

The evolution of land plants: a perspective from horizontal gene transfer

Qia Wang^{1,2}, Hang Sun¹, Jinling Huang^{3*}

¹ Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201, China

² University of Chinese Academy of Sciences, Beijing 10049, China

³ Department of Biology, East Carolina University, Greenville, NC 27858, USA

Abstract

Recent studies suggest that horizontal gene transfer (HGT) played a significant role in the evolution of eukaryotic lineages. We here review the mechanisms of HGT in plants and the importance of HGT in land plant evolution. In particular, we discuss the role of HGT in plant colonization of land, phototropic response, C₄ photosynthesis, and mitochondrial genome evolution.

Keywords: mechanisms of HGT; plant evolution; mitochondrial genome; adaptation

Introduction

Horizontal gene transfer (HGT) refers to the movement of genetic information between distinct species. Being different from vertical genetic transmission from parent to offspring, HGT circumvents normal mating barriers and may introduce novel genes into recipient genomes. As such, HGT may not only accelerate the genome evolution of recipient organisms, but also allow recipients to explore new resources and niches [1–4].

HGT was once thought to be frequent only in prokaryotes and certain unicellular eukaryotes [2,5]. During the past decade, horizontally acquired genes have been found in all major multicellular eukaryotic lineages (plants, animals, and fungi) [6–9], suggesting that HGT has occurred throughout the history of eukaryotic evolution and is critical for the adaptive evolution of some multicellular lineages. Here, we review cases of HGT in land plants, and discuss the genetic mechanisms and evolutionary importance of HGT in plant evolution. In particular, we focus on acquired genes of adaptive significance in plants, rather than genes that are selectively neutral or nearly neutral [10,11]. Because intracellular gene transfer (IGT) from organelles (mitochondria and plastids) to the nucleus has been discussed in multiple other articles [12–14], it will not be considered here.

Mechanisms of HGT in plants

A complete and successful HGT requires that a foreign gene first enters cells of the recipient organism, be integrated into the recipient genome and then transmitted to the offspring [7]. Because the physical isolation of germ cells may prevent foreign genes from being transmitted to the offspring [15,16], plants and animals were traditionally regarded to be resistant to HGT [3,15]. Nevertheless, the occurrence of HGT in all major eukaryotic lineages suggests that no barrier to HGT is insurmountable in eukaryotes [7]. Specifically for plants, their meristems, which represent the germline equivalent but can be formed through de-differentiation of somatic cells, are less protected and may result in a higher susceptibility to HGT [16]. Several mechanisms have also been proposed regarding how HGT may occur in plants [6,7,16–18] (Fig. 1).

INTIMATE PHYSICAL ASSOCIATION. Sustained contact such as symbiosis, parasitism, epiphytism, pathogen infection or plant grafting may offer opportunities to gene transfer. In particular, parasitism has been reported in several cases of HGT in plants [6,18–23]. In most of these documented examples, genes were transferred from host to parasitic plants. For instance, multiple mitochondrial and nuclear genes of Rafflesiaceae, a family of parasitic plants, were reportedly acquired from their host *Tetrastigma* (Vitaceae) [19–21]. Similar cases have also been observed in other parasitic plants such as *Cistanche deserticola* (Orobanchaceae) [23], *Orobanche aegyptiaca* (Orobanchaceae) and *Cuscuta australis* (Convolvulaceae) [18], all of which acquired genes from their hosts. Considering the main direction of nutrient transmission from host to parasitic plants, it is possible that genetic material may be carried within, thus offering opportunities for HGT to parasitic plants.

