Involvement of plastid, mitochondrial and nuclear genomes in plant-to-plant horizontal gene transfer

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Abstract

This review focuses on plant-to-plant horizontal gene transfer (HGT) involving the three DNA-containing cellular compartments. It highlights the great incidence of HGT in the mitochondrial genome (mtDNA) of angiosperms, the increasing number of examples in plant nuclear genomes, and the lack of any convincing evidence for HGT in the well-studied plastid genome of land plants. Most of the foreign mitochondrial genes are non-functional, generally found as pseudogenes in the recipient plant mtDNA that maintains its functional native genes. The few exceptions involve chimeric HGT, in which foreign and native copies recombine leading to a functional and single copy of the gene. Maintenance of foreign genes in plant mitochondria is probably the result of genetic drift, but a possible evolutionary advantage may be conferred through the generation of genetic diversity by gene conversion between native and foreign copies. Conversely, a few cases of nuclear HGT in plants involve functional transfers of novel genes that resulted in adaptive evolution. Direct cell-to-cell contact between plants (e.g. host-parasite relationships or natural grafting) facilitate the exchange of genetic material, in which HGT has been reported for both nuclear and mitochondrial genomes, and in the form of genomic DNA, instead of RNA. A thorough review of the literature indicates that HGT in mitochondrial and nuclear genomes of angiosperms is much more frequent than previously expected and that the evolutionary impact and mechanisms underlying plant-to-plant HGT remain to be uncovered.

Keywords: angiosperm; horizontal gene transfer; chimeric; gene conversion; parasitic

Introduction

Horizontal gene transfer (HGT), the exchange of genetic material between non-mating organisms, is widespread in prokaryotes and, to a lesser extent, in unicellular eukaryotes [1–3]. Most of the evidence for HGT in eukaryotes comes from genes derived from bacteria, describing transfers between phagotrophic, unicellular eukaryotes and their bacterial prey [1,4]. In the last few years, horizontal transfer in multicellular eukaryotes has been increasingly reported [5–8]. Plants in particular have been recognized as donors and targets of HGT involving the three domains of life [5,9]. Of the genetic exchanges reported between multicellular eukaryotes, the frequency of HGT between flowering plants is surprisingly elevated [10–16]. Most cases of plant-to-plant HGT comprise mitochondrial sequences (introns or genes) that were transferred to the mitochondrial genome of another angiosperm [15–20].

This review focuses on plant-to-plant HGT events involving the three DNA-containing compartments in plant cells,

with emphasis on transfers between angiosperm mitochondria, especially those involving host-parasite relationships.

## HGT among plants: impact in each of the three genomes

Horizontal transfers among angiosperms has been increasingly recognized and slowly accepted by the scientific community. HGT between two plants may involve any of the three DNA-containing compartments, though certain genomes are more prone to genetic exchanges than others (Fig. 1).

Mitochondria-to-mitochondria HGT

Angiosperm mitochondrial genomes (mtDNAs) engage in HGT remarkably often compared to all other organellar genomes and most nuclear genomes (Fig. 2) [10–12,15–18,20–27]. Several properties of plant mitochondria and their genomes contribute to this propensity for HGT. Plant mitochondria are capable of importing DNA or RNA [28,29] and readily undergo fusion [30,31]. Furthermore, plant mtDNAs have an active homologous recombination system [32,33] that is reflected in their structurally dynamic

