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ACHIEVEMENTS IN HORIZONTAL GENE TRANSFER STUDIES IN PARASITIC PLANTS

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Horizontal gene transfer (HGT) is a process that allows genetic material to flow between even distantly related organisms. It is primarily observed in bacteria and protists but also in different lineages of eucaryotes. The first HGT cases in plants were discovered at the beginning of the 21st century and have been intensively studied ever since. Researchers have placed particular emphasis on the plant kingdom, especially parasitic plants. This review presents the current state of knowledge about this phenomenon in plants, with a special focus on parasitic plants.

Among the described factors facilitating HGT, close physical contact between organisms is believed to be one of the most important. It is noted especially in the case of parasitism and similar relationships. For that reason, reported occurrences of this phenomenon in holoparasites, hemiparasites, and mycoheterotrophic plants are compared. The mechanisms responsible for HGT in plants still remain unclear, however, the studies described here suggest that both DNA and RNA may play a role as a carrier in that process. Also, the transfer between genomes of different organelles in the cell, intracellular gene transfer (IGT), and its relationships with HGT are described. The occurrence of the HGT and IGT phenomena concerning different genomes: nuclear, mitochondrial, and plastid is discussed in the review. Finally, some future areas of research in the field are proposed.

Keywords: evolution, HGT, horizontal gene transfer, hosts, parasitic plants.

INTRODUCTION

Horizontal gene transfer (HGT), also known as lateral gene transfer, is usually described as a process in which genetic material is passed between organisms in other ways than from parent to offspring, which can be regarded as "vertical". Contrary to crossing, in which generally only DNA from closely related species may be joined in one organism, HGT allows pieces of genomes or even whole genomes to move between organisms belonging to distant evolutionary lines. The phenomenon of horizontal gene transfer was initially described in bacteria and protists and is believed to be the most common and the main source of novel genes in these groups (Griffith, 1928; Freeman, 1951; Lawrence and Roth, 1996; Ochman et al., 2000; Koonin et al., 2001; Gogarten et al., 2002; Gogarten, 2003; Keeling and Palmer, 2008).

Later studies found many examples of its occurrence and importance in the evolution of multicellular eukaryotes, including fungi, plants, and animals (Koonin et al., 2001; Soucy et al., 2015; Wickell and Li, 2020). Considering plants, several evolutionary improvements were probably realized via HGT, for example, the adaptation of ferns to low-light conditions (Li et al., 2014) and high insect resistance (Li et al., 2018), C_4 photosynthesis in the grass lineage *Alloteropsis* (Christin et al., 2012), or even the synthesis of flavonoids and lignin, which was crucial for adaptation to terrestrial environments (Emiliani et al., 2009).

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Previous studies on HGT were conducted on particular genes and sequences, but the rapid development of new techniques such as NGS (Next-Generation Sequencing) enabled genome-wide insight into the HGT process (examples described below).

The main aim of our paper is to summarize and review the current state of studies and knowledge about the occurrence and significance of horizontal gene transfer with a focus on parasitic plants.

HGT AND LIFESTYLE OF PLANTS

Unicellular organisms are more susceptible to incorporation of foreign genes and more likely to pass them on to the next generations because when a gene is introduced into the cell's genome it is simply transferred to the descendant cells/organisms. It is more complicated in multicellular organisms because the transferred sequence must be included in the germline (at least when sexual reproduction is involved). Inheritance of the transferred gene is more likely when spores, zygotes, embryos, etc. are exposed to the environment, as was proposed in the "weak-link model" by Huang (2013). In other cases, as described below, other types of close contact between organisms may create opportunities for transfers.

One of the most striking examples of HGT in plants was found in *Amborella trichopoda* which has an enormous, 3.9-megabase mitochondrial genome. Detailed studies revealed traces of many HGT events; most of its mitochondrial genes have one or more copies acquired from green algae, mosses, and other angiosperms. Furthermore, according to the authors, many of these transfers were large, including whole mitochondria followed by mitochondrial fusion and genome recombination (Bergthorsson et al., 2004; Rice et al., 2013). The authors associate the reason why *A. trichopoda* is such a good receptor for alien-genes with the lifestyle of the plant. Growing in tropical forests, it is frequently covered by many species of epiphytes, including bryophytes. The close plant-to-plant contact, as in the case of epiphytism, may facilitate the transfer of genes between them (Bergthorsson et al., 2004).