* Corresponding author. Email: huangjl@ecu.edu

Handling Editor: Andrzej Bodył

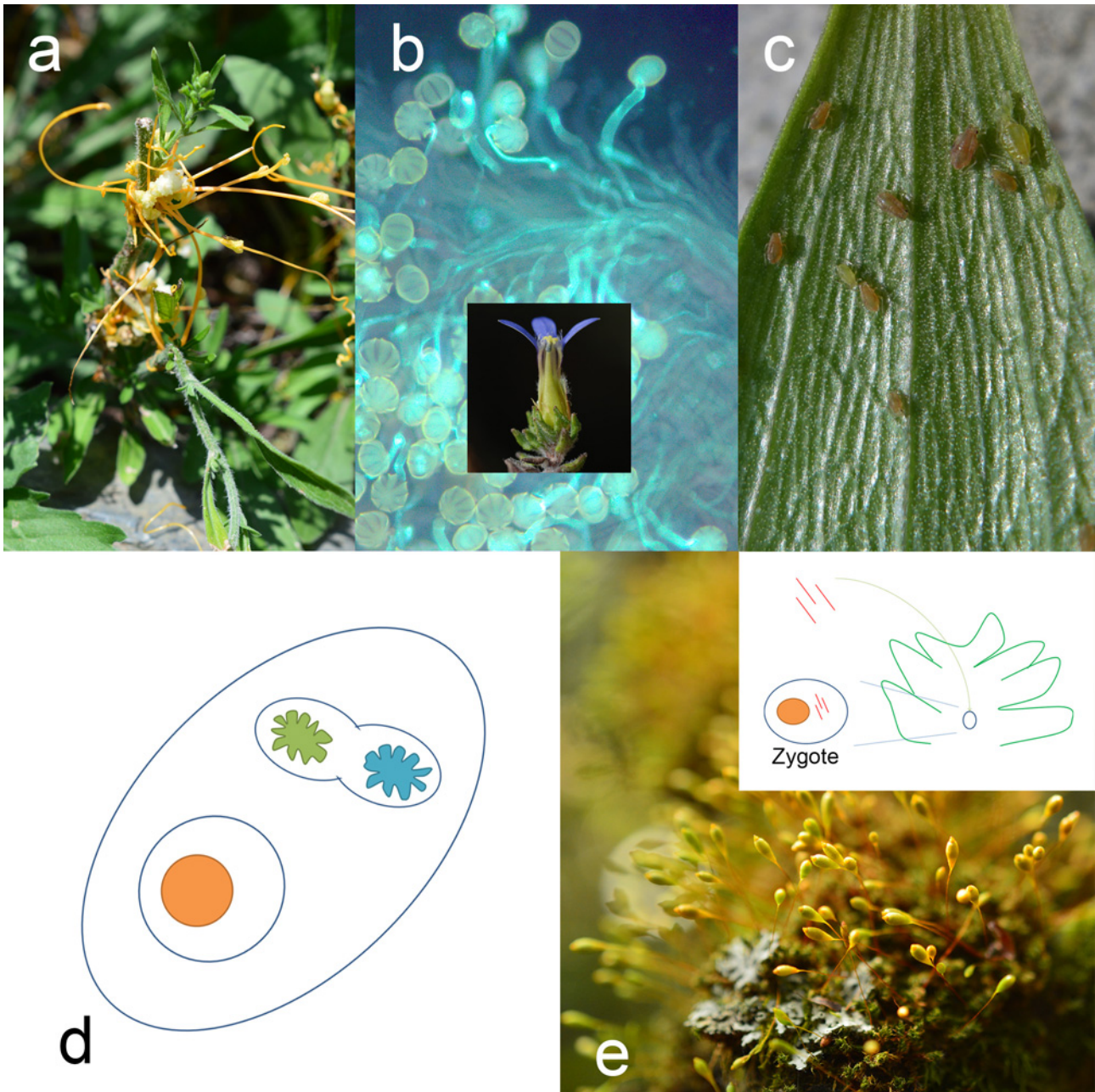


Fig. 1 Mechanisms of HGT in land plants. Several mechanisms may facilitate HGT in plants, some of which are shown here. **a** The intimate physical association of the parasite *Cuscuta* with host plants offers opportunities for gene transfer. **b** Pollen germination on stigma of *Cyananthus* (as shown by image of fluorescence labeled callose. Photo courtesy of Yang Niu, Kunming Institute of Botany). Genetic materials may be delivered to egg cells via elongated pollen tubes. **c** Aphids may serve as a gene transfer agent between two plant species (photo courtesy of Jianwen Zhang, Kunming Institute of Botany). **d** Horizontal transfer of entire genomes between green plants may be explained by mitochondrial fusion. **e** Weakly protected zygote may serve as an entry point for foreign genes into the moss genome according to the weak-link model.

However, even if gene transfer in the opposite direction (from parasitic to host plants) may be rare, there are still cases that have been reported. For instance, Mower and his colleagues described two HGT cases of the mitochondrial *atp1* gene from parasitic flowering plants, *Cuscuta* and *Bartsia* (Orobanchaceae), to their host plants of *Plantago* (Plantaginaceae) [22]. Therefore, the link between HGT direction and nutrient flow is not universal.

ILLEGITIMATE POLLINATION. This hypothesis presumes that pollen grains of one flowering plant species may germinate on the stigma of another species and, after pollination, some genes from the former may happen to be integrated into the latter species [16,24,25]. Such genetic materials may have been delivered to egg cells via elongated pollen tubes and, in some cases or under laboratory conditions, whole plastid and/or mitochondrial genomes

are involved [24,26]. Based on available data, HGT due to illegitimate pollination may happen between closely related species such as different *Alloteropsis* grasses [25], or even members from different genera of the grass family Poaceae [27,28].

