



Horizontal gene transfer in parasitic plants

Charles C Davis and Zhenxiang Xi

Horizontal gene transfer (HGT) between species has been a major focus of plant evolutionary research during the past decade. Parasitic plants, which establish a direct connection with their hosts, have provided excellent examples of how these transfers are facilitated via the intimacy of this symbiosis. In particular, phylogenetic studies from diverse clades indicate that parasitic plants represent a rich system for studying this phenomenon. Here, HGT has been shown to be astonishingly high in the mitochondrial genome, and appreciable in the nuclear genome. Although explicit tests remain to be performed, some transgenes have been hypothesized to be functional in their recipient species, thus providing a new perspective on the evolution of novelty in parasitic plants.

Address

Department of Organismic and Evolutionary Biology, Harvard University, 22 Divinity Avenue, Cambridge, MA 02138, USA

Corresponding author: Davis, Charles C (cdavis@oeb.harvard.edu)

Current Opinion in Plant Biology 2015, **26**:14–19

This review comes from a themed issue on **Biotic interactions**

Edited by **Uta Paszkowski** and **D Barry Scott**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 3rd June 2015

<http://dx.doi.org/10.1016/j.pbi.2015.05.008>

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Introduction

Parasitism has evolved multiple times across the tree of life. Parasitic plants obtain some or all of their water and nutrients, including carbohydrates and minerals, through a specialized feeding apparatus called the haustorium, which attaches to roots or shoots of their hosts (Figure 1). Parasitic plants exhibit a range of diversity, including species with the ability to photosynthesize (hemiparasites) and those that cannot (holoparasites). Despite the direct haustorial connection parasitic plants establish with their hosts, most grow predominantly exterior to their hosts. The exceptions include a small group of endophytic holoparasites, which emerge only during sexual reproduction (Figure 1). These species otherwise grow embedded in their hosts and have no discernable roots, shoots, or leaves, persisting largely as a mycelium-like body consisting of a greatly reduced strand of cells [1*].

Owing to their extreme vegetative reduction and modified reproductive morphology, the phylogenetic placement of

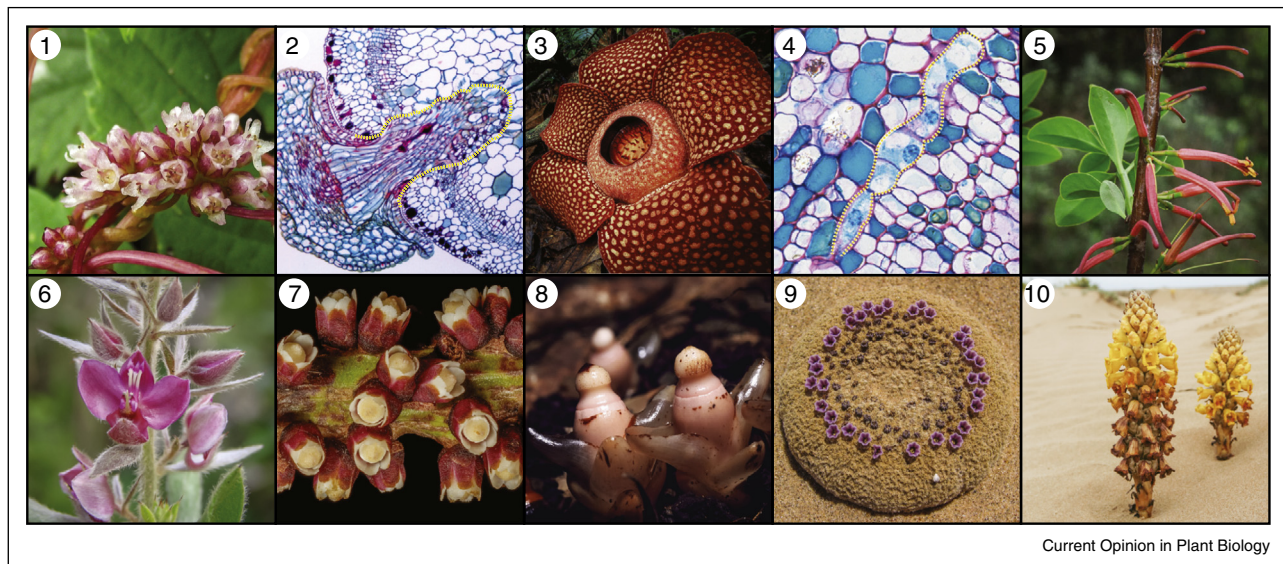
parasitic plants among their free-living relatives was long a mystery. This is especially true for the endophytic holoparasites, most of which have been historically grouped together to include species variously placed today in Apodanthaceae, Cytinaceae, Mitrastemonaceae, and Rafflesiaceae. Recent phylogenetic investigations, however, have greatly challenged this traditional view of classification by demonstrating that these families are not closely related. Instead, the most comprehensive analyses indicate that parasitism in angiosperms has evolved at least 11 times from free-living ancestors [2].

