



# What we know so far and what we can expect next: A molecular investigation of plant parasitism

Juliane Karine Ishida<sup>1</sup>  and Elaine Cotrim Costa<sup>2</sup> 

<sup>1</sup>Universidade Federal de Minas Gerais (UFMG), Instituto de Ciências Biológicas, Departamento de Botânica, Belo Horizonte, MG, Brazil.

<sup>2</sup>Universidade Federal do Rio Grande (FURG), Instituto de Ciências Biológicas, Rio Grande do Sul, RS, Brazil.

## Abstract

The review explores parasitic plants' evolutionary success and adaptability, highlighting their widespread occurrence and emphasizing the role of an invasive organ called haustorium in nutrient acquisition from hosts. It discusses the genetic and physiological adaptations that facilitate parasitism, including horizontal gene transfer, and the impact of environmental factors like climate change on these relationships. It addresses the need for further research into parasitic plants' genomes and interactions with their hosts to better predict environmental changes' impacts.

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## Introduction

Windsor (1998) asserts that the parasitic lifestyle is the prevailing survival tactic on Earth. Notably, even among flowering plants, this strategy is found, with approximately 292 genera and 4750 species capable of exhibiting parasitic behavior (Nickrent, 2020). The repeated occurrence of parasitism in plants, seen around 12 or 13 times throughout evolution (Westwood *et al.*, 2010), emphasizes its remarkable adaptative capability and versatility. Indeed, this group is present in many ecosystems, including lush tropical forests and challenging habitats like dry and semi-arid areas, plains, savannas, and wetlands (Press and Graves, 1995). Their ability to adapt and use different survival tactics demonstrates their outstanding potential to navigate and thrive in response to various ecological stresses efficiently.

A common feature shared by all plants that adopted this alternative nutrient-acquisition strategy is the presence of a new organ known as haustorium (plural haustoria). This organ is the primary interface for exchanging materials between the parasite and its host plant. The structure, typically a modified root or stem, forms a physical and physiological link that aids the attachment of parasitic plants to their hosts, enabling them to draw water, nutrients, and other vital resources (Yoshida *et al.*, 2016). Haustoria are the defining feature of parasitic plants. For instance, the mycoheterotrophs that do not form haustoria are not classified as true parasitic plants (Hershey, 1999). Mycoheterotrophs are plants adapted to survive in dimly lit forests by deriving nutrients through parasitism on mycorrhizal fungi (Merckx *et al.*, 2009). Parasitized fungi have a symbiotic relationship with photosynthetic plants. In this

parasitism, mycoheterotrophs indirectly get organic carbon from green plants, using a fungus as an intermediary. Parasites exhibit higher transpiration rates (Ackroyd and Graves, 1997; Bell *et al.*, 2011; Amutenya *et al.*, 2023). It increases suction tension between the host-parasite link, creating a gradient that aids water transport by dragging nutrients towards the parasite in the xylem sap (Ackroyd and Graves, 1997; Jiang *et al.*, 2003; Jiang *et al.*, 2007). *Rhinanthus minor* and *R. alectorolophus* (Orobanchaceae) maintain open stomata throughout the day and night as a transpirational sink to maximize xylem sap extraction from its host plants (Jiang *et al.*, 2007; Světlíková *et al.*, 2018).

The specific structure and function of the haustorium vary depending on the type of parasitism. The haustorium in holoparasitic plants is the primary means for acquiring all necessary nutrients from the host through phloem-based connections, compensating for their inability to photosynthesize autonomously due to the lack of chlorophyll (Nickrent and Musselman, 2004). Conversely, in hemiparasitic plants, the haustorium aids in absorbing water and nutrients from the host (Nickrent and Musselman, 2004). Although this parasite can engage in photosynthesis, the rates often remain limited in some species compared to nonparasitic plants. Hemiparasites can be further categorized into obligate and facultative parasites based on the degree of dependency on the host. An obligatory parasitic plant cannot complete its life cycle without establishing a connection with a host. On the other hand, a facultative parasitic plant can live as an autotrophic plant, but it will benefit from having a nearby host. Another distinguishing feature among parasites is the extent of parasitic tissues that develop inside and externally within the host. Most species introduce specialized cells into their host to provide nourishment for the parasite. However, in certain species, vegetative growth primarily occurs within the host organism (endophytically), with the parasite emerging just for the purpose of flowering (Thorogood *et al.*, 2021).

Scientific investigations have advanced in the last 15 years and provided a deeper understanding of the complex molecular and physiological adaptations that enable parasitic plants to thrive. Studying how parasitic plants establish and maintain their reliance on host plants offers valuable insights into the intricate relationships and interdependencies within natural ecosystems. This review provides an overview of the current understanding of the modifications occurring in these plants' nuclear, mitochondrial, and plastid genomes, which have enabled them to achieve repeated success throughout evolution. We examine the current understanding of the haustorium induction mechanism and the extrinsic elements that can impact its development.