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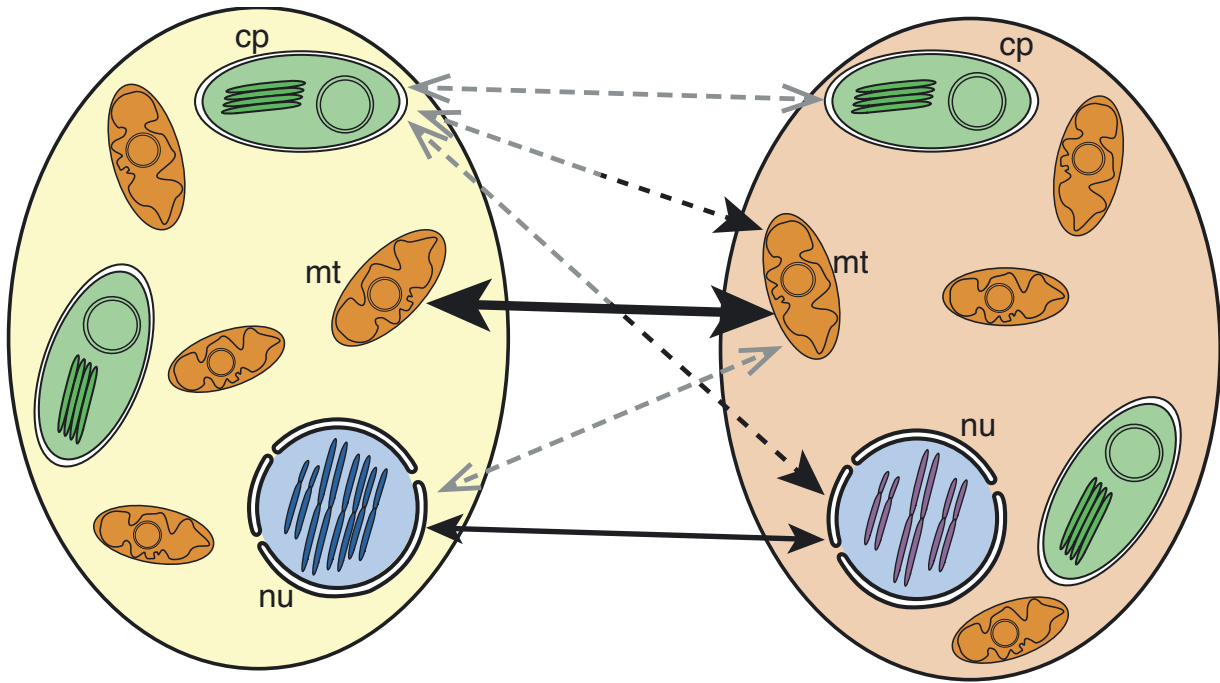
Fig. 1 Horizontal gene transfers (HGT) between two plant species. Solid black lines depict the number of reported HGT events between those cell compartments. Thicker lines indicate more frequent events than thinner lines. Dashed black and grey lines depict putative transfers or lack of evidence for such transfers, respectively. mt: mitochondria; cp: chloroplast; nu: nucleus.

and rearranged genomes [34–36], allowing for a high frequency of intracellular gene transfer (IGT) of chloroplast and nuclear DNA into the mitochondria [37,38]. Plant mitochondrial genomes have generally very low substitution rates [39,40] and relatively large and variable sizes (from 222 kb to 11.3 Mb) [41–43]. Regardless of the genome length, plant mtDNAs encode only 37–67 genes surrounded by long intergenic regions of, mostly, unknown origin with no similarity to any other sequenced DNA [41]. These large intergenic regions facilitate the acquisition of foreign DNA without disruption of the expression of native genes.

In most cases, foreign genes acquired by plant mitochondria are mitochondrial genes donated by another angiosperm species via mitochondria-to-mitochondria horizontal transfer (Fig. 1). Only rarely foreign genes from a non-land plant [44] or from prokaryotes [15] were found in plant mtDNAs.

The most frequently documented case of HGT in multicellular eukaryotes, and the first one to be reported for plants, involves an intron present in the mitochondrial gene *cox1* of flowering plants, which had spread among many diverse angiosperms via an estimated 73 separate plant-to-plant transfer events (Fig. 2) [16,45]. This constitutes the most rampant case of horizontal transmission known among multicellular, if not all eukaryotes, with multiple lines of evidence strongly supporting the highly frequent horizontal transfer of this intron [16,19,45,46].