Recent papers focusing on grasses revealed multiple HGT events between species belonging to that group. Possible mechanisms facilitating the movement of genes between grasses propounded by the authors include large pollen dispersal (that may result in contact of pollen tubes, belonging to different species, growing on the same stigma) and direct contact of plants growing close together, especially by root-to-root inosculation in perennial plants (Dunning et al., 2019; Hibdige et al., 2020).

Indeed, considering conditions enabling the transfer of genetic material between multicellular organisms belonging to different species, close physical contact between them seems to be an important factor. Such a close connection is observed also between parasites and their hosts. Cell-to-cell contact with their hosts is the main reason why parasites are regarded as especially probable recipients (less frequent donors) of genes (Wijayawardena et al., 2013). Except for the small group of endophytic holoparasites that grow inside their hosts, parasitizing plants usually develop outside their hosts and are connected to them by haustoria. In some cases, they infiltrate the host's roots in other cases - its shoots (Davis and Xi, 2015). For some species, parasitism is indispensable for survival and development (obligatory parasites), in other cases it is optional (facultative parasites). Due to the type of dependence on their hosts, parasites may be divided into hemiparasites and holoparasites. The first group includes photosynthesizing plants that uptake mainly water and mineral nutrients from the host, however, they may also get some organic substances. The latter have lost the ability of photoautotrophy, so due to lack of chlorophyll, they are not green and depend on their hosts for water, mineral nutrients, and organic ingredients. The uptake of organic substances requires a direct connection to the living cells of the host, which may also facilitate the movement of genetic material fragments between cells and, consequently, organisms. For that reason, holoparasites seem to be a good subject for identifying HGT cases and studying the mechanisms of the process (Davis and Xi, 2015; Schneider et al., 2018).

Plant parasites use different parts of their bodies to connect with the hosts, which may decide whether the transferred genes become inherited by the next generations. Yang et al. (2019) in their research, observed a higher rate of HGT events in *Cuscuta* (Convolvulaceae) compared to holoparasitic Orobanchaceae, and proposed that it may be caused by the type of connection between the parasite and the host. Whereas Orobanchaceae are connected by haustoria attached to roots, *Cuscuta* forms haustorial stem connections. This is an important difference because in the latter case, there is a shorter distance from the haustoria to flowers, and consequently, to cells that form gametes. The presence of the transferred gene in the gamete is indispensable to pass them on to the next generations of parasites. Although Orobanchaceae form haustoria at the early stages of their development (Joel et al., 2013) and so, initially the distance between the connection and the apical meristem, which eventually builds the stem and flowers is not distant, this timeframe may be too short to be as effective as the permanently close placement of haustoria and floral meristematic tissues observed in *Cuscuta*.

Mycoheterotrophs are another group of heterotrophic plants. They do not obtain nutrients from other plants directly like parasites, but via a fungus. Despite HGT being very common in parasitic plants and the recent publication of a number of mitochondrial and nuclear genomes of mycoheterotrophs (see references in Petersen et al., 2020; Shtratnikova et al., 2020), there is almost no indication of horizontal gene transfer in those plants. Because they both share some morphological features and have a limited or nonexistent ability of photosynthesis, plant parasites and mycoheterotrophs are often grouped together. The nature of their interaction and connection with the host is, however, profoundly distinct. Mycoheterotrophs do not form any structures similar to haustorium that would integrate them with the host plant tissues. There is also no evidence of transfer of RNA through mycorrhizal connections (Shtratnikova et al., 2020), contrary to the bidirectional flow of nucleic acids observed in parasitic plants (Kim and Westwood, 2015).

Mycoheterotrophic plants' genomes could, in theory, contain transfers of foreign genetic material from both the fungus and the plant, that is the indirect donor of carbon. However, because in that case the plant to plant HGT would require two plant-fungal HGTs, it seems unlikely that mycoheterotrophs will show higher rates of foreign plants DNA than the autotrophic plants (Petersen et al., 2020). HGT from a fungus requiring just a single step event seems more probable, although, for years the only examples of fungal HGT found in the angiosperms have involved the *cox1* intron (Vaughn et al., 1995) and some linear plasmids (see references in Sinn and Barrett, 2020). This may be explained by possible barriers between angiosperms and fungi, as was suggested by Richards et al. (2009). A new paper published by Sinn and Barrett in 2020 describes the first example of a genome-scale HGT between fungi and angiosperm plants (ancestors of the orchids). Interestingly, the fungi that were most probably the donors of the horizontally transferred genes were parasites themselves and not the species involved in mycoheterotrophic relations with orchids. Sinn and Barrett propose that while mycoheterotrophic organisms are establishing mycorrhizal connections, they may have a diminished defense response, which may make them less resistant to fungal infection and increase the probability of HGT.