### How did parasitic plants evolve?

The growing amount of large-scale sequencing information on parasitic plants enables us to address essential inquiries about the modifications and evolutionary mechanisms that enabled the shift from nonparasitic to parasitic behavior. At least 12 independent evolutionary occurrences of plant parasitism have been documented (Westwood *et al.*, 2010), leading to the question of how parasitic plants managed to evolve multiple times during angiosperm evolution. This observation has sparked the hypothesis that common strategies might underlie the independent evolution of parasitic plants. In support of this argument, the genomes of distantly related lineages of parasitic plants (*Striga asiatica*, *Scurrula parasitica*, *Cuscuta australis*, two species of *Balanophora*, and *Sapria himalayana*) have shared genetic alterations that indicate a tendency towards parasitism (Chen *et al.*, 2023). Some species exhibiting high levels of host dependency often experience a progressive loss of genes associated with carbon synthesis, circadian rhythm, flower and root development, nitrogen transporters, and Abscisic acid (ABA) biosynthesis (Chen *et al.*, 2023). The lack/reduced ability to synthesize ABA and respond to the circadian rhythm is intriguing. The genome comparison of mycoheterotrophic orchids *Gastrodia elata* and *Apostasia shenzhenica* (Zhang *et al.*, 2017) with parasitic plants (*C. australis*, *S. asiatica*, and *Sapria himalayana*) revealed a reduction in homologs associated with functional categories such as photosynthesis, light perception, circadian clock, flowering time regulation, nutrient uptake, leaf, and root development (Xu *et al.*, 2021). Parasitism syndrome appears to promote a decreased sensitivity to environmental changes. As the parasite establishes a closer relationship with its host, it becomes increasingly dependent on the host's external perception.

Another significant aspect that contributes to the success of parasitism is the frequency of horizontal gene transfer (HGT) (Ding *et al.*, 2012). The HGT is a prevalent mechanism for directly introducing new genes to recipient species that are distantly related (Wickell and Li, 2020; Ma *et al.*, 2022). As a result, this process can lead to the emergence of novel features, which in turn can contribute to the adaptation of species to new ecological niches (Ding *et al.*, 2012; Wickell and Li, 2020; Ma *et al.*, 2022). HGT has been demonstrated in the nuclear genomes of parasitic plants (Yoshida *et al.*, 2010), as well as in their mitochondrial (Mower *et al.*, 2004; Mower *et al.*, 2010; Xi *et al.*, 2013) and plastidial (Sanchez-Puerta *et*

*al.*, 2023) genomes. The nuclear genome of eukaryotic cells differs from organellar genomes in mitochondria and plastids. Mitochondrial DNA (mtDNA) and plastid DNA (ptDNA) are circular, double-stranded polymers with essential genes for organelle function. MtDNA produces energy, whereas plastid ptDNA photosynthesizes (Oldenburg and Bendich, 2015). Maternal inheritance is the predominant pattern for mtDNA and ptDNA (Sato and Sato, 2013; Sakamoto and Takami, 2024), although biparental or paternal transmission has been observed (Weihe *et al.*, 2009; Shen *et al.*, 2015; Sakamoto and Takami, 2024). Both mitochondrial DNA (mtDNA) and plastid DNA (ptDNA) have higher mutation rates in comparison to nuclear DNA and can experience gene transfer events (Cui *et al.*, 2021).

An extensive search for HGT in parasitic systems belongs to Orobanchaceae has been conducted, relying primarily on phylogenetic approaches. HGT is therefore suspected when a DNA sequence from a parasite is phylogenetically aggregated with its host instead of its nearest relatives. Examining eight host species in Fabaceae and six in Poaceae, no HGT events were detected in the facultative parasites in *Pedicularis keiskei*, *Phtheirospermum japonicum*, and *Melampyrum roseum* (Kado and Innan, 2018). In contrast, over 100 events were documented in the obligate holoparasites *Orobanche minor* and *Aeginetia indica* (Kado and Innan, 2018), indicating that the amount of HGT is directly proportional to a higher degree of host dependency. A similar pattern emerged when studying the facultative (*Triphysaria versicolor*), obligate hemiparasite (*Striga hermonthica*), and holoparasite (*Phelipanche aegyptiaca*) (Yang *et al.*, 2016). However, with a more significant number of host species (22 representatives of land plants), the authors noted three potential events in the facultative parasite (Yang *et al.*, 2016). Furthermore, convergence is observed in the horizontally acquired sequences of two unrelated parasites: one belonging to the Convolvulaceae and the other belonging to the Orobanchaceae (Yang *et al.*, 2019). Therefore, it is likely that HGT genes, which are expressed and advantageous for the parasite, are preserved during evolution. In contrast, those that do not benefit the host are eliminated.

The high occurrence of intronic sequences and sections surpassing 100 kb, which preserve synteny between host and parasite sequences, indicates that the principal method for gaining sequences from the host includes processes mediated by DNA rather than mRNA via retro-transfer (Mower *et al.*, 2004; Xi *et al.*, 2012; Kado and Innan, 2018). While RNA exchange occurs through the haustorium (Westwood *et al.*, 2009; Leblanc *et al.*, 2012; Kim *et al.*, 2014; Van and Alamy, 2018; Kaga *et al.*, 2020; Zangishei *et al.*, 2022), however, one possible explanation for the infrequent occurrence of RNA-mediated HGT is that the mRNA must undergo reverse transcription to DNA before it can be incorporated into a plant genome. However, the efficiency of this reverse transcription process is exceedingly low. Another factor is the quick turnover of RNA in comparison to DNA, making it susceptible to rapid destruction by RNases. The mechanism underlying the incorporation of host-derived DNA into the parasite genome remains unclear. The movement of large DNA fragments is not limited to parasites. This phenomenon is also found in grafted

tissues of nonparasitic plants (Stegemann and Bock, 2009; Stegemann *et al.*, 2012). Indeed, the haustorial connection closely resembles graft junctions, as both structures are involved in the vascular connection between two organisms (Kokla and Melnyk, 2018; Kurotani *et al.*, 2020). Thus, close association is likely crucial in transferring DNA fragments.