In the past two decades, more than 24 different angiosperm species were found to contain foreign genes in their mitochondrial genomes (not counting *cox1* intron transfers). From those, two well-studied angiosperm lineages stand out for their extraordinarily large numbers of foreign

mitochondrial genes (Fig. 2). The complete sequence of the ~3.9 Mb mtDNA of *Amborella trichopoda* revealed the presence of two mitochondrial genome equivalents from other
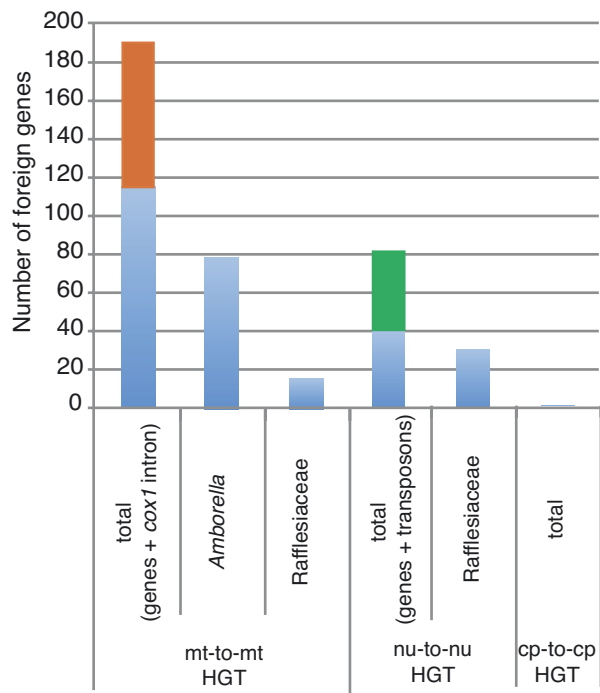
Fig. 2 Number of foreign genes transferred by HGT between nuclear (nu), chloroplast (cp) and mitochondrial (mt) genomes of angiosperms, respectively. It is possible that several foreign genes were transferred together in a single HGT event. Blue, orange and green bars represent coding genes, *cox1* introns and transposable elements, respectively.

angiosperms (~80 mitochondrial genes; Fig. 2), one from mosses and three from green algae – all acquired by HGT [15]. Foreign genes in *Amborella* mtDNA are predominantly pseudogenes, while the native homologs remain intact and presumably functional [15]. A next-generation sequencing study on three endophytic holoparasites of the angiosperm family Rafflesiaceae uncovered a minimum of 16 foreign mitochondrial genes (Fig. 2) presumably obtained from their host plants in a number of, both ancient and recent, independent horizontal transfers [47]. In contrast to *Amborella*, a fraction of the foreign genes appear to be functional in the parasite and may have replaced the native genes via homologous recombination [47].

Most foreign mitochondrial transfers, including those in *Amborella* and holoparasites within the Rafflesiaceae, were inferred to occur as genomic DNA, with no evidence of RNA-transfer followed by retrotranscription [15,23,24,47]. Evidence for this comes from the presence of introns, long tracts of foreign mitochondrial sequences encompassing genes and intergenic regions, or unedited cytidine nucleotides at sites known to undergo RNA editing in plant mitochondria.

Nuclear genes

An increasing number of reports on plant nuclear genes horizontally transferred to the nuclear genome of a foreign plant have been published (Fig. 1). Nuclear-to-nuclear transfers involve both genes [22,48–52] and transposable elements [14,53,54] exchanged between angiosperms (Fig. 2) and also between bryophytes and ferns [55]. The most striking example of nucleus-to-nucleus HGT involves the holoparasitic plant *Rafflesia cantleyi* (Rafflesiaceae), whose nuclear genome contains a minimum of 31 genes obtained from its plant host, *Tetrastigma rafflesiae* (Vitaceae) [22]. The foreign genes, transferred as DNA, are expressed and many of them are probably functional [22].