TRANSFER AGENTS. Vectors such as viruses, bacteria, fungi or insects could transfer genes between organisms. Although concrete evidence is still scarce by now, the possibility that a vector with a wide host range may serve as a gene transfer agent between two unrelated plant species should not be dismissed prematurely [6,16].

MITOCHONDRIAL FUSION. HGT in land plant mitochondria is frequent and sometimes involves large pieces of DNA or even whole genomes (discussed below). Mitochondrial fusion has been suggested as a mechanism to explain these observations [29]. The mitochondrial genomes of green plants may be incompatible with those of fungi or animals, thus limiting the donors of mitochondrial fusion events to other green plants [29].

THE WEAK-LINK MODEL. To explain how foreign genes may overcome the isolation of germ cells and reach the offspring, Huang recently proposed a weak-link model [7]. This model suggests that foreign genes may enter recipient cells at weakly protected unicellular or early developmental stages of the lifecycle (e.g. zygotes, embryos or spores). These stages represent the weak link in recipient organisms for the entry of foreign genes. Subsequent cell proliferation and differentiation may spread foreign genes to other tissues, including germ cells. As such, foreign genes could ultimately be transmitted to the offspring and then fixed in the population through drift or positive selection on newly acquired functions [7].

Some of the above mechanisms (e.g., illegitimate pollination) are only applicable to plants, whereas others (physical association and weak-link model) may explain HGT from miscellaneous donors such as viruses, fungi and prokaryotes. These mechanisms also are not mutually exclusive. For instance, the entry of weakly protected unicellular or early developmental stages of land plants may be facilitated by transfer agents or physical associations. In other words, transfer agents, intimate physical association, and illegitimate pollination concern how foreign genes may be carried from donor to recipient organisms, while the weak-link model focuses on how the barrier of germ cells may be circumvented and foreign genes be integrated into recipient genomes. Even boundaries of these mechanisms may not be clear-cut. For example, a common host plant could serve as an intermediate vector for horizontally transferred genes between different parasites [16,30].

Currently, our knowledge about how HGT happened in land plants is still limited. Future work and new technologies are needed in this research area.

The impacts of HGT on land plant evolution

HGT in plant colonization of land

Fossil data and molecular evidence suggest that land plants emerged from a pioneer green algal ancestor about

480–500 million years ago [31]. Compared with aquatic environments, terrestrial habitats brought many challenges to early land plants (e.g., desiccation, UV radiation, and microbial attack). During their colonization of land, plants evolved some complex regulatory systems, body plans, and other phenotypic novelties that facilitated their adaptation and radiation in a hostile terrestrial environment [32,33]. The origin and evolution of these novelties were aided through acquisition of genes from other organisms [32–34].

The phenylpropanoid pathway is responsible for the production of compounds such as flavonoids and lignin. The first and essential step of the phenylpropanoid pathway is catalyzed by phenylalanine ammonia lyase (PAL) [35,36]. At 2009, Emiliani et al. reported that plants acquired the *PAL* gene from soil bacteria or fungi during their early stages of land colonization [32]. Given the role of lignin in xylem formation and flavonoids in protecting plants from microbial infection and/or UV radiation, the acquisition of *PAL* might have been crucial for plant adaptation to terrestrial environments. A more comprehensive genome analysis of the moss *Physcomitrella patens* identified 57 gene families that were transferred from prokaryotes, fungi or viruses to the most recent common ancestors of land plants or green plants [33]. These genes are involved in some essential or plant-specific activities such as xylem formation, plant defense or nitrogen recycling [33,34]. Nineteen of these identified gene families also appear to be specific to mosses, suggesting that recent HGT events may not be rare. Further analyses also show that the origin of plant auxin biosynthesis was shaped by HGT [37]. Since these acquired genes were identified based on analyses of a single genome using stringent phylogenomic approaches, it is reasonable to believe that more horizontally acquired genes will be found in land plants [34].

The origin of vascular tissues is a significant event in land plant evolution. By ensuring long-distance transport of water, nutrients and organic compounds and increasing the mechanical support for plants, vascular tissues enable land plants to overcome some of the major challenges in terrestrial habitats (e.g., anchorage of plants in the ground, absorption of water and nutrients, support for upright growth) [33,38]. Several horizontally acquired genes are involved in the development of vascular tissues. For instance, the vein patterning 1 (*VEP1*) gene in land plants, presumably acquired from bacteria, is involved in vascular strand formation [33,39]. Most recently, Yang et al. investigated the evolution of TAL-type transaldolase (*TAL*) gene and found that land plant *TAL* genes are derived from actinobacteria [40]. *TAL* is ubiquitous in land plants and positively selected [40]. Transgenic experiments in rice showed that *TAL* is specifically expressed in vascular tissues. Importantly, knockdown of *TAL* expression leads to fewer, smaller and immature vascular bundles in culms, suggesting that the acquisition of *TAL* genes have played a pivotal role in plant vascular development and, therefore, adaptation to land environments.