Fungi are also frequently involved in symbiotic relationships with plants, which opens another opportunity for different plant species that share the same fungal symbiont. This is one of the possible explanations of HGT between parasitic Loranthaceae and the fern *Botrychium virginianum*, suggested by Davis et al. (2005).

Grafting is another method of a direct connection between plants, which may facilitate the movement of genetic material. First, the possibility of transfer was reported for plastids (Stegemann and Bock, 2009; Stegemann et al., 2012), and later, experiments on *Nicotiana* grafts showed that nuclear genomes accompanied by plastid and mitochondrial ones may also be transferred between species, eventually even leading to new species formation (Fuentes et al., 2014).

Finally, it has been suggested that a close evolutionary relationship, which is important for genetic compatibility, may play an important role in HGT and the fixation of alien sequences (Skippington and Ragan, 2012; Soucy et al., 2015).

HGT BETWEEN PARASITIZING PLANTS AND THEIR HOSTS

Parasitism in angiosperms has evolved independently at least 11 (Barkman et al., 2007) or (most probably) even 12 times (Westwood et al., 2010; Zervas et al., 2019; Nickrent, 2020). Genetic studies of plant parasites are frequently focused on plastid and mitochondrial genomes. Plastid genomes often show signs of degradation, especially of genes connected with photosynthesis, and mitochondrial genomes, as explained below, are regarded as good receivers of alien DNA (Wicke et al., 2013; Cusimano and Wicke, 2015; Arimura, 2018). Because parasitic plants are believed to be a promising model for HGT studies due to their intimate contact with hosts, horizontal gene transfer in that group has been the subject of numerous studies since the first decade of the 21st century (Davis and Xi, 2015). Below we summarize the studies on horizontal gene transfer in different species and groups with the focus on hemiparasites and holoparasites.

Hemiparasites are not as dependent on their hosts as holoparasites and uptake less substances from them. Consequently they may be considered as less frequent HGT recipients. Several studies seem to confirm this hypothesis. About a decade ago Yoshida et al. (2010) used large-scale expressed sequence tag analysis to search for grass-like genes in the nuclear genome of *Striga hermonthica*. This member of the Orobanchaceae family is a parasite of species belonging to the Poaceae family, including crops such as *Sorghum bicolor* and *Oryza sativa*. They found a gene (*ShContig9484*) that encodes a 448-amino acid protein with an unknown function that was probably transferred from sorghum or a related grass species to the common ancestor of *S. hermonthica* and *S. gesnerioides*. This sequence was probably transferred as mRNA, then reverse transcribed to DNA, and finally integrated into the nuclear genome.

Five years later, a complex analysis of the mitochondrial genome of hemiparasitic *Viscum scurruloideum* was completed and published by Skippington et al. (2015). The authors described many interesting features of that mitogenome, including its reduction and gene loss. They also tried to find sequences that could have been horizontally transferred, but the only evident case was the *cox1* intron, which was probably acquired recently.

The mitochondrial *cox1* intron is a sequence frequently found in different species as transferred from other lineages. It was probably originally transferred from fungi and then transferred many times independently in different angiosperm lineages (Sanchez-Puerta et al., 2008; Sanchez-Puerta, 2014). Detailed studies on parasitic plants showed that it is common in the examined species (with few exceptions), but not related to the parasitic style of life (Barkman et al., 2007; Fan et al., 2016).

Also in 2015, the mitogenome of *V. album* was published (Petersen et al., 2015). The results indicate that in this species the mitochondrial genome is also very divergent and multiple genes were lost. However, later studies (Skippington et al., 2017) on *V. album* revealed evidence of a recent acquisition of *matR* and *ccmB* genes via horizontal gene transfers, probably from two different donors (Ericales and Santalales).

