few cell divisions, while the nuclei duplicate their genome only once in each cell cycle (Kuroiwa et al., 1992; Suzuki et al., 1992; Fujie et al., 1994). These transient mitochondrial fusions might be related to mitochondrial DNA replication in preparation for the following massive cell proliferation (see below).

MAINTENANCE OF MITOCHONDRIAL DNA WITH DYNAMIC MITOCHONDRIA

In plant somatic cells, the number of mitochondrial genomes is less than the number of mitochondria (Bendich and Gauriloff, 1984; Kuroiwa et al., 1992; Preuten et al., 2010; Wang et al., 2010). During the latter part of leaf development or leaf senescence, the integrity and amount of organellar DNA decrease (for review, see Oldenburg and Bendich, 2015). One of the nucleases identified originally in pollen (DPD1 nuclease) is suggested to contribute to the degradation of organellar DNA during leaf senescence too (Sakamoto and Takami, 2014). Each Arabidopsis mesophyll cell has more than 500 mitochondria (Sheahan et al., 2005) and about 50 copies of mitochondrial genomes (Preuten et al., 2010; Wang et al., 2010). Some mitochondria seem to have no nucleoids (DNA-protein complexes in mitochondria; Arimura et al., 2004b; Takanashi et al., 2006; Wang et al., 2010). Many of the mitochondria with nucleoids have only a part of the mitochondrial genome (Kuroiwa et al., 1992; Satoh et al., 1993; Takanashi et al., 2006; Wang et al., 2010). The shortage of genetic information in the individual mitochondrion is thought to be overcome by constant fission and fusion (Arimura et al., 2004b; Logan, 2006).

Plant mitochondrial genomes are much larger (from around 200 kb to more than 10 Mb) than the 16.5-kb single circular molecules of human and animal mitochondrial genomes (Kubo and Newton, 2008; Sloan, 2013; Gualberto and Newton, 2017). Two different structures have been proposed for plant mitochondrial genomes. They are usually depicted as circles, called master circles. Homologous sequences in different regions actively recombine, resulting in a multipartite genome structure consisting of many kinds of DNA (Palmer and Shields, 1984; Kubo and Newton, 2008). The circular structure was deduced from the mapping of sequences or restriction fragment length polymorphisms. However, the physical structure of mitochondrial DNA is now thought to be mostly linear with

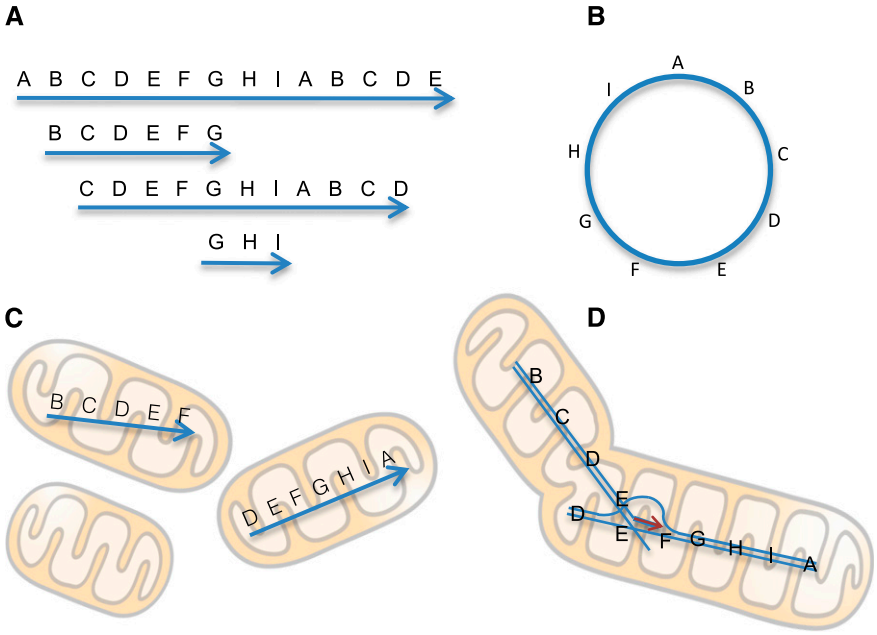

Figure 2. Mitochondrial genome structures, mitochondrial fusion, and DNA replication. A, In vivo variable-length linear DNA structures with circularly permutated sequences. B, A master circle of the mitochondrial genome deduced from these sequences, although such circles are probably rare. C, Individual mitochondria having zero or some portions of the genome as linear DNA molecules. Double-strand breaks that form linear DNA fragments might be generated by respiration-induced reactive oxygen species. D, Mitochondrial fusion provides an opportunity for recombination of DNA fragments. DNA replication by recombination-dependent replication (RDR) may start at this stage. Fusion is dominant where organellar DNA synthesis is active, such as in shoot apical meristems, and during germination and regeneration.