HGT in phototropic response and C₄ photosynthesis

Millions of years after the initial plant invasion of land, vascular plants arose (during Silurian) [41]. Ferns dominated the earth's land surface antecedently, and their dominance

was then replaced by angiosperms. Surprisingly, ferns did not die out. Instead, they mostly adapted to a shade-dwelling habit created by angiosperms-dominated forest canopies and then went through another round of diversification, which led to the emergence of the majority of living ferns. Neochrome, a novel chimeric photoreceptor derived from the fusion of red-sensing phytochrome and blue-sensing phototropin modules [42,43], is considered as a key innovation that allows ferns to thrive under low-light conditions [44,45]. In order to understand the origin of fern neochrome, Li and his colleagues [46] performed some comprehensive phylogenetic analyses of neochrome and related gene families. After ruling out other causes (e.g., phylogenetic artifacts and independent origins), they concluded that neochrome originated in hornworts and then was transferred to ferns horizontally. This finding suggests that HGT may have had a profound evolutionary impact on the diversification of ferns and, without it, the fern lineages we see today would likely be dramatically different.

C₄ photosynthesis evolved multiple times from C₃ ancestors independently [47]. HGT also has affected the evolution of C₄ photosynthesis in Poaceae [25]. *Alloteropsis*, a genus of the grass family that includes five C₄ species and one C₃ subspecies (*A. semialata* subspecies *eckloniana*), is an excellent example for studying the evolution of C₄ photosynthesis [48,49]. Christin and his colleagues [25] reported that two essential genes of the C₄ pathway in *Alloteropsis* grasses were acquired from other C₄ taxa within the same family (Poaceae). A reasonable mechanism for the gene transfer events in *Alloteropsis* grasses was illegitimate pollination. This study also demonstrates that, even without sustained physical associations like parasitism or epiphytism, occasional contact such as pollination may offer opportunities for HGT in flowering plants.

HGT in plant organellar genomes

Although HGT to plastid genomes has rarely been reported (but see [50,51]), mitochondrial genes of land plants are subject to widespread, sometimes in a large scale, gene transfers [24,52,53]. For instance, up to 41% of mitochondrial genes in the parasitic family Rafflesiaceae were reportedly subject to HGT events [21]. Such massive mitochondrial gene transfers in Rafflesiaceae are not entirely unexpected, considering the frequent reports of HGT in plant mitochondrial genes and in parasitic plants.

An unprecedented case of HGT in flowering plants is related to *Amborella trichopoda* (Amborellaceae), a basal

flowering plant. The mitochondrial genome of *Amborella* reportedly contains six genome equivalents of foreign mitochondrial DNA, including entire mitochondrial genomes from three green algae and one moss [29]. What makes *Amborella* so rich in foreign mitochondrial genes? The authors postulated that direct contact between *Amborella* and epiphytes, meristem regeneration through wounding, mitochondrial fusion, as well as a lower rate of DNA loss might have contributed to the large number of foreign genes in *Amborella* mitochondrial genome [17,29]. On the other hand, the distinctive phylogenetic position of *Amborella* (it diverged the earliest from other lineages of flowering plants [54]) allows researchers to confidently detect genes acquired from other plants [17]. The massive HGT in *Amborella* also highlights the tendency of plant mitochondrial genomes to take up foreign DNA, for there is no evidence of HGT in the chloroplast genome of *Amborella* [17,29].

HGT of mitochondrial genes is traditionally considered neutral or nearly neutral and, therefore, insignificant for plant adaptive evolution. However, because acquired mitochondrial genes can be transferred to the nucleus or recombine with endogenous organellar DNA fragments, they may increase genetic variation of the recipient plant taxon [14,55,56]. Indeed, it has been demonstrated that gene acquisition and subsequent recombination/gene conversion led to some mosaic mitochondrial genes in plants [53,55,56]. Therefore, it is premature to dismiss the functional implications of mitochondrial HGT.