In 2016, a study reported HGT findings in four members of Orobanchaceae with an increasing degree of parasitic dependence, including two hemiparasites: *S. hermonthica* and *Triphysaria versicolor* (Yang et al., 2016). The study, which focused on the nuclear genome, showed that transfers were found in all tested species, and what is especially interesting, as host dependence increased, so did the number of transfers. More of them were identified in the holoparasite *Phelipanche aegyptiaca* (32 cases) than in the obligate hemiparasite *S. hermonthica* (10); in the facultative hemiparasite *T. versicolor* two transfers were found, and only one case in the free-living *Lindenbergia*.

In a similar study, two holoparasites (*Orobanche minor* and *Aeginetia indica*) and three facultative parasites (*Pedicularis keiskei*, *Phtheirospermum japonicum*, and *Melampyrum roseum*) from the Orobanchaceae family were examined to check for HGT cases in the nuclear genome (Kado and Innan, 2018). Whereas in holoparasites, a total of 106 transferred genes was found (22 in *O. minor* and 84 in *A. indica*), there were no traces of HGT in the facultative parasites. In addition, the latest analysis of the non-nuclear genomes of *Aeginetia indica* conducted by Choi and Park (2021) showed that the *atpI* gene within the mitochondrial genome and the *atpH* gene within the plastid genome were obtained via HGT, with the host plant as the probable *atpI* donor. They also found intracellular transfer of two genes (*ndhB* and *cemA*) from the plastid genome to the mitogenome.

Other studies focused on holoparasite *Cuscuta* where multiple transfers were detected through analyses of genomes and transcriptomes (Vogel et al., 2018; Yang et al., 2019) (see below).

Because parasites uptake nutrients from hosts, it could be assumed that genes are only transferred from host to parasite. However, the opposite direction is also possible. In the early years of HGT studies which focused on plants, such a phenomenon was reported for two transfers of the *atp1* gene to *Plantago* from their parasites *Cuscuta* and *Bartsia* (Mower et al., 2004). More detailed studies found two more mitochondrial genes (in addition to the previously found *atp1*), *atp6* and *matR*, transferred from *Cuscuta* to the common ancestor of *Plantago coronopus*, *P. macrorhiza*, and *P. subspathulata* (Mower et al., 2010). The authors suppose that these genes were transferred as a rather long DNA string, maybe even a complete genome, and shortly afterwards the genes degenerated into pseudogenes. Likewise, studies on the evolution of the *Geranium* mitogenome revealed many genes that derived via HGT from parasitic plants (mainly *Cuscuta* and *Bartsia*) (Park et al., 2015).

DILEMMA: RNA OR DNA?

Considering the possible mechanisms of horizontal gene transfer, one of the most fundamental questions is what kind of genetic information carrier is responsible for HGT. Generally, there are two possibilities: DNA and (m)RNA. In the first case, fragments of DNA strands or even whole genomes (see *Amborella* case above) are transferred from plant to plant and integrated with the recipient's genome. The second possibility is a movement of mRNA from donor to recipient, followed by reverse transcription and insertion in the target DNA.

The key to understanding the HGT mechanism, at least in the case of host-parasite interaction, may be the observation of which molecules are transferred through the host-parasite connection. Such studies were reported for several parasites, such as *Cuscuta* (*C. reflexa*, *C. pentagona,* and *C. campestris*) (Haupt et al., 2001; David-Schwartz et al., 2008; Westwood et al., 2009; Kim and Westwood, 2015; Shahid et al., 2018) where, besides other molecules, many mRNAs were found.

Another way to resolve the "DNA or RNA?" question is to analyze the genes acquired by HGT. Some of their features may indicate their origins. The clue in this case may be the presence of introns. If a gene is found as an undivided strain of exons and was composed of exons and introns in the donor genome, then it may be regarded as reverse-translated mRNA. Other features may also indicate the mRNA-origin of a gene, like traces of poly-A tail, such as in the *ShContig9484* sequence in *Striga hermonthica* (Yoshida et al., 2010), or enhanced nucleotides by mRNA edition.

Later studies on *Cuscuta* (Yang et al., 2019), which based on genome sequencing, indicate that due to the presence of introns, at least functional genes (108 cases) received by HGT were transferred via DNA, rather than as retroprocessed RNA. More examples of DNA-mediated transfers were reported, e.g., for *Rafflesia cantleyi* (Xi et al., 2012), species of *Orobanche*, *Phelipanche,* and *Cuscuta* (Zhang et al., 2013; Zhang et al. 2014) and some Orobanchaceae members (Yang et al., 2016; Kado and Innan, 2018).