HGT can be a powerful evolutionary tool for plants. It allows them to acquire new genes, potentially introducing novel functionalities that improve their overall fitness. A large-scale study revealed that green plants (Archaeplastida) obtained many of their Glycosyl Hydrolase (GH) genes through HGT, primarily from bacteria and fungi (Kfoury *et al.*, 2024). These enzymes are crucial for breaking down carbohydrates and are essential for various cellular processes (Garron and Henrissat, 2019). Interestingly, the acquisition of these “foreign” genes was followed by a shift in how GH enzymes were distributed within plant cells (Kfoury *et al.*, 2024). There was a significant increase in GH proteins targeted to the extracellular space (Kfoury *et al.*, 2024). This strategic positioning likely played a key role in the diversification of plant cell wall polysaccharides and the development of more effective defense mechanisms against pathogens. The impact of HGT for parasitic lifestyle was documented in various organisms, including nematodes (Haegeman *et al.*, 2011) and oomycetes (Richards *et al.*, 2011). These gene transfers involve incorporating genes that can degrade plant cell walls. This suggests that the evolution of parasitic life in plants might have occurred via multiple acquisitions of sequences from other species, fungi being a particular focus (Richards *et al.*, 2011; Alexander *et al.*, 2016). The nuclear gene HGT played a relevant role in some parasitic plants, while the horizontal transfer of mitochondrial genes seems even more widespread (Davis and Xi, 2015; Zervas *et al.*, 2019). These findings underscore the substantial degree of HGT in the mitochondrial genome of parasitic species, potentially involving genes acquired from their hosts over evolutionary timescales. However, the precise biological functions of these transferred genes in the context of plant parasitism necessitate further in-depth studies.

Interestingly, it was reported that two unrelated parasite species, *P. aegyptiaca* and *C. australis*, acquired genes encoding for Strictosidine Synthase-Like (*SSL*) from Brassicaceae independently (Zhang *et al.*, 2014). The function of these *SSL* genes remains to be revealed. Significantly, the *SSL* genes found in parasitic plants are under positive selection and exhibit continuous transcription throughout various phases of development (Zhang *et al.*, 2014). This indicates that the foreign *SSL* genes in these species may have contributed to their adaptation to a parasitic lifestyle or environment and subsequent evolution.

### Paradox of genome size of parasitic plant species

The variation in genome size within parasitism has prompted various studies investigating its correlation with evolutionary alterations in parasitism and patterns of host usage. A shift towards parasitism is generally associated with a shrink in genome size, with parasites showing smaller genomes than nonparasitic organisms (Poulin and Randhawa,

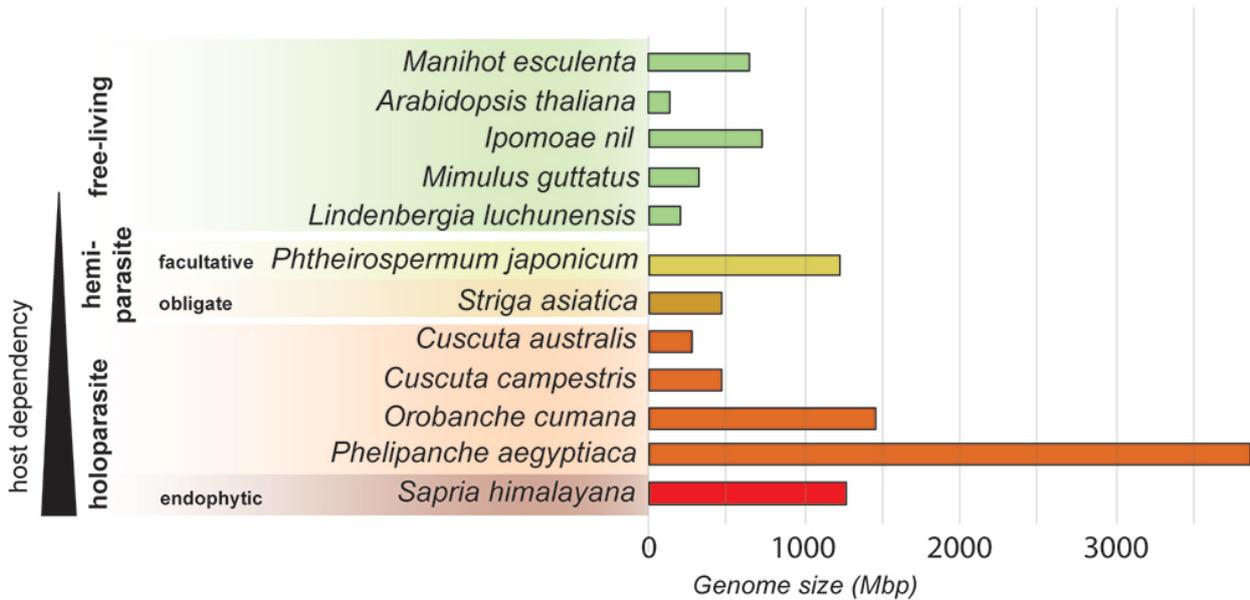
2015; Coghlan *et al.*, 2018). However, this generalization does not hold true for all parasitic organisms; the genomes of parasitic plants serve as a counterpoint (Lyko and Wicke, 2021). Parasitic plants may exhibit larger genomes (Figure 1). For example, the highly host-dependent endophytic parasite, *Sapria himalayana*, has a genome size of 1,280 Mbp, which is on par with that of the facultative hemiparasite *P. japonicum*, which has a genome of 1,227 Mbp (Figure 1). Similarly, the holoparasites *P. aegyptiaca* and *Orobanche cumana* exhibit even larger genomes, with sizes of 3,877 Mbp and 1,463 Mbp, respectively (Figure 1). This is in stark contrast to their free-living relatives, such as *Mimulus guttatus* with a 313 Mbp genome and *Lindenbergia luchunensis* with a 212 Mbp genome (Figure 1). This inconsistency necessitates further investigation into the factors influencing genome size variation within parasitic plant lineages.