Conclusions

The foregoing cases suggest that HGT happened in all major land plant lineages (mosses, ferns and flowering plants). The acquired genes may also be derived from different donor groups including viruses, bacteria, fungi, and other plants [6,33,57,58]. Many other cases of HGT have been reported in land plants, but cannot be detailed here [37,52,59–64]. To sum up, while HGT in plants may not be as frequent as in prokaryotes or unicellular eukaryotes, it still plays an important role in some essential or plant-specific activities and has had a significant impact on the evolution of land plants. In the end, it should be noted that most of the HGT cases discussed above were detected through analyses of whole genomes or transcriptomic data. In view of the increasing amount of genomic data that become available, we will have a better understanding of the frequency and the role of HGT in land plants.

Acknowledgments

We thank three reviewers for their comments and suggestions. This work is supported by a NSF “Assembling the tree of life” grant (DEB 0830024), an NSFC Oversea, Hong Kong, Macao collaborative grant (31328003), and the CAS/SAFEA “International partnership program for creative research teams”.

Authors' contributions

The following declarations about authors' contributions to the research have been made: contributed to the writing of this review: QW, HS, JH.

Competing interests

No competing interests have been declared.

References

- Ochman H, Lawrence JG, Groisman EA. Lateral gene transfer and the nature of bacterial innovation. *Nature*. 2000;405(6784):299–304. <http://dx.doi.org/10.1038/35012500>
- Gogarten JP, Doolittle WF, Lawrence JG. Prokaryotic evolution in light of gene transfer. *Mol Biol Evol*. 2002;19(12):2226–2238.