ROLE OF HGT IN PARASITE-HOST INTERACTION

Studies on gene transfers between organisms inevitably lead to another important question: Do sequences acquired by HGT play an adaptive role? That question may be formulated more specifically when relationships between hosts and parasites are considered: Can sequences obtained by parasites play an important role in their parasitism?

The transcriptome analysis of *R. cantleyii* (Xi et al., 2012) revealed that this holoparasite probably acquired several dozens of transcribed genes from its host *Tetrastigma rafflesiae*. In the authors' opinion, the raised rate of unidirectional HGT could indicate that it may be beneficial for the parasite. They hypothesize that host-originated genes that are expressed in *Rafflesia* may be engaged in "genomic deception" that aims to minimize the ability of the host to detect the parasite and mount a defense against it. This is undoubtedly an interesting idea, however, as the authors suggest, it needs further confirmation.

One of the most interesting discoveries in this field was made by Yang et al. (2019) in their study on *Cuscuta campestris*. They found that many of the genes acquired by HGT are expressed in haustoria and are involved in the defense response and amino acid metabolism. That may indicate that horizontal transfer plays an adaptive role in parasite-host interaction. Also, their observations, together with previous results reported by Shahid et al. (2018), imply that HGT may be a source of mobile small RNAs that influence the host's gene expression. Such observations correspond with other reports regarding RNA flow between pathogens and hosts that have been observed, even between kingdoms. Generally, gene silencing via RNAs in pathogen-hosts relationships has already been described for many organisms, including plants, and is used by both hosts against parasites and pathogens to confer the host's resistance (for reviews see e.g., Weiberg et al., 2014; Weiberg and Jin, 2015). In most cases, it includes one-way RNA flow, but there are exceptions. Pathogen fungi *Botrytis cinerea* and *Verticillium dahliae* deliver small RNAs to host plants to silence their immunity genes, while also uptaking the hosts' RNAs (Weiberg et al., 2013; Wang et al., 2016). Because this phenomenon concerns nucleic acids transfer between organisms, it may be an interesting subject in HGT studies, however, it is probably restricted to a narrow set of genes.

Another interesting conclusion of the study on *Cuscuta* (Yang et al., 2019) is that 18 functional genes, that were acquired by this parasite through HGT, belong to the same gene families as the sequences that were independently horizontally transferred to parasites belonging to the Orobanchaceae family (Yang et al., 2016). Moreover, most of these genes are expressed in the haustoria of these two groups of parasites. All these observations strongly support the possibility of an adaptive role of HGT in the parasitic style of life.

Recently, Cai et al. (2021) analyzed the genome of endoparasite *Sapria himalayana* (Rafflesiaceae) and found that at least 1.2% of its content, including both genic and intergenic sequences, was transferred via HGT from the host. The authors suggest that some of transferred genes are potentially adaptive for parasitism.

SOURCE AND TARGET GENOMES OF HGT

Plant cells possess three genomes that can be potential sources and/or targets of gene transfer: nuclear, mitochondrial, and plastid; each has different features and different abilities to be the donor or recipient of foreign genes. Since the beginnings of their endosymbiotic coexistence, many gene transfers have occurred between these organelles. This process, similar to HGT in which DNA is moved between different genomes of the cell, e.g., between mitochondria and nucleus, is called intracellular gene transfer (IGT). Generally, IGT is restricted to a single species (organism), however, it is possible that the sequence transmitted by HGT may be transferred not only between species but also between different types of organella (Bergthorsson et al., 2003). Considering three organelles, there are six theoretically possible transfer directions. Mainly, during evolution genes have migrated from mitochondria and plastids to the nucleus, which allowed, for example, a better coordination of gene expression in cells (Woodson and Chory, 2008; Kleine et al., 2009; Wolf, 2009). Both plastid and mitochondrial genomes resemble those of prokaryotes, because of their bacterial origins (Sagan, 1967). That similarity may suggest that the frequency of IGT and HGT events is comparable in these organelles, but such an assumption would be misleading due to several fundamental differences between them. The most important is that whereas mitochondria frequently fuse, fission, and recombine, plastids do it only in rare exceptions (Arimura et al., 2004; Stegemann et al., 2012; Arimura, 2018). Moreover, angiosperm mitochondria have more noncoding DNA (72-89%) than plastids (40-45%), which provides more space where alien sequences may be integrated without disrupting the function of present genes (Rice and Palmer, 2006). Consequently, mitochondria are reported as frequent internal gene recipients (Koulintchenko et al., 2003; Zhao et al., 2019; Petersen et al., 2020), contrary to plastids. Comprehensive studies of 136 diverse species conducted by Gandini and Sanchez-Puerta (2017) revealed almost 1400 sequences transferred from plastids to mitochondria. The authors hypothesized that the plastid sequences were probably transferred by IGT from plastid to mitochondria in the same taxon and later between mitochondria of different species.