These insights have greatly stimulated research relating to genome evolution in parasitic plants [3**,4], and the investigation of the adaptations that have enabled the origin of parasitism [5**,6,7]. One of the most exciting discoveries to emerge from this body of research is the finding that parasitic plants and their hosts undergo horizontal gene transfer (HGT) — the exchange of genetic materials between distantly related, non-mating organisms. More generally, the hypothesis of HGT in autotrophic plants was invoked in two landmark studies [8,9], in which gene phylogenies were identified as strongly incongruent with well-established species relationships based on various lines of molecular and morphological evidence. In this regard, phylogenies that are incongruent with accepted species relationships have been deemed the ‘gold standard’ for deducing HGT [10] (Figure 2). Since that time, HGT has been identified in a variety of autotrophic plant clades [10,11**,12], most notably in bryophytes [13], ferns [14,15*], basal angiosperms [16,17**], and grasses [18].

Parasitic plants are exemplary systems for studying HGT

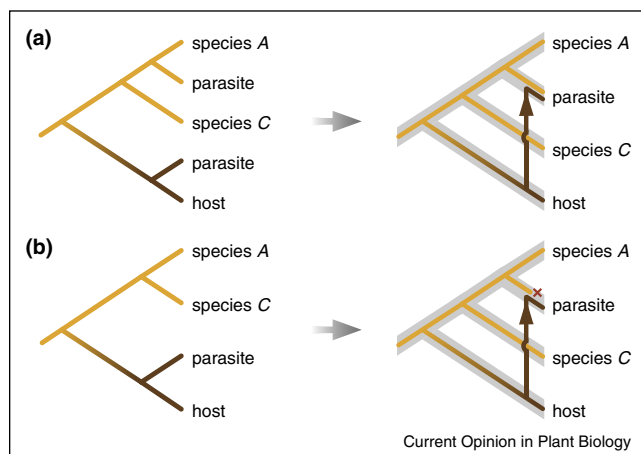
Following the two initial discoveries of HGT in autotrophic plants, investigations in parasitic plants have provided important insights into HGT [14,19–21]. Several studies ranging from single to hundreds of genes demonstrate that the parasitic mode of life may enable HGT in plants, which is thought to be facilitated by the intimate physical association between the parasite and its host [19]. This intimacy makes parasitic plants a potential model system for HGT related research. Here, the donor and recipient lineages are often well characterized, making it much easier to discern HGT. By contrast, explanations of HGT in autotrophic plants tend to be less clear from a mechanistic perspective. Up until now, both host-to-parasite [e.g., 19] and parasite-to-host gene transfers [e.g., 14,20] have been identified in parasitic plants (Table 1). In addition, the possibility that parasitic plants act as bridges for gene flow between diverse autotrophic

Figure 1



Parasitic plant diversity. (1) Holoparasitic *Cuscuta europaea* (Convolvulaceae); (2) *Cuscuta campestris* (Convolvulaceae) penetrating host tissue via a haustorium (highlighted with dotted yellow lines); (3) Holoparasitic *Rafflesia arnoldii* (Rafflesiaceae), which produces the world's largest flowers; (4) Holoparasitic *Rhizanthus lowii* (Rafflesiaceae) showing its very reduced endophyte (marked with dotted yellow lines) in the phloem of the host — the only remnants of a vegetative body; (5) Hemiparasitic *Taxillus delavayi* (Loranthaceae, Santalales); (6) Hemiparasitic *Krameria argentea* (Krameriaceae); (7) Holoparasitic *Pilostyles hamiltonii* (Apodanthaceae); (8) Holoparasitic *Mitrastema yamamotoi* (Mitrastemonaceae); (9) Holoparasitic *Pholisma sonorae* (Lennoaceae); and (10) Holoparasitic *Cistanche phelyphaea* (Orobanchaceae). Images copyright Dave, M. Costea, J. Holden, L. Nikolov, J. Lundberg, J. Medeiros, K. Thiele, C. Tada, J. Bartel, and P. Precey, respectively.

