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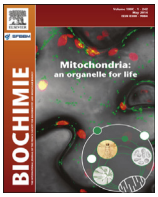

Review

The plant mitochondrial genome: Dynamics and maintenance

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ABSTRACT

Plant mitochondria have a complex and peculiar genetic system. They have the largest genomes, as compared to organelles from other eukaryotic organisms. These can expand tremendously in some species, reaching the megabase range. Nevertheless, whichever the size, the gene content remains modest and restricted to a few polypeptides required for the biogenesis of the oxidative phosphorylation chain complexes, ribosomal proteins, transfer RNAs and ribosomal RNAs. The presence of autonomous plasmids of essentially unknown function further enhances the level of complexity. The physical organization of the plant mitochondrial DNA includes a set of sub-genomic forms resulting from homologous recombination between repeats, with a mixture of linear, circular and branched structures. This material is compacted into membrane-bound nucleoids, which are the inheritance units but also the centers of genome maintenance and expression. Recombination appears to be an essential characteristic of plant mitochondrial genetic processes, both in shaping and maintaining the genome. Under nuclear surveillance, recombination is also the basis for the generation of new mitotypes and is involved in the evolution of the mitochondrial DNA. In line with, or as a consequence of its complex physical organization, replication of the plant mitochondrial DNA is likely to occur through multiple mechanisms, potentially involving recombination processes. We give here a synthetic view of these aspects.

1. Introduction

Mitochondria are key players in plant development, fitness and reproduction. Their contribution to energy production, metabolism and cell homeostasis relies on the performance of their own genetic system that makes them semi-autonomous. As in other organisms, the mitochondrial genome in plants encodes a series of essential polypeptides that build up the complexes of the oxidative phosphorylation chain, together with nuclear-encoded subunits. But plant mitochondrial DNAs (mtDNAs) have remarkable features that distinguish them from their animal and fungal counterparts. In particular, higher plants harbor large mtDNAs that are highly variable in size and structural organization. On top of that, in many plant species, mitochondria contain various forms of plasmids that replicate independently from the main chromosome. In most plant species, the mtDNA gene sequences evolve very slowly, as compared to animal mtDNA sequences, and point mutations are rare. It is believed that this is because plant mitochondria contain an active DNA recombination system that allows copy correction of mutations. Indeed, numerous studies have shown that plant mitochondrial genomes undergo extensive and high frequency homologous recombination (HR). Such processes make plant mtDNA prone to rearrangements. When not lethal, mtDNA mutations/rearrangements can generate severe phenotypes or cause cytoplasmic male sterility (CMS). Hence the requirement for efficient DNA repair and maintenance pathways in a context where oxidative pressure, replication defaults or environmental hazard generate base modifications and strand breaks. Finally, mitochondrial genome dynamics generates heteroplasmy, with alternative mtDNA configurations coexisting with the main mtDNA. Segregation of alternative mitotypes significantly contributes to the rapid evolution of the plant mtDNA structure. The present review addresses these issues, with special emphasis on the specificities of the plant mitochondrial genetic system.

2. Plant mitochondrial DNA structure and organization

2.1. Genome size and content

The structure of higher plant mitochondrial genomes has a number of unique features. Whereas most animals possess circular mtDNAs of 15–17 kb in size, the mitochondrial genomes of plants

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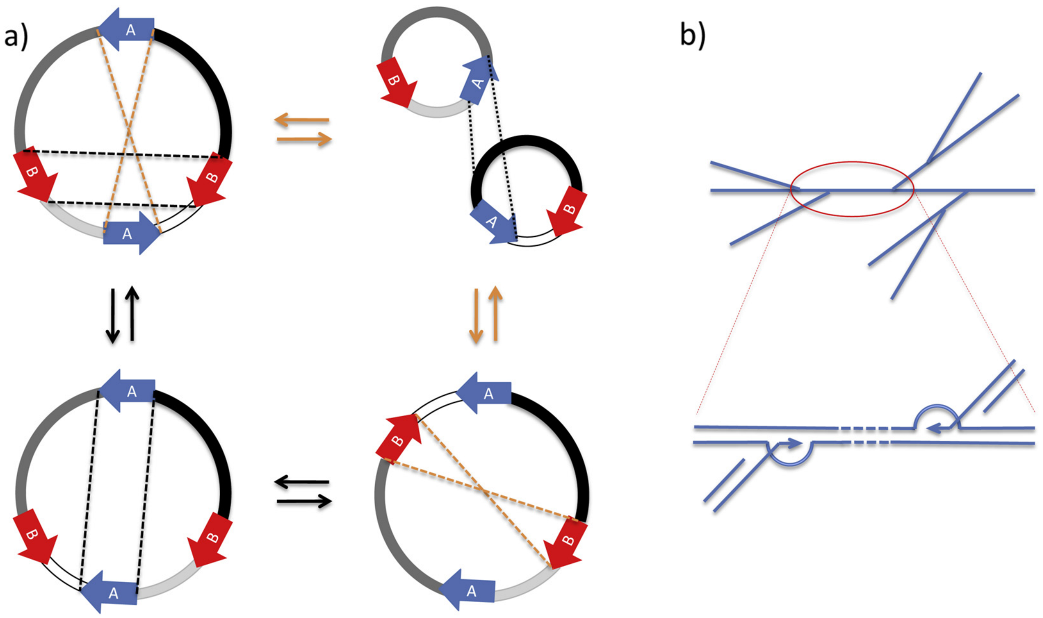