One important consideration when interpreting genome size data for parasitic plants depicted in Figure 1 lies in the inherent challenges associated with sequencing and annotating exceptionally large genomes. These technical difficulties often lead researchers to prioritize species with more manageable characteristics, such as smaller genomes, lower heterozygosity (genetic variation within an individual), reduced repetitive DNA content, and a lack of polyploidy (multiple sets of chromosomes). Supporting this notion is the observation that despite significant advancements in sequencing technology and a substantial increase in the number of sequenced plant species over the past two decades, there appears to be a relative stagnation in the range of reported genome sizes. The minimum, maximum, and median values observed in the last three years (12.40 Mb, 27.60 Gb, and 489.65 Mb, respectively) are not drastically different from those documented in the preceding twenty years (Xie *et al.*, 2024). This lack of significant change in the spectrum of sequenced genome sizes suggests a potential bias towards species with more easily analyzed genomes (Xie *et al.*, 2024). Consequently, the data presented in Figure 1 might not fully capture the true extent of genome size variation within parasitic plants, particularly for those harboring exceptionally large genomes.

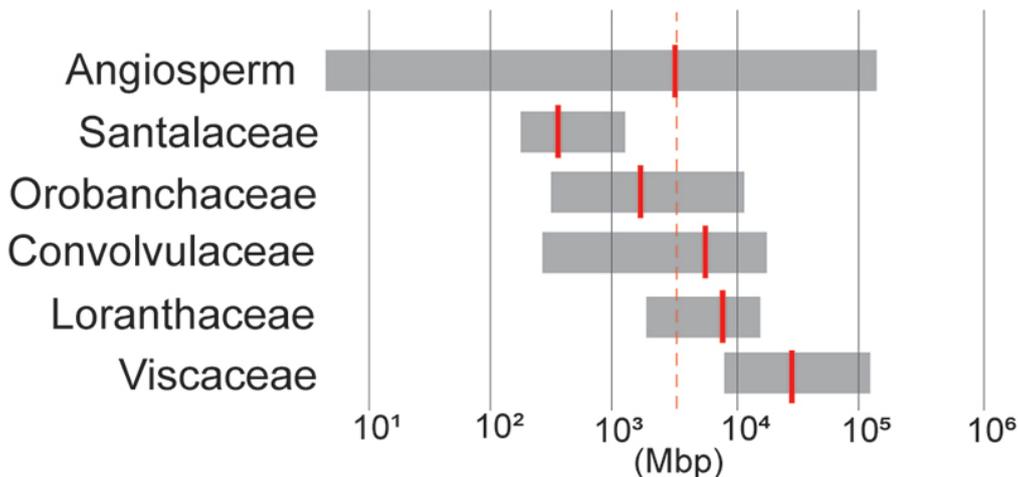
To address this potential bias, we sought to broaden the scope of our analysis by incorporating data from the Plant DNA C-value database (<http://cvalues.science.kew.org/>). This resource provides genome size estimates for a wider range of plant species. Restricting our analysis to families containing at least two genera with parasitic representatives, we observed a range of genome sizes within parasitic plant lineages (Figure 2) and compared them to the average genome size in Angiosperms. While some families, such as Santalaceae (average: 569 Mb) and Orobanchaceae (average: 2747 Mb), exhibit average genome sizes below the angiosperm average. However, a different observation was indicated by Piednoël *et al.* (2012) that suggested that within Orobanchaceae, obligate parasitic species have larger genomes than autotrophic and hemiparasitic species (Piednoël *et al.*, 2012). These divergent findings may arise from limitations in both analyses; in our case, it's linked to the chosen methodology and the comprehensiveness of the database. Therefore, further investigation is warranted to gain deeper insights into this inconsistency. In our approach, we observed larger genomes

in *Cuscuta* spp. (average: 7,028 Mb) and Loranthaceae (average: 8,849 Mb), with Viscaceae notably possessing the highest average genome size on record (44,656 Mb) (Figure 2). Our analysis reveals a remarkable diversity in genome size among parasitic plant species, challenging the previously held notion of a universal reduction in genome size associated with