Given their high abundance in nuclear genomes and their ability to move and become functional in a new host genome [56], transposable elements are often maintained in the recipient genome after being horizontally transferred [57]. Therefore, transposable elements, and other forms of selfish DNA, are expected to be the predominant type of DNA transferred among eukaryotes once enough comparative data is available across this domain of life. Nuclear-to-nuclear plant HGT likely occurs in a higher (even extremely higher) frequency than we are able to detect today given the paucity of plant nuclear genome sequences available for comparison. It is likely that most nuclear transfers are non-functional and therefore transient, disappearing before detection.

Plastid genes

Chloroplast genomes (cpDNAs) from photosynthetic eukaryotes are only rarely involved in HGT. This is likely not an underestimation because cpDNAs have been thoroughly sequenced across the diversity of the eukaryotic tree of life and phylogenetic analyses of plastid genes intensively performed [5,58]. Even though it is an unusual event, a few confirmed cases of foreign plastid genes in algal cpDNAs exist [59–62], whereas no convincing evidence is available for HGT between angiosperm plastid genomes and only

few examples are available for horizontal transfers of plastid genes involving different compartments in two plant species (Fig. 1).

Angiosperm plastid genomes are highly resistant to acquiring genes from other cellular compartments, as well as from other organisms. Two examples of IGT into to the plastid genome of angiosperms include a mitochondrial fragment and possible retrotransposon in the cpDNA of *Daucus carota* [63,64] and a 2.4 kb mitochondrial segment transferred to an intergenic spacer in the cpDNA of the milkweed *Asclepias syriaca* [65]. The limited acquisition of sequences from other compartments or other organisms by angiosperm chloroplasts relates to their particular properties: the absence of plastid fusion or uptake mechanisms, and the reduced plastid genome with minimal intergenic regions. However, once a foreign DNA fragment enters the plastid, this DNA can be incorporated into the cpDNA by homologous recombination [35,66].

There are a few examples of horizontally transferred plastid genes found in angiosperms, but it is not always clear in which cellular compartment they reside or whether the transfer occurred directly from the chloroplast genome of the donor (Fig. 1). A cp-to-cp HGT of the plastid gene *rps2* identified in parasitic angiosperms of the genus *Phelipanche* [13] cannot be ruled out (Fig. 2). However, the recently sequenced plastid genome of *P. ramosa* [67] showed that the foreign copy of *rps2* is not present in its cpDNA. In other cases, foreign plastid genes were located in the mitochondrial genomes of the fabid *Phaseolus vulgaris* [68], the early-diverging angiosperm *Amborella trichopoda* [15], the holoparasite *Sapria himalayana* [47], and in the Solanaceae *Hyoscyamus niger* [69]. The route by which these plastid genes entered the recipient mitochondria remains unknown, but given the frequency of mt-to-mt HGT, it has been proposed that plastid genes were first transferred to the mitochondrial genome within the donor plant by IGT and then horizontally transferred via mitochondrial HGT. Likewise, the presence of foreign plastid genes in the nuclear genome of the holoparasite *Rafflesia lagascae* (Rafflesiaceae) has been described [70]. IGT from the chloroplast to the nucleus of the host followed by nucleus-to-nucleus HGT could have occurred.

A thorough study of the three genomes of plant parasites in the holoparasitic plant family Rafflesiaceae indicated that mitochondrial HGT is more frequent than nuclear HGT in these host-parasite relationships, with no strong evidence for plastid-to-plastid transfers [47].

Mechanisms of HGT among plants

A long-standing question in plant evolutionary biology relates to the mechanisms of gene transfer among angiosperms. Postulated natural mechanisms that facilitate HGT include direct transmission involving parasitic or epiphytic plants, tissue grafts, illegitimate pollination, or indirect transmission via a vector intermediate, such as virus, bacteria, insects, and fungi [5,11,12,16,18,21,25,71]. These proposed mechanisms can explain the horizontal transfer across the three cellular compartments (Fig. 1).