Fig. 1. Circular and linear models of the mtDNA structure in plants. The dynamics of the mtDNA of plants allow several models. a) A circular genome model representing the different organisations of the mtDNA of *A. thaliana* ecotype C24. The two pairs of large, frequently recombining repeats (A and B) and their orientations are represented by blue and red arrows. The different parts of the genome are colored in a range of gray scale. Intramolecular recombination events are represented with dashed lines, and in orange, recombination leading to subgenomic molecules. Dotted line shows possible intermolecular recombination. b) The mtDNA has been observed as predominantly constituted by a complex array of linear molecules. Branched forms of the mtDNA could be intermediates of recombination-dependent processes: 3′ single-stranded sequences resulting from the recession of double-strand breaks can invade homologous double-stranded DNA, forming a D-loop and leading to the establishment of replication forks.

are much larger and differ greatly in size, even between very close species or within species [1,2]. They commonly range between 200 and 750 kb in angiosperms [1], but with a tremendous further extension in some lineages. As an example, proliferation of dispersed repeats, expansion of existing introns and acquisition of sequences (including sequences of nuclear, plastid, viral and bacterial origin) account for the expansion of the cucumber (*Cucumis sativus*) mitochondrial genome into a tri-chromosome structure with components of 1556, 84, and 45 kb in size [3]. Sequencing of the mtDNA from two *Silene* species with exceptionally high mutation rate revealed enormous mitochondrial genomes of 6.7 (*Silene noctiflora*) and 11.3 (*Silene conica*) megabase-pairs resulting from massive proliferation of non-coding content [4]. Moreover, these genomes are distributed into a large number of circular chromosomes: 59 for *S. noctiflora* and over 128 for *S. conica*. These chromosomes range themselves in size from 44 to 192 kb. As a comparison, the more typical, slowly evolving mitochondrial genome of *Silene latifolia* accounts for a single chromosome of 253 kb [4]. Remarkably, plant mitochondrial genomes are large but their ploidy appears to be low. Whereas thousands of mtDNA copies can be present in a mammalian cell, much lower mtDNA levels were detected in plants. Preuten et al. [5] analyzed the ploidy of several individual mitochondrial genes in various samples of *Arabidopsis thaliana*, *Nicotiana tabacum* and *Hordeum vulgare*, using real time quantitative PCR. The copy numbers of the investigated genes both differed from each other and varied greatly between organs or during development, with the highest estimates around 280 copies per cell for the *atp1* gene in mature leaves. This was actually less than the mean number of mitochondria per cell, which was around 450 in protoplasts derived from mature leaves. Thus, individual mitochondria in plants may contain only part of the genome or potentially no DNA [5].

Despite their large sizes, land plant mtDNAs do not contain a significantly greater number of genes than mitochondrial genomes of other lineages. The known genes usually range between 50 and 60, while multiple *cis*- or *trans*-spliced introns and large intergenic regions complete the genomes. Protein genes in plant mtDNAs encode subunits of the oxidative phosphorylation chain complexes but also proteins involved in the biogenesis of these complexes, as well as several ribosomal proteins. First to be entirely sequenced, the 367 kb *A. thaliana* mtDNA (ecotype C24) codes for 32 proteins, 3 ribosomal RNAs (5S, 18S and 26S rRNAs) and 22 tRNAs [6], while the 16.5 kb human mtDNA codes for 13 proteins, 2 rRNAs (12S and 16S) and 22 tRNAs [7]. With a total of 57 genes versus 37, this makes a 1.5 fold difference in gene content for a 22 fold difference in size. Identified genes represent a minor part of the plant mtDNA content (10% in *A. thaliana*), whereas the major part (60% in *A. thaliana*) has no recognizable origin and function [6]. Introns and duplications expand (8% and 7% in *A. thaliana*, respectively), as well as integrated nuclear and plastid sequences (5% as a whole in *A. thaliana*). Further putative open reading frames of significant length can be detected, which also add up to 10% of the genome in *A. thaliana* [6].

Differences in gene content among plant species are also not linked to genome size. The large cucumber mtDNA carries just 4 more protein genes than the *A. thaliana* genome within 1.3 megabase of extra sequence [3]. On the other hand, it can be noted that the cucumber mitochondrial genome has integrated 7 more tRNA genes of plastid origin, whereas 2 tRNA genes of authentic mitochondrial origin present in other species are missing. Similarly, the 253 kb mtDNA of *S. latifolia* and the 11.3 megabase mtDNA of *S. conica* carry the same reduced set of 25 protein genes and, while the *S. latifolia* mtDNA contains 9 tRNA genes, that of *S. conica* has only 2 [4]. The intergenic sequences with no recognizable origin or function thus represent 91.5% (10.3 megabase) of the *S. conica* mitochondrial genome. With the emergence of second-generation sequencing technologies, the number of completed plant mitochondrial genome sequences rapidly increased in the last few years,