Figure 2



Using phylogeny to infer horizontal gene transfer (HGT). **(a)** Inferred gene tree on the left depicts transgene in parasite (placed with host clade), coexisting with its vertically inherited homolog (i.e., duplicative HGT). Outer species tree (in grey) on the right with inner gene tree demonstrating host-to-parasite HGT. **(b)** Inferred gene tree on the left depicts transgene in parasite (placed with host clade). Outer species tree on the right with inner gene tree demonstrating host-to-parasite HGT, followed by loss of vertically inherited homolog (red 'x'; i.e., replacement HGT).

plants has been invoked [16]. Because most HGTs reported to date involve host-to-parasite transfers, we focus our review on transgenes identified in parasitic plants, and draw upon broader HGT studies in autotrophic plants when they are especially relevant. These include: the phylogenetic breadth and magnitude of HGT in parasitic plants, the genomic compartmentalization of transgenes including potential mechanisms for how these events occur, the functionality of transgenes in their recipient species, and lastly, insights into past parasite–host associations from HGT.

Parasitic plants show high rates of HGT

Evidence of HGT has been identified in 10 of the 11 parasitic lineages to date (Table 1) and overwhelmingly involve mitochondrial DNA, which is consistent with most studies from autotrophic plants [17^{**},22]. This is likely due to several unique properties of mitochondria, including their ability to actively uptake DNA [23], and to undergo frequent fusion and fission [24]. Additionally, plant mitochondrial genomes possess massive intergenic regions [25], allowing for foreign genes to be inserted without disturbing expressed native genes. In the first broad genomic study to comprehensively assess the magnitude of HGT involving host–parasite mitochondrial genomes, Xi *et al.* [3^{**}] identified that up to 41% of mitochondrial genes in Rafflesiaceae demonstrate evidence of HGT. Here, four mitochondrial genes maintain

Table 1

Summary of horizontal gene transfer (HGT) involving parasitic plants

Clade	Reference	Transgenes
Apodanthaceae	[21]	1 mitochondrial gene
	[2]	2 mitochondrial genes
<i>Cassytha</i> (Lauraceae)	[2]	1 mitochondrial gene
<i>Cuscuta</i>	[20]	1 mitochondrial gene
(Convolvulaceae)	[22]	3 mitochondrial genes
	[30]	1 nuclear gene
Cynomoriaceae	[2]	2 mitochondrial genes
Hydnoraceae	[2]	1 mitochondrial gene
Lennooideae	[2]	1 mitochondrial gene
(Boraginaceae)		
Mitrastemonaceae	[21]	1 mitochondrial gene
	[2]	2 mitochondrial genes
Orobanchaceae	[20]	1 mitochondrial gene
	[42]	1 plastid gene
	[29]	1 nuclear gene
	[43]	1 plastid gene
	[31**]	1 nuclear gene
	[30]	1 nuclear gene
Rafflesiaceae	[19]	1 mitochondrial gene
	[21]	1 mitochondrial gene
	[2]	1 mitochondrial gene
	[4]	47 nuclear and 2 mitochondrial genes
	[3**]	11 mitochondrial and 14 plastid genes
	[26*]	15 plastid genes
Santalales	[14]	2 mitochondrial genes
	[2]	1 mitochondrial gene

both horizontally and vertically transferred homologs (duplicative HGT, sensu [11**]), and seven include only transgenic sequences (Figure 2). Moreover, at least some of these transgenes maintain synteny with their hosts, suggesting that native genes were likely displaced via homologous recombination (replacement HGT, sensu [11**]). Subsequent efforts to assemble a mitochondrial genome in Rafflesiaceae support these findings [26*], and further point towards the complete loss of the plastid genome in these endophytic holoparasites. Although these results of HGT are lower than the nearly six mitochondrial genome equivalents of DNA content transferred into the autotrophic species *Amborella trichopoda* [17**], they clearly indicate that a parasitic mode of life can significantly reshape the content of mitochondrial genomes via HGT.