3. Andersson JO. Lateral gene transfer in eukaryotes. *Cell Mol Life Sci*. 2005;62(11):1182–1197. <http://dx.doi.org/10.1007/s00018-005-4539-z>
4. Keeling PJ, Palmer JD. Horizontal gene transfer in eukaryotic evolution. *Nat Rev Genet*. 2008;9(8):605–618. <http://dx.doi.org/10.1038/nrg2386>
5. Andersson JO. Gene transfer and diversification of microbial eukaryotes. *Annu Rev Microbiol*. 2009;63:177–193. <http://dx.doi.org/10.1146/annurev.micro.091208.073203>
6. Richardson AO, Palmer JD. Horizontal gene transfer in plants. *J Exp Bot*. 2006;58(1):1–9. <http://dx.doi.org/10.1093/jxb/erl148>
7. Huang J. Horizontal gene transfer in eukaryotes: the weak-link model. *Bioessays*. 2013;35(10):868–875. <http://dx.doi.org/10.1002/bies.201300007>
8. Dunning Hotopp JC. Horizontal gene transfer between bacteria and animals. *Trends Genet*. 2011;27(4):157–163. <http://dx.doi.org/10.1016/j.tig.2011.01.005>
9. Boto L. Horizontal gene transfer in the acquisition of novel traits by metazoans. *Proc Biol Sci*. 2014;281(1777):20132450. <http://dx.doi.org/10.1098/rspb.2013.2450>
10. Gogarten JP, Townsend JP. Horizontal gene transfer, genome innovation and evolution. *Nat Rev Microbiol*. 2005;3(9):679–687. <http://dx.doi.org/10.1038/nrmicro1204>
11. Huang J, Gogarten JP. Concerted gene recruitment in early plant evolution. *Genome Biol*. 2008;9(7):R109. <http://dx.doi.org/10.1186/gb-2008-9-7-r109>
12. Selosse MA, Albert B, Godelle B. Reducing the genome size of organelles favours gene transfer to the nucleus. *Trends Ecol Evol*. 2001;16(3):135–141. [http://dx.doi.org/10.1016/S0169-5347\(00\)02084-X](http://dx.doi.org/10.1016/S0169-5347(00)02084-X)
13. Timmis JN, Ayliffe MA, Huang CY, Martin W. Endosymbiotic gene transfer: organelle genomes forge eukaryotic chromosomes. *Nat Rev Genet*. 2004;5(2):123–135. <http://dx.doi.org/10.1038/nrg1271>
14. Kleine T, Maier UG, Leister D. DNA transfer from organelles to the nucleus: the idiosyncratic genetics of endosymbiosis. *Annu Rev Plant Biol*. 2009;60(1):115–138. <http://dx.doi.org/10.1146/annurev.arplant.043008.092119>
15. Kurland CG, Canback B, Berg OG. Horizontal gene transfer: a critical view. *Proc Natl Acad Sci USA*. 2003;100(17):9658–9662. <http://dx.doi.org/10.1073/pnas.1632870100>
16. Bock R. The give-and-take of DNA: horizontal gene transfer in plants. *Trends Plant Sci*. 2010;15(1):11–22. <http://dx.doi.org/10.1016/j.tplants.2009.10.001>
17. Bergthorsson U, Richardson AO, Young GJ, Goertzen LR, Palmer JD. Massive horizontal transfer of mitochondrial genes from diverse land plant donors to the basal angiosperm *Amborella*. *Proc Natl Acad Sci USA*. 2004;101(51):17747–17752. <http://dx.doi.org/10.1073/pnas.0408336102>
18. Zhang D, Qi J, Yue J, Huang J, Sun T, Li S, et al. Root parasitic plant *Orobanche aegyptiaca* and shoot parasitic plant *Cuscuta australis* obtained Brassicaceae-specific strictosidine synthase-like genes by horizontal gene transfer. *BMC Plant Biol*. 2014;14(1):19. <http://dx.doi.org/10.1186/1471-2229-14-19>
19. Davis CC, Wurdack KJ. Host-to-parasite gene transfer in flowering plants: phylogenetic evidence from Malpighiales. *Science*. 2004;305(5684):676–678. <http://dx.doi.org/10.1126/science.1100671>
20. Xi Z, Bradley RK, Wurdack KJ, Wong K, Sugumaran M, Bombliks K, et al. Horizontal transfer of expressed genes in a parasitic flowering plant. *BMC Genomics*. 2012;13:227. <http://dx.doi.org/10.1186/1471-2164-13-227>
21. Xi Z, Wang Y, Bradley RK, Sugumaran M, Marx CJ, Rest JS, et al. Massive mitochondrial gene transfer in a parasitic flowering plant clade. *PLoS Genet*. 2013;9(2):e1003265. <http://dx.doi.org/10.1371/journal.pgen.1003265>
22. Mower JP, Stefanović S, Young GJ, Palmer JD. Plant genetics: gene transfer from parasitic to host plants. *Nature*. 2004;432(7014):165–166. <http://dx.doi.org/10.1038/432165b>
23. Li X, Zhang TC, Qiao Q, Ren Z, Zhao J, Yonezawa T, et al. Complete chloroplast genome sequence of holoparasite *Cistanche deserticola* (Orobanchaceae) reveals gene loss and horizontal gene transfer from its host *Haloxylon ammodendron* (Chenopodiaceae). *PLoS ONE*. 2013;8(3):e58747. <http://dx.doi.org/10.1371/journal.pone.0058747>