The frequency of HGT events between plant mitochondria is biased towards host-parasite systems [51], even though more than 55 mitochondrial genomes from free-living angiosperms have been sequenced and only a draft assembly of the mtDNA of the parasitic plant *Rafflesia lagascae* is available [70]. This bias suggests the importance of direct physical contact as a mechanism for plant-to-plant HGT. Parasitic plants form vascular connections with the host plant that allow transfer of water, nutrients, proteins, mRNAs, and pathogens [72–74]. Even though the exchange of genomic DNA in host-parasite relationships has not been shown, it is not hard to imagine that DNA fragments can occasionally travel through the haustorium.

A few studies focused on an experimental model of HGT through grafting. Natural grafting may enable HGT between two plants [9,15]. In a recent study, three HGT events were observed on axillary shoots of grafted cotton plants, but the genetic variations were not stably inherited across three generations [75]. Two research groups recreated HGT by grafting two lines or species of tobacco and found that nuclear genomes, entire chloroplasts and organellar DNA travelled across the graft junction through plasmodesmata [71,76–78]. These observations demonstrate that plant grafting can result in the exchange of DNA from the three DNA-containing compartments.

Regardless of how mitochondrial genes physically reach a recipient plant, a mitochondrial-fusion model for HGT in plants has been proposed [15]. According to this model, plant mitochondrial HGT occurs by capture of entire mitochondria from foreign, donor plants, followed by fusion of native and foreign mitochondria, and then recombination of their genomes. The fusion of foreign and native mitochondria seems to be restricted to phylogenetically related taxa, such as those that belong to the Viridiplantae, due to putative incompatibilities in the mechanism of mitochondrial fusion with other lineages [15]. This restriction would explain the almost exclusive occurrence of foreign mitochondrial genes from plants integrated in angiosperm mitochondrial genomes.

To study the cellular and molecular processes of plant-to-plant transfers, experimental assays recreating HGT events have been undertaken [69,71,76–78]. In one study, the effects of mitochondrial fusion followed by mtDNA recombination were assessed in a cybrid (cytoplasmic hybrid) plant between two Solanaceae [69]. It has been known for decades that mitochondrial genomes recombine after protoplast fusions between two plant species [79]. Recently, the complete sequence of the mtDNA of a cybrid plant indicated that the two parental genomes recombined intensely after protoplast fusion to form an intensely chimeric mtDNA that encodes a single allele of most of its genes, including nine chimeric genes [69].

Outcomes of HGT in plants

The evolutionary implications of HGT in land plants are still largely unknown. Examples of putative adaptive roles of HGT in plants have been recently reviewed [7,8]. Most cases involve genes obtained from bacteria [80–83], viruses [81]

and fungi [6,81], and reside in the plant nuclear genome. Only a handful of nuclear genes were acquired through plant-to-plant HGT [22,48,55], and a few of those represent novel, functional genes in the recipient genome that may lead to ecological adaptations [48,55].

Horizontal transfers between flowering plant mitochondria generally results in the initial duplication of a mitochondrial gene, in which two different copies (the foreign and the native) co-exist for some time in the recipient mtDNA. Over time, this initial situation may have different outcomes (Fig. 3):