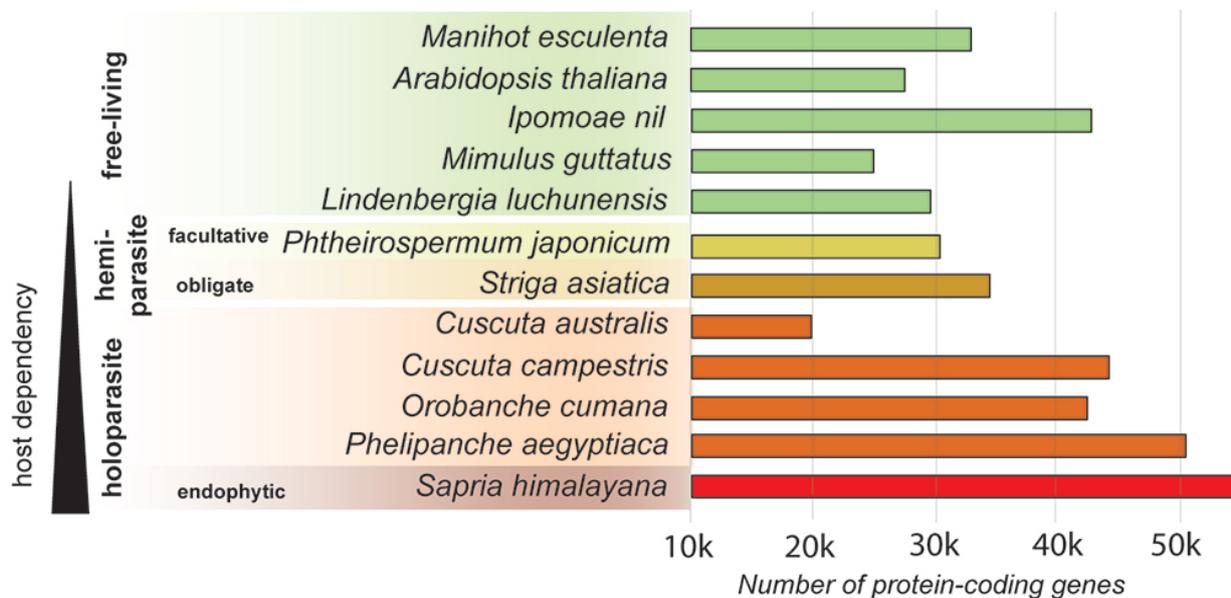
parasitism (Poulin and Randhawa, 2015; Coghlan *et al.*, 2018). This underscores the paradox of parasitic plant genomes being larger and more complex than anticipated (Figures 1 and 2) (Lyko and Wicke, 2021). Importantly, it also emphasizes that the observed paradox might not be universally applicable across all parasitic plant groups (Figure 2).



**Figure 1** – Genome size of parasitic plants compared to nonparasitic plants. Only those with fully sequenced and assembled genomes. The arrangement reflects the degree of host dependence. At the top, in green, are the free-living plants, which include *Manihot esculenta* (Alaba *et al.*, 2014), *Arabidopsis thaliana* (Lamesch *et al.*, 2012), *Ipomoea nil* (Hoshino *et al.*, 2016), *Mimulus guttatus* (Hellsten *et al.*, 2013) and *Lindenbergia luchunensis* (Xu *et al.*, 2022). In light yellow is the facultative hemiparasite *Phtheirospermum japonicum* (Cui *et al.*, 2020)— the obligate hemiparasite *Striga asiatica* (Yoshida *et al.*, 2019) in dark yellow. Holoparasites are depicted in orange/red and include *Cuscuta australis* (Sun *et al.*, 2018), *C. campestris* (Vogel *et al.*, 2018), *Orobanche cumana* (Xu *et al.*, 2022), and *Phelipanche aegyptiaca* (Xu *et al.*, 2022). Lastly, the endophytic holoparasite *Sapria himalayana* (Cai *et al.*, 2021) is shown in red, representing the most extreme parasitism.



**Figure 2** – Estimated genome size (C-value) of parasitic plants. The C-values were obtained from Plant DNA C-values Database (Leitch *et al.*, 2019) maintained by Kew Royal Botanic Garden. The prime estimated c-value (in Mbp) from the database was compared with a list of parasitic plant genera (U.S. DEPARTMENT OF AGRICULTURE, 2024). Only families that have a minimum of two genera of parasitic plant species with documented C-values in the database were examined in this analysis. The grey bars represent the range of C-values observed in each group, from the lowest to the largest, while the red bars indicate the average genome size. The dashed line indicates the average genome size of all angiosperm plants recorded in the database. For Santalaceae, the genera included were *Rhoicarpus* sp., *Santalum* sp. and *Comandra* sp. In Orobanchaceae, the listed genera were *Bartsia* sp., *Bellardia* sp., *Cistanche* sp., *Euphrasia* sp., *Melampyrum* sp., *Nothobartsia* sp., *Odontitella* sp., *Parentucellia* sp., *Pedicularis* sp., *Phelipanche* sp., *Phelypaea* sp., *Schwalbea* sp., *Orobanche* sp., *Pedicularis* sp., *Odontites* sp. and *Rhinanthus* sp. Convolvulaceae included *Cuscuta* sp. Loranthaceae encompassed the genera *Alepis* sp., *Amylothea* sp., *Benthamina* sp., *Decaisnina* sp., *Dendrophthoe* sp., *Diplatia* sp., *Amyema* sp., *Nuytsia* sp., *Loranthus* sp., *Lysiana* sp., *Macrosolen* sp., *Ileostylus* sp., *Muellerina* sp., *Peraxilla* sp., *Sogerianthe* sp. and *Tupeia* sp. Finally, Viscaceae comprised *Viscum* sp. and *Arceuthobium* sp.



**Figure 3** – Number of protein-coding genes in the genome of parasitic plants compared to nonparasitic plants. Only those with fully sequenced and assembled genomes. The arrangement reflects the degree of host dependence. At the top, in green, are the free-living plants, which include *Manihot esculenta* (Alaba *et al.*, 2014), *Arabidopsis thaliana* (Lamesch *et al.*, 2012), *Ipomoea nil* (Hoshino *et al.*, 2016), *Mimulus guttatus* (Hellsten *et al.*, 2013) and *Lindenbergia luchunensis* (Xu *et al.*, 2022). In light yellow, facultative hemiparasite *Phtheirospermum japonicum* (Cui *et al.*, 2020). The obligate hemiparasite *Striga asiatica* (Yoshida *et al.*, 2019) in dark yellow. Holoparasites are depicted in orange/red and include *Cuscuta australis* (Sun *et al.*, 2018), *Cuscuta campestris* (Vogel *et al.*, 2018), *Orobanche cumana* (Xu *et al.*, 2022), and *Phelipanche aegyptiaca* (Xu *et al.*, 2022). Lastly, the endophytic holoparasite *Sapria himalayana* (Cai *et al.*, 2021) is shown in red, representing the most extreme parasitism.