However, some examples of IGT to plastids were also described. Studies on the mitochondrial and plastid genomes of *Daucus* (Iorizzo et al., 2012a, 2012b) showed that a mitochondrial sequence was transferred to the plastid by a retrotransposon. Other examples of IGT to plastids were reported in *Asclepias syriaca* (Straub et al., 2013), bamboos (Ma et al., 2015), and *Paspalum* (Burke et al., 2016).

Mitochondrial genomes, as mentioned above, are regarded as quite good targets of alien genes, so it is not surprising that HGT events are also frequently reported in these organelles. The first reports of HGT in plants that did not involve mobile genetic elements or *cox1* intron were reported for mitochondrial genes: *atp1* (in *Amborella*), *rps2* (in *Actinidia*), and *rps11* (one case in *Sanguinaria*, second in Caprifoliaceae and one possible in Betulaceae) (Bergthorsson et al. 2003). One year later, a massive HGT was described in *A. trichopoda* (Bergthorsson et al., 2004), in which 20 of 31 mitochondrial genes tested had one or more copies acquired from other species, mostly Angiosperms, but also from other groups of plants, including mosses. Later studies brought other reports of HGT to non-parasitic plants, but we will focus on parasites.

The first report of HGT to mitochondria of parasitic plants (Davis and Wurdack, 2004) referred to Rafflesiaceae from plants of the order

Malpighiales. The analyses showed that, whereas phylogenetic trees based on mitochondrial *matR* and nuclear 18S ribosomal DNA and PHYC loci place Rafflesiaceae in Malphigiales, on the *nad1B-C* tree they are grouped with Vitaceae, close to *Tetrastigma*, which is their obligate host. Also, studies published in the same year (Nickrent et al., 2004) suggested that *matR* and *atp1* genes were transferred to Rafflesiaceae.

HGT of a mitochondrial gene in Orobanchaceae was first reported by Kwolek et al. (2017). *Orobanche coerulescens*, and probably three species of *Phelipanche,* contain *atp6* genes acquired in two independent events from *Asteraceae*. The gene sequences suggest that the currently existing *atp6* genes in these species are the result of recombination of the original parasite gene and the one received from the host. While *O. coerulescens* sequences contain rather long fragments of the alien gene, the transferred segment of the gene found in the *Phelipanche* species is short and located in the terminal region of the analyzed DNA sequence.

Some interesting studies were recently conducted on *Cynomorium coccineum*, which is one of the most widespread (from western China to the Canary Islands) parasitic flowering plants and parasites species from at least 10 angiosperm families from different orders (Bellot et al., 2016; Cusimano and Renner, 2019). The tested samples belonged to different populations spread along its range. The authors found 10 horizontal transfers of five mitochondrial genes (*atp1*, *atp8*, *cox1*, *cox2,* and *ccmFn*) that occurred at different stages of the species evolution. They reported different types of HGT gene integration or their coexistence with the original copies. Some alien and native copies coexisted and both remained functional. Moreover, more than one copy, independently acquired from different hosts, may accompany the original, working gene. Other transferred genes remained alone, replacing the native copies. Recently, Sanchez-Puerta et al. (2019) sequenced the mitochondrial genome of *Lophophytum mirabile* (Balanophoraceae). The authors found that in nine of 60 circular-mapping chromosomes, over 80% DNA is of alien origin, probably acquired by HGT from legumes.

As mentioned previously, plastids are considered as less receptive targets for HGT than mitochondria. However, some reports indicate that this phenomenon may also be observed for these organelles. Although so far most known cases have not concerned parasites, we report them shortly to demonstrate the possibility of such a process.