(*i*) deletion of the foreign gene copy: in this case, the process of HGT goes unseen (silent HGT);
(*ii*) deletion of the native gene copy once the foreign copy becomes functional in the recipient genome (replacement HGT);
(*iii*) both copies are maintained in the recipient mtDNA (duplicative HGT);
(*iv*) homologous recombination and gene conversion between the two copies lead to a single functional chimeric copy of the gene (chimeric HGT).
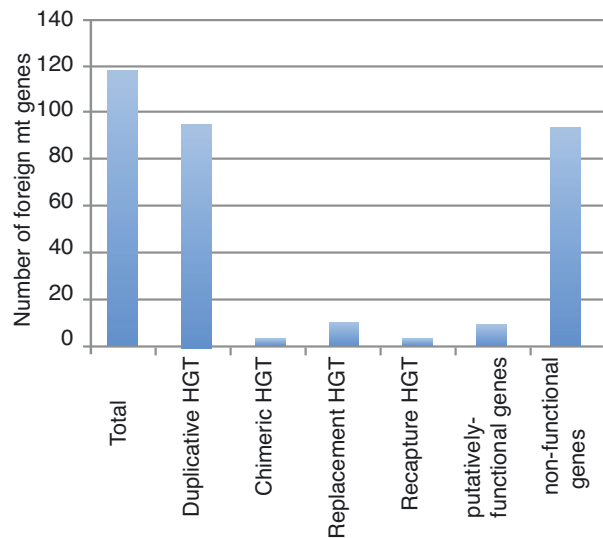
Fig. 3 Number of foreign genes acquired by HGT between angiosperm mitochondria. The total number of foreign mitochondrial (mt) genes are subdivided by HGT type and whether they are putatively functional or not (genes with undetermined functional status are not shown). Non-functional genes include those foreign genes that are pseudogenes, not significantly expressed, or not fully edited.

Foreign mitochondrial genes are commonly found as extra genes, coexisting with native mitochondrial copies of the same gene (duplicative HGT). In those cases, transferred genes usually become pseudogenes while the native alleles remain functional. Occasionally, the foreign and native copies may undergo continuous or discontinuous gene conversion, leading to one or two chimeric gene copies, but often with a single functional allele (chimeric HGT). The functional chimeric gene may translate into a protein with novel residues in the recipient genome. This increase in genetic diversity through HGT could impact the evolution of plant

mitochondria [20,23]. A duplicative HGT and differential gene conversion (DH-DC) model has been postulated [23] in which gene conversion of foreign (from other organisms or organelles) and native genes generates mitochondrial genetic variability. A striking case of chimeric HGT has been recently discovered in an extensive survey of the mitochondrial *cox1* gene across almost 900 angiosperms (Sanchez-Puerta et al., unpublished). A divergent short region of the gene *cox1* has most likely been horizontally acquired and gene converted about 20 times during the evolution of the angiosperms examined. The chimeric *cox1* genes are the only *cox1* alleles present in the mtDNAs analyzed and are therefore most likely functional (Sanchez-Puerta et al., unpublished).

In a few cases, a gene that has been functionally transferred to the nuclear genome of the recipient angiosperm is reacquired by its mtDNA via HGT (recapture HGT). On the other hand, introducing a novel gene into angiosperm mitochondria is uncommon because plant mitochondria contain a reduced gene repertoire, unless it brings a gene that was, in turn, acquired from another cell compartment, such as a plastid or nuclear gene (as discussed in the previous section).

In the plant mtHGTs described to date, no clear evidence for an adaptive gain of function was found. It is likely that genetic drift rather than selection has fixed mitochondrial HGT events. Most foreign genes are non-functional pseudogenes due to truncation of the gene or presence of premature stop codons, while those that have a complete open reading frame may not be significantly expressed or efficiently edited (Fig. 3). About nine cases have been reported where chimeric [10,23] or foreign [47] genes are full-length, transcribed and edited in the recipient mtDNA suggesting they are functional (plus the 20 chimeric *cox1* genes described above; unpublished results). The chimeric or foreign functional genes do not show any apparent increase in fitness due to the genetic diversity introduced by HGT. On the contrary, HGT could impair overall gene expression through gene conversion with a foreign allele or when two alleles (a foreign and a native) are simultaneously present and functional in a single mitochondrion [69].

Conclusions

Little is known about the functional implications of horizontal gene transfer among plants, in addition to the real incidence of nuclear and mitochondrial HGT in the plant kingdom. This phenomenon raises a number of questions regarding the extent and mechanism of the exchange of genetic material between plants, its consequences for transgene containment, and the co-evolution of organellar DNA with the nuclear genome. The current accelerated generation of comparative genomic data will contribute to quickly uncover evolutionary aspects of plant-to-plant HGT, such as the expected prevalence of nuclear HGT.

Competing interests
No competing interests have been declared.

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