By contrast, HGT involving plastid DNA is rare [11**,27]. This is likely due to the fact that plastids do not have DNA uptake mechanisms, and plastid genomes have few intergenic regions. A recent HGT was invoked for the plastid gene *rps2* in *Phelipanche* (Orobanchaceae; in this case HGT involved parasite-to-parasite transfer). Here, the researchers were agnostic on the genomic localization of *rps2*. One possibility is that the transgene moved directly from the host's plastid genome to the parasite's mitochondrial genome. A second is that this transgene

resulted from intergenomic transfer, first involving plastid-to-mitochondrion transfer within the donor lineage, followed by mitochondrion-to-mitochondrion host-to-parasite transfer. With regard to the second possibility, a clearer example was demonstrated in Rafflesiaceae, where *Sapria himalayana* [3**] and *Rafflesia lagascae* [26*] acquired an astonishing 14 and 15 plastid genes from their grapevine hosts (*Tetrastigma*, Vitaceae), respectively. Based on the availability of a previously assembled mitochondrial genome of the host lineage [28], it was confidently determined that these transgenes were likely resident in the host's mitochondrial genome at the time of transfer. These results collectively establish that most transgenes to date have been acquired from the mitochondrial genome rather than the plastid genome [11**].

Although a larger picture of rampant HGT involving mitochondrial DNA in parasitic plants is emerging, our knowledge of HGT involving nuclear DNA is still in its infancy. This is partly due to the paucity of deeply sequenced genomes available to address this topic in a broad, comparative framework. Yoshida *et al.* [29] used genome scanning approaches to demonstrate that the gene *ShContig9483* in the purple witchweed, *Striga hermonthica* (Orobanchaceae), was acquired from a member of the grass family (Poaceae). Similar host-to-parasite transfers have subsequently been identified in *Cuscuta australis* and *Orobanche aegyptiaca* (Convolvulaceae and Orobanchaceae, respectively; involving the *strictosidine synthase-like* gene) [30] and *Phelipanche aegyptiaca* (involving the *albumin 1* gene) [31**]. More focused efforts investigating hundreds of genes indicate that host-to-parasite transfer involving nuclear genes may be prevalent. For example, several dozen genes were identified via phylotranscriptomics as likely candidates for nucleus-to-nucleus transfers between Rafflesiaceae and their hosts [4]. These authors additionally sought to establish background rates of non-HGT causes of phylogenetic incongruence (e.g., gene duplication, gene loss, and incomplete lineage sorting). This is likely to become especially relevant as more genomic data become available. Promising new analytical approaches have been developed to identify HGT in the face of these confounding effects using parsimony [32,33] or Bayesian methods [34,35*].

In summary, these results suggest that while the relative magnitude of HGT involving the nuclear genome in parasitic plants is appreciable, transfers involving the mitochondrial genome are likely to be potentially much more frequent.

Mechanisms and functionality of transgenes in parasitic plants

One outstanding question involves the uptake mechanisms of foreign DNA. Although vectors remain unclear, fungi, bacteria, and viruses have been invoked [9,10]. More recently, transposable elements have also been

implicated as a vector for HGT in autotrophic plants [36[•]]. Although many nutrients and macromolecules, including mRNAs, are trafficked between host and parasite [5^{••},37,38], the evidence points primarily to direct uptake of DNA, rather than mRNA. This is demonstrated in various studies of parasitic plants [3^{••},4,22,30,31^{••}], as well as in autotrophic ones. In Rafflesiaceae, evidence for direct DNA uptake is supported by the presence of introns in transgenes and the inclusion of cytosine-to-uracil RNA editing sites in mitochondrial transgenes. One exception is in *Striga* where the putative transgene mentioned above possesses no intron and has consecutive adenine nucleotides at the 3' end, suggesting that this transgene was RNA-mediated and then incorporated into the genome via reverse transcription [29]. Given the unique properties of the mitochondrial genome and recent observation of exchange of whole plastid genomes in plant grafting experiments [39,40], it appears that the intimate association between parasites and their hosts greatly facilitates HGT via the direct incorporation of large fragments of DNA, rather than shorter mRNAs. Finally, as broader comparative data becomes available on the sizes of plasmodesmatal connections between hosts and parasites, we may gain insight into which symbioses are likely to confer more or less HGT.

A second outstanding question relates to the functionality of transgenes in parasitic plants. Although the magnitude of HGT involving nuclear genes is lower, on average, than that of the mitochondrial genome, nuclear transgenes may nevertheless confer key evolutionary advantages in their recipient lineages. Most of the acquired DNAs identified in mitochondrial genomes are introns or pseudogenes. Whether these pseudogenes are inherited as such at the time of transfer, or whether gene death takes place subsequent to their transfer via deterioration of the foreign DNA remains unclear [12]. However, several recently identified nuclear transgenes maintain reading frame, and in some cases have been shown to be actively transcribed. The *Rafflesia cantleyi* transcriptome, for example, exhibits dozens of expressed transgenes that represent a wide range of cellular functions as determined by gene annotation data, including roles related to respiration, metabolism, mitochondrial translation, and protein turnover [4]. Although the extent to which these transgenes are functional awaits further exploration, these results raise the possibility that transcripts acquired via HGT may express host-like genes to better manipulate their host. Similarly, a transgene closely related to the *albumin 1* gene was discovered in *Phelipanche aegyptiaca* [31^{••}]. *Albumin 1* genes encode seed storage proteins and insect toxins, and appear to have been acquired via HGT in the ancestor of *Phelipanche* from one of its legume hosts. In this case, the transfer appears to have given rise to a family of duplicated, differentially expressed genes in their recipient lineage. This suggests the intriguing possibility that differential function of these copies may have