These comparisons underscore a significant discrepancy: the size of the genome of a parasitic plant does not appear to directly correlate with its level of host dependency (Figures 2-3) which is consistent with the findings of Neumann *et al.* (2021). The variation in protein-coding gene numbers across different parasitic plant species (Figure 3) strengthens the evidence against a direct correlation between genome size and host dependency (Figure 3). The HGT and the mobility of large DNA fragments have been proposed as potential contributors to the expansion of genome sizes in parasitic plants (Lyko and Wicke, 2021). These mechanisms could potentially explain the observed variation between parasitic plant species. Furthermore, a recent study suggests a potential link between genome size and the type of centromere organization (Neumann *et al.*, 2021). This hypothesis is supported by observations in *Cuscuta* spp., where the transition to holocentricity (where centromeres are diffusely distributed along the chromosome) coincided with significant changes in several key features. The changes include the composition of centromeric chromatin, the makeup of repetitive DNA sequences, and even the overall number of chromosomes. The observed variation suggests that the transition to holocentricity might have been accompanied by multiple rearrangements in chromosome structure (karyotype rearrangements) (Neumann *et al.*, 2021). This finding aligns with the existing hypothesis that holocentric chromosomes exhibit a higher tolerance for chromosome fusions and fissions, potentially facilitating the observed changes in *Cuscuta*. Despite these advancements in understanding genome size variation in parasitic plants, the paradox of their larger genomes compared to typical free-living relatives remains unsolved. Research efforts should be directed towards unraveling the biological significance of

these large genomes and identifying the key factors driving the observed variation within this diverse group of organisms.

### Mitochondrial genomes in parasitic plants

Plant mitochondria's primary function is producing energy through oxidative phosphorylation (OXPHOS) (Braun, 2020). In aerobic eukaryotes, OXPHOS typically involves four respiratory-chain complexes (I to IV) and an ATP synthase (complex V). The complexes within the inner membrane of plant mitochondria facilitate electron movement through redox reactions, forming the Electron Transport Chain (ETC). This process ultimately results in a proton gradient, allowing for the synthesis of ATP through the activity of the ATP-synthase protein (Schertl and Braun, 2014). Complex I serve as the primary entry point for most electrons in the respiratory chain, facilitating their transfer from matrix NADH to ubiquinone (Braun, 2020). Complex I subunits were previously considered essential for multicellular eukaryotes' energy production and survival. However, it has been challenged by the parasitic mistletoe, whose mitogenomes lack all the *nad* genes encoding subunits of complex I in addition to *ccmB* and *matR* (Skippingtona *et al.*, 2015; Petersen *et al.*, 2015; Zervas *et al.*, 2019). Strikingly, the mitochondrial genes were not transferred to the host genome, and biochemical evidence indicates that the assembly of these respiratory complexes did not occur in the membranes of parasite mitochondria (Senkler *et al.*, 2018). Mistletoes are not a monophyletic group (Vidal-Russell and Nickrent, 2008; Nickrent, 2011) and are presently categorized into three families in Santalales (Santalaceae, Loranthaceae, and Misodendraceae) (Nickrent, 2011; Chase *et al.*, 2016). Currently, five species (*Viscum scurruloideum*,

*V. album*, *V. minimum*, *V. crassulae*, and *Phoradendron liga*) in Santalaceae exhibit the absence of complex I (Skippingtona *et al.*, 2015; Petersen *et al.*, 2015; Zervas *et al.*, 2019), a trait not observed in *Loranthus europaeus* (Loranthaceae) (Zervas *et al.*, 2019). This suggests that the loss of complex I occurred during the evolutionary path of parasitic mistletoes within Santalaceae and not in Loranthaceae. The confirmation or refutation of this observation may be possible with further analysis of complete mitogenomes of other mistletoe species.

The peculiar situation of mitochondria from the parasitic mistletoe plant raises questions about how OXPHOS works in these species. How can these organelles provide enough energy for the parasite? The response is that they are probably not. The organization of mitochondrial complexes in *V. album* differs from that of nonparasitic species (Senkler *et al.*, 2018). Complexes II and IV are often coupled to form a supercomplex, whereas complexes II and V are in smaller amounts (Senkler *et al.*, 2018). This reorganization seems to impact the activity levels in the respiratory chain, resulting in reduced ATP levels in *V. album* compared to nonparasitic plants. The impaired energy production seems to be compensated by a rise in sugar intake from the host (Maclean *et al.*, 2018).

Aside from their essential role in energy metabolism, plant mitochondria also have a vital function in other cellular processes, including apoptosis (Scott and Logan, 2008) and cell proliferation (Kianian and Kianian, 2014). In addition, these organelles play a role in regulating signaling pathways that include crucial secondary messengers such as calcium signaling and reactive oxygen species (ROS) (Logan, 2006; Scott and Logan, 2008; Schwarzländer and Finkemeier, 2013; van Aken, 2021). The mitogenomes of parasitic plants were shown to include foreign sequences derived from several host plant species' nuclear and mitochondrial genomes (Bellot *et al.*, 2016; Sanchez-Puerta *et al.*, 2019; Cusimano and Renner, 2019). The presence of HGT in the mitogenome raises concerns about its potential influence on parasitism efficiency. An initial observation attempting to address this question suggests that there is seemingly no correlation between the degree of the parasite's reliance on the host and the frequency of HGT events in the mitogenomes. Notably, there are significant variations of host-derived sequences in mitogenomes across parasitic plants. For example, in *Rafflesia cantleyi* (Rafflesiaceae), up to 40% of the mitochondrial genes are acquired from their host's mitochondrial genome (Xi *et al.*, 2013).