24. Sanchez-Puerta MV, Cho Y, Mower JP, Alverson AJ, Palmer JD. Frequent, phylogenetically local horizontal transfer of the *coxI* group I intron in flowering plant mitochondria. *Mol Biol Evol*. 2008;25(8):1762–1777. <http://dx.doi.org/10.1093/molbev/msn129>
25. Christin PA, Edwards EJ, Besnard G, Boxall SF, Gregory R, Kellogg EA, et al. Adaptive evolution of C₄ photosynthesis through recurrent lateral gene transfer. *Curr Biol*. 2012;22(5):445–449. <http://dx.doi.org/10.1016/j.cub.2012.01.054>
26. Svab Z, Maliga P. Exceptional transmission of plastids and mitochondria from the transplastomic pollen parent and its impact on transgene containment. *Proc Natl Acad Sci USA*. 2007;104(17):7003–7008. <http://dx.doi.org/10.1073/pnas.0700063104>
27. Diao X, Freeling M, Lisch D. Horizontal transfer of a plant transposon. *PLoS Biol*. 2006;4(1):e5. <http://dx.doi.org/10.1371/journal.pbio.0040005>
28. Vallenback P, Jaarola M, Ghatnekar L, Bengtsson BO. Origin and timing of the horizontal transfer of a *PgiC* gene from *Poa* to *Festuca ovina*. *Mol Phylogenet Evol*. 2008;46(3):890–896. <http://dx.doi.org/10.1016/j.ympev.2007.11.031>
29. Rice DW, Alverson AJ, Richardson AO, Young GJ, Sanchez-Puerta MV, Munzinger J, et al. Horizontal transfer of entire genomes via mitochondrial fusion in the angiosperm *Amborella*. *Science*. 2013;342(6165):1468–1473. <http://dx.doi.org/10.1126/science.1246275>
30. Park JM, Manen JF, Schneeweiss GM. Horizontal gene transfer of a plastid gene in the non-photosynthetic flowering plants *Orobanche* and *Phelipanche* (Orobanchaceae). *Mol Phylogenet Evol*. 2007;43(3):974–985. <http://dx.doi.org/10.1016/j.ympev.2006.10.011>
31. Sanderson MJ, Thorne JL, Wikström N, Bremer K. Molecular evidence on plant divergence times. *Am J Bot*. 2004;91(10):1656–1665. <http://dx.doi.org/10.3732/ajb.91.10.1656>
32. Emiliani G, Fondi M, Fani R, Gribaldo S. A horizontal gene transfer at the origin of phenylpropanoid metabolism: a key adaptation of plants to land. *Biol Direct*. 2009;4:7. <http://dx.doi.org/10.1186/1745-6150-4-7>
33. Yue J, Hu X, Sun H, Yang Y, Huang J. Widespread impact of horizontal gene transfer on plant colonization of land. *Nat Commun*. 2012;3:1152. <http://dx.doi.org/10.1038/ncomms2148>
34. Yue J, Hu X, Huang J. Horizontal gene transfer in the innovation and adaptation of land plants. *Plant Signal Behav*. 2013;8(5). <http://dx.doi.org/10.4161/psb.24130>
35. Dixon RA, Achnine L, Kota P, Liu CJ, Reddy MSS, Wang L. The phenylpropanoid pathway and plant defence – a genomics perspective. *Mol Plant Pathol*. 2002;3(5):371–390. <http://dx.doi.org/10.1046/j.1364-3703.2002.00131.x>
36. Dixon RA, Paiva NL. Stress-induced phenylpropanoid metabolism. *Plant Cell*. 1995;7(7):1085–1097. <http://dx.doi.org/10.1105/tpc.7.7.1085>
37. Yue J, Hu X, Huang J. Origin of plant auxin biosynthesis. *Trends Plant Sci*. 2014;19(12):764–770. <http://dx.doi.org/10.1016/j.tplants.2014.07.004>
38. Ligrone R, Duckett JG, Renzaglia KS. Major transitions in the evolution of early land plants: a bryological perspective. *Ann Bot*. 2012;109(5):851–871. <http://dx.doi.org/10.1093/aob/mcs017>
39. Jun JH, Ha CM, Nam HG. Involvement of the *VEP1* gene in vascular strand development in *Arabidopsis thaliana*. *Plant Cell Physiol*. 2002;43(3):323–330. <http://dx.doi.org/10.1093/pcp/pcf042>
40. Yang Z, Zhou Y, Huang J, Hu Y, Zhang E, Xie Z, et al. Ancient horizontal transfer of transaldolase-like protein gene and its role in plant vascular development. *New Phytol*. 2014 (in press). <http://dx.doi.org/10.1111/nph.13183>
41. Cai C, Ouyang S, Wang Y, Fang Z, Rong J, Geng L, et al. An Early Silurian vascular plant. *Nature*. 1996;379(6566):592–592. <http://dx.doi.org/10.1038/379592a0>
42. Möglich A, Yang X, Ayers RA, Moffat K. Structure and function of plant photoreceptors. *Annu Rev Plant Biol*. 2010;61:21–47. <http://dx.doi.org/10.1146/annurev-arplant-042809-112259>
43. Kawai H, Kanegae T, Christensen S, Kiyosue T, Sato Y, Imaizumi T, et al. Responses of ferns to red light are mediated by an unconventional