various sizes, some even longer than the genome size (Oldenburg and Bendich, 1996; Backert and Börner, 2000; Sloan, 2013; Cheng et al., 2017). Such linear structures are thought to have random fragments of a long head-to-tail concatemer sequence of the mitochondrial genomes (Fig. 2; Bendich, 1993; for review, see Sloan, 2013). For example, if the circular genome has the sequence ABCDE, the linear molecules would have sequences like ABCDEABCDEABCDEA or a mixture of ABC, DEABCD, BCDEA, and so on. Such structures that are physically linear but with a circularly permutated sequence are similar to those of some viruses and bacteriophages. The replication of plant mitochondrial genomes has been suggested to be similar to one of the replication mechanisms of T4 bacteriophages, called RDR (Backert and Börner, 2000; Maréchal and Brisson, 2010). At first, a T4 bacteriophage starts DNA replication from Ori sequences inside a host cell at the early stage of infection, generating one or a few copies (Kreuzer and Brister, 2010). However, when the copy number reaches about 20, replication depends mainly on RDR. In RDR, DNA synthesis starts from the 3′ end of each linear molecule, with other molecules acting as templates. In other words, both 3′ ends of each linear molecule function as primers for DNA synthesis, resulting in massive amplification of the genome (Broker and Doermann, 1975; Mosig, 1998; Kreuzer, 2000; Kreuzer and Brister, 2010). An advantage of RDR for circularly permutated linear molecules is that the DNAs are able to replicate without telomeres, which are necessary for the replication of the linear DNAs in nuclear chromosomes. Replication origins have not yet been identified in plant mitochondrial genomes. If they do not exist, replication might occur only by RDR.

Cheng et al. (2017) recently observed the physical structures of DNA molecules isolated from mitochondria during the early germination of mung bean (*Vigna radiata*) seeds. At first, the DNA was in the form of simple linear molecules with sizes shorter than the genome size. Subsequently, during stratification, imbibition, and germination, the DNAs became more branched and longer, gradually acquiring sizes longer than the genome. Finally, the DNAs reverted to simple short linear molecules. These changes may reflect the gathering and recombination of short linear molecules at the start of RDR during germination. Similar changes in mitochondrial DNA structures have been observed in the growth cycles (but not cell cycles) of cultured tobacco cells in pioneering studies by Oldenburg and Bendich (1996; for review, see Oldenburg and Bendich, 2015) and *Chenopodium album* cells (Backert and Börner, 2000). Rapid amplification of organellar DNAs has been observed around meristems (Kuroiwa et al., 1992; Fujie et al., 1994) and at specific stages, such as during germination (Cheng et al., 2017) and at the start of cell culture (Satoh et al., 1993). The rapid amplification of organellar DNA independent of the host cell cycle also seems to be like that in phages that use RDR for DNA synthesis.

As stated above, fusion-dominant tentacle-shaped mitochondria have been observed in shoot apical meristems, and transient mitochondrial fusions have been observed in germinating cells and culture-starting protoplasts. These are the regions during the organellar DNA amplifications. A model of the relationship between mitochondrial fusion and DNA replication is shown in Figure 2. The mitochondria in plant somatic cells have linear DNA molecules, each containing a portion of the genome. Before the start of consecutive cell divisions (e.g. before the start of culture or the start of germination), mitochondria fuse to bring their DNA molecules together. The ends then undergo homologous recombination to start replication by RDR and to obtain the sequences that their genome lacks.

CONCLUSION

Many questions remain about the molecular factors and mechanisms of mitochondrial fission and fusion in plants (see Outstanding Questions box). Since the discovery of the balance between mitochondrial fission and fusion and the identification of molecular factors in yeast and mammals more than 15 years ago, research in this area has expanded enormously. Some of the new fields of study include mitophagy, mitochondrial quality control, submitochondrial structures, sites of contact with other organelles, cell death, and Parkinson's and other neurodegenerative diseases. Plant mitochondria have many characteristics that distinguish them from other mitochondria, such as smallness, abundance, fast movement, and roles in photorespiration and cytoplasmic male sterility. These plant-specific

OUTSTANDING QUESTIONS

- What is the role of FIS1 homologs in plants? Do FIS1 homologs in animals have roles similar to those in plants?
- Do plant mitochondria with different genomes have different functions (division of labor)?
- What proteins are directly involved in mitochondrial fusion in plants? How do they achieve fusions of the inner and outer membranes?
- Do plants, like animals, have mitochondrial quality control mechanisms, such as specific autophagy (mitophagy) of degraded mitochondria?
- How do plant cells faithfully replicate at least one complete mitochondrial genome for every daughter cell?

characteristics present many challenging and exciting opportunities for future research.

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