The first possibility of a plastid genome transfer is a process called "organelle capture" in artificial and natural grafts (Stegemann and Bock, 2009; Stegemann et al., 2012). As a result, whole plastid genomes may be transferred between species, however, to our knowledge, this has not been yet observed in plant parasites. The transfer of individual genes requires other mechanisms. Additionally, smaller parts of plastid genome may be transferred as shown by Rice and Palmer (2006), who reported the transfer, replacing the original, of the bacterial *rpl36* gene to the chloroplast in algae, which, in the author's opinion, required homologous recombination.

Studies on *Orobanche* and *Phelipanche* species by Park et al. (2007) suggest that the latter might have a horizontally acquired plastid region including the *rps2, trnL-trnF,* and *rbcL* plastid genes from the former, however, the target genome was not determined, and the vector remained speculative. The results of later studies concerning the plastid genome evolution (Wicke, 2013) suggest that the transferred fragment does not reside in the plastid genome.

The nuclear genome, the largest of the three, is also involved in HGT. The studies on *Striga hermonthica* (Yoshida et al., 2010) mentioned above were the first discovery of such cases in parasitic plants. During the next years, other reports revealed more examples, including the previously described analysis of transcriptomes of holoparasite *Rafflesia cantlei* (Xi et al., 2012). In 2013 Zhang et al. demonstrated a transfer of a gene encoding albumin 1 KNOTTIN-like protein from legumes to *Phelipanche aegyptiaca* and related species. Moreover, they found an independent transfer of that gene to *Cuscuta pentagona*. A year later, two independent transfers of strictosidine synthase-like (SSL) genes from Brassicaceae were described in *P. aegyptiaca* and *Cuscuta australis* (Zhang et al., 2014).

Nowadays, such studies mainly rely on techniques, such as NGS, that allow analyzing complete genomes or transcriptomes. These methods allow to investigate all genes in the genome, indicate the length of the transferred sequences, estimate the frequency of the process, study other aspects of HGT, genome structure and evolution. This approach was used, for example, in studies on members of Orobanchaceae family (Kado and Innan, 2018), which were described above.

Furthermore, many cases of HGT were detected with the use of these techniques for *Cuscuta*. Vogel et al. (2018) found 64 high confidence HGT candidates in holoparasitic *C. campestris*. Yang et al. (2019) reported in their study 108 transcribed and probably functional HGT events in *C. campestris* and related species, accompanied by 2 regions with host-derived transposons, pseudogenes, and noncoding sequences. Also, recent studies on *Sapria himalayana* showed that at least 1.2% of its the genome was acquired by HGT (Cai et al., 2021).

FINAL QUESTIONS AND THOUGHTS

As described above, the phenomenon of horizontal gene transfer in parasitic plants (and non-parasitic plants) was in the past decades and is presently the subject of many studies that focus on different aspects of this phenomenon. Our knowledge of the topic is growing every year, but many aspects are still unexplained, and what is more, some of them are yet untouched. One of the most fundamental questions is why HGT occurrences are relatively frequent in some species and rare in others. Some organism features mentioned here, such as the type of connection between plants or the level of parasitism appear to facilitate HGT, but perhaps, we should also look for other causes, even beyond the organismal level.

The transfer of the alien gene to the organism's cell, its integration into the cellular genome, and the transfer to the next generation are just first steps and do not guarantee the spread and fixation of the newly acquired gene in the population and in the species. If such changes are beneficial to the carrier, its frequency should be increased in the next generations due to natural selection, just as other types of advantageous mutations. However, especially in the case of neutral genetic changes, genetic drift may play an important role. This mechanism is particularly strong in small populations, so they may be liable to fixation of different genetic changes from point mutation to wider genome changes (Lynch, 2007; Fontdevila, 2011). This phenomenon may also be important in the spread of HGT events, so it is worth examining whether there is a connection between the frequency of transfers in genomes and the population sizes of their carriers. However, such studies would be practically difficult and rather restricted to recent HGT events.

Genetic drift may also be considered at the subcellular level. In that case particular mitochondria or plastids may be regarded as individuals in the population of organelles. When a genetic change occurs in mitochondrial or plastid DNA, whether from HGT or by other means, it starts in just a single organelle; one of dozens, hundreds or thousands. Therefore, the outcome depends on spreading of organelles in the population where evolutionary mechanisms such as natural selection and genetic drift work as well. It is worth remembering that mitochondrial and plastid numbers may significantly differ between tissues and cells and may be inherited from only one of the parents (Cole, 2016 and citations herein).

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