- photoreceptor. *Nature*. 2003;421(6920):287–290. <http://dx.doi.org/10.1038/nature01310>
44. Schneider H, Schuettelpelz E, Pryer KM, Cranfill R, Magallón S, Lupia R. Ferns diversified in the shadow of angiosperms. *Nature*. 2004;428(6982):553–557. <http://dx.doi.org/10.1038/nature02361>
 45. Schuettelpelz E, Pryer KM. Evidence for a Cenozoic radiation of ferns in an angiosperm-dominated canopy. *Proc Natl Acad Sci USA*. 2009;106(27):11200–11205. <http://dx.doi.org/10.1073/pnas.0811136106>
 46. Li FW, Villarreal JC, Kelly S, Rothfels CJ, Melkonian M, Frangedakis E, et al. Horizontal transfer of an adaptive chimeric photoreceptor from bryophytes to ferns. *Proc Natl Acad Sci USA*. 2014;111(18):6672–6677. <http://dx.doi.org/10.1073/pnas.1319929111>
 47. Osborne CP, Beerling DJ. Nature's green revolution: the remarkable evolutionary rise of C₄ plants. *Philos Trans R Soc Lond B Biol Sci*. 2006;361(1465):173–194. <http://dx.doi.org/10.1098/rstb.2005.1737>
 48. Ibrahim DG, Burke T, Ripley BS, Osborne CP. A molecular phylogeny of the genus *Alloteropsis* (Panicoideae, Poaceae) suggests an evolutionary reversion from C₄ to C₃ photosynthesis. *Ann Bot*. 2009;103(1):127–136. <http://dx.doi.org/10.1093/aob/mcn204>
 49. Christin PA, Freckleton RP, Osborne CP. Can phylogenetics identify C₄ origins and reversals? *Trends Ecol Evol*. 2010;25(7):403–409. <http://dx.doi.org/10.1016/j.tree.2010.04.007>
 50. Rice DW, Palmer JD. An exceptional horizontal gene transfer in plastids: gene replacement by a distant bacterial paralog and evidence that haptophyte and cryptophyte plastids are sisters. *BMC Biol*. 2006;4:31. <http://dx.doi.org/10.1186/1741-7007-4-31>
 51. Moszczynski K, Mackiewicz P, Bodyl A. Evidence for horizontal gene transfer from bacteroidetes bacteria to dinoflagellate minicircles. *Mol Biol Evol*. 2012;29(3):887–892. <http://dx.doi.org/10.1093/molbev/msr276>
 52. Bergthorsson U, Adams KL, Thomason B, Palmer JD. Widespread horizontal transfer of mitochondrial genes in flowering plants. *Nature*. 2003;424(6945):197–201. <http://dx.doi.org/10.1038/nature01743>
 53. Mower JP, Stefanović S, Hao W, Gummow JS, Jain K, Ahmed D, et al. Horizontal acquisition of multiple mitochondrial genes from a parasitic plant followed by gene conversion with host mitochondrial genes. *BMC Biol*. 2010;8(1):150. <http://dx.doi.org/10.1186/1741-7007-8-150>
 54. Soltis PS, Soltis DE. Angiosperm phylogeny: a framework for studies of genome evolution. In: Greilhuber J, Dolezel J, Wendel JF, editors. *Plant genome diversity*. Vienna: Springer; 2013. p. 1–11. (vol 2). http://dx.doi.org/10.1007/978-3-7091-1160-4_1
 55. Hao W, Palmer JD. Fine-scale mergers of chloroplast and mitochondrial genes create functional, transcompartmentally chimeric mitochondrial genes. *Proc Natl Acad Sci USA*. 2009;106(39):16728–16733. <http://dx.doi.org/10.1073/pnas.0908766106>
 56. Hao W, Richardson AO, Zheng Y, Palmer JD. Gorgeous mosaic of mitochondrial genes created by horizontal transfer and gene conversion. *Proc Natl Acad Sci USA*. 2010;107(50):21576–21581. <http://dx.doi.org/10.1073/pnas.1016295107>
 57. Maumus F, Epert A, Nogué F, Blanc G. Plant genomes enclose footprints of past infections by giant virus relatives. *Nat Commun*. 2014;5:4268. <http://dx.doi.org/10.1038/ncomms5268>
 58. Richards TA, Soanes DM, Foster PG, Leonard G, Thornton CR, Talbot NJ. Phylogenomic analysis demonstrates a pattern of rare and ancient horizontal gene transfer between plants and fungi. *Plant Cell*. 2009;21(7):1897–1911. <http://dx.doi.org/10.1105/tpc.109.065805>
 59. Won H, Renner SS. Horizontal gene transfer from flowering plants to Gnetum. *Proc Natl Acad Sci USA*. 2003;100(19):10824–10829. <http://dx.doi.org/10.1073/pnas.1833775100>
 60. Yoshida S, Maruyama S, Nozaki H, Shirasu K. Horizontal gene transfer by the parasitic plant *Striga hermonthica*. *Science*. 2010;328(5982):1128–1128. <http://dx.doi.org/10.1126/science.1187145>
 61. Intrieri MC, Buiatti M. The horizontal transfer of *Agrobacterium rhizogenes* genes and the evolution of the genus *Nicotiana*. *Mol Phylogenet Evol*. 2001;20(1):100–110. <http://dx.doi.org/10.1006/mpev.2001.0927>
 62. Nickrent DL, Blarer A, Qiu YL, Vidal-Russell R, Anderson FE. Phylogenetic inference in Rafflesiales: the influence of rate heterogeneity and horizontal gene transfer. *BMC Evol Biol*. 2004;4(1):40. <http://dx.doi.org/10.1186/1471-2148-4-40>
 63. Schönenberger J, Anderberg AA, Sytsma KJ. Molecular phylogenetics and patterns of floral evolution in the Ericales. *Int J Plant Sci*. 2005;166(2):265–288. <http://dx.doi.org/10.1086/427198>
 64. Davis CC, Anderson WR, Wurdack KJ. Gene transfer from a parasitic flowering plant to a fern. *Proc Biol Sci*. 2005;272(1578):2237–2242. <http://dx.doi.org/10.1098/rspb.2005.3226>