Another example is *Ombrophytum subterraneum* (Balanophoraceae), with 14% of mitogenome acquired from the host species (Roulet *et al.*, 2020). However, the most striking example is found in *Lophophytum mirabile* (Balanophoraceae), where 80% of the mitochondrial sequences are derived from the hosts (Sanchez-Puerta *et al.*, 2017; Sanchez-Puerta *et al.*, 2019). A shared characteristic among them is that most foreign genes have complete reading frames and are actively transcribed. Host-derived sequences frequently replace their native homologs in parasitic organelles, appearing in clusters as large fragments while maintaining the synteny with their donor sequence. Therefore, this evidence suggests that the transfer occurs in DNA molecules, potentially through a homologous recombination process (Mower *et al.*, 2004; 2010).

Based on this logic, for recombination to occur, DNA fragments must be able to move between host and parasite cells. The structure of certain mitogenomes reveals a clue to the potential mechanism. In the highly HGT-prone parasite *L. mirabile*, its mitogenome (822 kb) is segmented into 54 subgenomes—circular chromosomes ranging from 7.2 to 580 kb, with 29 of them carrying intact genes (Sanchez-Puerta *et al.*, 2017). Three other holoparasitic plants in Balanophoraceae, *Rhopalocnemis phalloides* (Yu *et al.*, 2022), *Ombrophytum subterraneum* (Roulet *et al.*, 2020) and *Thonningia sanguinea* (Zhou *et al.*, 2023), are reported to consist of 21, 54 and 18 minicircular chromosomes, respectively. These small circular chromosomes share a conserved region containing a replication origin, implying they may replicate independently. The exact mechanism of this replication remains elusive. One potential explanation is the rolling circle mechanism (Yu *et al.*, 2022), a strategy previously demonstrated in yeast DNA (Prasai *et al.*, 2017), worms (Lewis *et al.*, 2015), and other flowering plants (Backert *et al.*, 1996; Backert, 2002). The multichromosomal mitochondrial genome is not a unique property observed in parasites. In soybeans, for example, it is estimated that the mitochondrial DNA is segmented into small circular structures (Synenki *et al.*, 1978). The genus *Silene* (Caryophyllaceae) has been shown to contain the most extensive and most intricate multichromosomal mitogenomes, distributed into 24 chromosomes. However, many of them do not possess the ability to code for proteins. In addition, *Amborella trichopoda* has a total of five circular chromosomes (Rice *et al.*, 2013). Three chromosomes are found in *Populus simonii* (Salicaceae) (Bi *et al.*, 2022) and two in hybrid sugarcane (Shearman *et al.*, 2016). However, the close connection between a parasite and its host via the haustorium may serve as a channel to transmit foreign autonomous chromosomes across species.

The prevalence of a substantial amount of HGT described for *L. mirabile* and *R. cantleyi* is not a universal trend among parasitic plants. HGT has little or no influence on the mitogenome in several host-parasite partnerships. For instance, in *Sapria himalayana* (Rafflesiaceae), the HGT level is approximately 0.33%, while *Castilleja paramensis* (Orobanchaceae) shows 1.5%. In the case of the hemiparasite *V. scurruloideum* (Santalaceae), the HGT level is 4.7%. Additionally, there is a lack of clear evidence of HGT in mitogenomes from *Cuscuta* spp. (Convolvulaceae) (Anderson *et al.*, 2021; Lin *et al.*, 2022).

## Plastid genome

The plastid genome of parasitic plants serves as a prime example of evolutionary adaptation and genomic plasticity resulting from a relaxation of evolutionary pressures (Bromham *et al.*, 2013). The plastid genome has undergone notable modifications in parasitic plants due to their distinctive lifestyle and evolutionary adaptations. In some species, like *Cuscuta* spp., these alterations include size reduction, changes in nucleotide composition resulting in a higher AT percentage compared to nonparasitic plants, and a bias in codon usage (Chen *et al.*, 2024).

Heterotrophic plants, such as mycoheterotrophy and parasitic plants, experience continuous deterioration of their functional plastome, often correlated with their dependence on

a host. The most significant proportion of plastid inactivation genes is in endophytic holoparasites, less often lost in facultative plants. Commonly lost genes in heterotrophic organisms include genes like NAD(P)H dehydrogenase complex (*ndh* genes), plastid-encoded polymerase (PEP), and photosynthesis genes, while the most conservative sequences are those involved in translation machinery (Wicke and Naumann, 2018). The *ndh* genes encode multiple complexes that enable cyclic electron transport across thylakoid membranes. They provide extra ATP to organisms in stressful environments to repair stroma over-reduction and maintain redox system balance in the electron transfer chain (Ma *et al.*, 2021). The lack of *ndh* genes is reported in the plastome of the holoparasite *Cuscuta* spp. (Convolvulaceae) (Braukmann *et al.*, 2013; Banerjee and Stefanović, 2020; 2023); and Orobanchaceae species, such as *Aeginetia indica* (Chen *et al.*, 2020), and in the facultative parasites *Pedicularis* spp. (Li *et al.*, 2021). In contrast, *P. japonicum*, a facultative parasite in the same tribe as *Pedicularis* (Pedicularideae), has not shown any loss of plastid genes (Li *et al.*, 2021). An extreme case of plastid genome reduction can be seen in the endophytic parasitic plant *Pilostyles boyacensis* (Apodanthaceae), which retains only seven functional genes in its plastome: *accD*, *rpl2*, *rrn16*, *rrn23*, *rps3*, *rps12* and *PbOx* (Arias-Agudelo *et al.*, 2019). Conversely, total loss of the plastome has been documented in Rafflesiaceae species, such as *Rafflesia lagascae* (Molina *et al.*, 2014) and *Sapria himalayana* (Cai *et al.*, 2021). The potential loss has also been reported in *Cuscuta* subgenus *Grammica* (Banerjee and Stefanović, 2023).