arisen in the parasites subsequent to their transfer. In these cases, the functional relevance of transgenes remains unclear, but parasitic plants need to avoid host defenses as well as resist herbivores, bacteria, fungi, and abiotic environmental stresses. Follow-up studies may reveal that these transgenes provide an evolutionary advantage in this regard.

Finally, an additional discovery to emerge is that codon usage patterns of native genes in some parasites demonstrate a very strong genome wide bias towards coding properties more like those of their hosts rather than their closest relatives [4]. This apparent form of molecular convergence may help to explain why HGT is so high in some parasitic lineages: the similarity in their genetic machinery relative to their hosts may greatly facilitate gene uptake. Why this convergence exists remains an open topic for investigation, and should be investigated in other lineages.

Detecting former host associations with HGT

Perhaps one of the most exciting possibilities offered by HGT in parasitic systems is their ability to provide insights into current and past host associations. In a recent broad survey of Rafflesiaceae mitochondrial genomes [3^{••}], gene transfers fell within two distinct categories — transfers that were ancient, perhaps dating back to the late Cretaceous, and those that were more recent. For the ancient transfers, transgenes were broadly shared and maintained synteny across related parasitic plants. This combination of factors suggests that they were likely the result of a single, ancient host-to-parasite transfer event. In other cases, however, transgenes from these parasitic plants were broadly dispersed among more recently derived host lineages, suggesting recent transfers. Interestingly, in the case of the ancient transfers, the transgenes did not group near to their current host lineages, suggesting that HGT involved former host associations, subsequently followed by a host shift. This is further supported by molecular divergence estimates, which demonstrate that the origin of the parasitic plants greatly predates that of their extant hosts [3^{••}]. By contrast, the more recent transfers tended to group with their current hosts. In these regards, HGT can serve as the 'ghost of transfers past', and will aid us in identifying former host associations. As more and better comparative genome data become available we will be able to time these HGT events with greater precision to better identify former host associations. In addition, by identifying these former associations we can begin to clarify fundamental host requirements of these parasitic plants.

Conclusions and future directions

Studies to date indicate that parasitic plants represent an active area of HGT. These symbioses are ideal for studying this phenomenon owing to the intimacy of their symbiotic interactions, and our ability to more confidently

invoke HGT when phylogenies are incongruent with accepted species relationships. In general, HGT in parasitic plants is reflective of what we see in autotrophic plants [10,11^{••}]: gene transfers involving mitochondrial genomes are high, and appreciable in nuclear genomes. The functionality of these transgenes is unknown, but seems likely in at least some instances. Along these lines, establishing functionality of transgenes in their recipient genomes will be a key goal going forward. Despite lower overall rates of HGT in the nuclear genome, these events could have a major influence on the evolution of novelty in their recipient lineages. The difficulty in elucidating function is not trivial, however, owing to their two-parted symbiosis and the challenges of growing these plants in controlled environments. In this regard, some taxa, such as *Cuscuta*, are likely to be more suitable for this purpose [41]. These species possess a simple anatomical structure, seed germination requiring only water, and a wide range of host tolerances. In addition to these more phylogenetically focused experiments, HGT remains largely unexplored for numerous parasitic clades at the genomic level. Future explorations should generate genomic data for these neglected clades to further discern the magnitude of HGT, especially by sequencing regions outside of transgenes to identify putative vectors from genomic signatures. These exercises in genomic surveillance should prove useful for understanding differential rates of HGT among genomes, common patterns of genes that are transferred (and lost in recipient genomes following transfer), and the prevalence of HGT among different modes of parasitism.

Acknowledgements

CCD and ZX were supported by National Science Foundation (NSF) Assembling the Tree of Life grant DEB-0622764 and NSF DEB-1120243 (to CCD). Members of the Davis laboratory provided helpful feedback on an early draft of this paper.

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