The accelerated pace of molecular evolution in the three genomes, including the mitochondrial, nuclear, and chloroplast genomes, is a defining characteristic of the shift from autotrophic to heterotrophic (Bromham *et al.*, 2013). This increased mutation rate in parasitic plants, which may be the result of relaxed environmental pressure, is followed by a decrease in the amount of GC content that is present in the genomes of plastids (Wicke *et al.*, 2016; Wicke and Naumann, 2018). An abundance of A+T in plant sequences is linked to a reduction of genome complexity and a higher ratio of structural organization (Müller *et al.*, 1999; Sundararajan *et al.*, 2016; Bowers *et al.*, 2022), which may be the driving force behind the influence on the reduction of the size of the plastid genome in parasitic plants. The parasitic plants *Balanophora reflexa* and *B. laxiflora* (Balanophoraceae) exhibit notably high AT-rich plastomes, with AT percentages of 88.4% and 87.8%, respectively. Notably, their protein-coding genes show an even higher inclination towards AT content, approximately 91% (Su *et al.*, 2019). In an unusual genetic twist, *B. reflexa* and *B. laxiflora* have altered their genetic code, reassigning the universally recognized stop codon TAG to code for tryptophan while still using TAA as a stop codon (Su *et al.*, 2019). It is not a unique example of the variant genetic code *Mycoplasma capricolum* similarly reassigned TGA to encode tryptophan (Yamao *et al.*, 1985). Yet, it remains a seldom observed phenomenon (Kim *et al.*, 2023). The presence of a TA-rich genome in these cases could be attributed to constraints related to nitrogen scarcity and energy demands. Notably, the plastid proteins of both *B. reflexa* and *B. laxiflora* do not show a reduction in nitrogen-rich amino acids or energy costs (Roy Smith, 2019; Su *et al.*, 2019).

## Reshaping the parasitic cell fate during the haustorium formation

Studying parasitic plants at the molecular level remains a challenging task. It happens because the targeted parasitic species must have certain features, such as small size, ease of cultivation, and a short life cycle. Species like mistletoes, for example, have a life cycle that exceeds three years (Reid *et al.*, 1995), making them unsuitable for use in several daily laboratory routines. Seed production is further constrained, particularly for obligatory plants, which rely on a host organism to produce seeds. Additionally, the time and substantial budget required to develop genetic information and manipulation tools present significant obstacles. Orobanchaceae encompasses a range of plant types, including free-living plants and hemi- and holoparasitic species, each displaying varying degrees of reliance on a host. *Triphysaria versicolor* and *P. japonicum* are widely recognized as essential models in the field of parasitic plant research (Tomilov *et al.*, 2007; Yoshida *et al.*, 2020; 2019; Ishida *et al.*, 2011; 2015; 2017 a, b; Cui *et al.*, 2016; Yoshida *et al.*, 2016; Spallek *et al.*, 2017; Cui *et al.*, 2020; Masumoto *et al.*, 2021). Currently, it is available the *P. japonicum* genome (Cui *et al.*, 2020), multiple transcriptome datasets (Ichihashi *et al.*, 2015; 2016; Cui *et al.*, 2016), genetic transformation (Ishida *et al.*, 2011), and *in vitro* assays of haustorium formation make *P. japonicum* (Ishida *et al.*, 2017a) an attractive model organism for studying the mechanisms underlying cell destiny and cellular reshaping in the development of parasitic organ haustorium.

### *Phtheirospermum japonicum*

*P. japonicum* is a facultative root hemiparasite that attaches to host plants through the development of lateral haustoria (Westwood *et al.*, 2010). Host root compounds trigger host perception of haustorium-inducing factors (HIFs) by the *P. japonicum* root, such as 2,6-dimethoxybenzoquinone (DMBQ), lignin units, and flavonoids (Goyet *et al.*, 2019), which are derived from the lignin biosynthetic pathway (Cui *et al.*, 2018). After signal perception of HIFs by *P. japonicum* root, the prehaustorium begins through divisions and expansion of the epidermal and outermost cortical cells regulated by the auxin biosynthesis gene *PjYUC3* (Ishida *et al.*, 2016). This regulation promotes the formation of haustorium hairs that differentiate from epidermal cells (Cui *et al.*, 2016), which secrete mucilage that helps the parasite attach to the host surface (Yoshida *et al.*, 2016). The cell specificity of the haustorium hairs has been demonstrated by an *AtPGP4* epidermis marker gene (Wakatake *et al.*, 2018). In the haustorium organogenesis, the epidermis, endodermis, and most cortical cells of the parasite roots are genetically reprogrammed, originating new cell fates that cell identities confirmed by cell type-specific marker genes (Wakatake *et al.*, 2018).

In the early haustorium development stages, the epidermal cells of the haustorium apex lose their identities and differentiate into elongated intrusive cells with palisade-like shapes and thin walls, which invade the host root tissues toward the vascular system (Wakatake *et al.*, 2018) (Figure 4). The intrusive cells express intrusive-cell-specific genes,

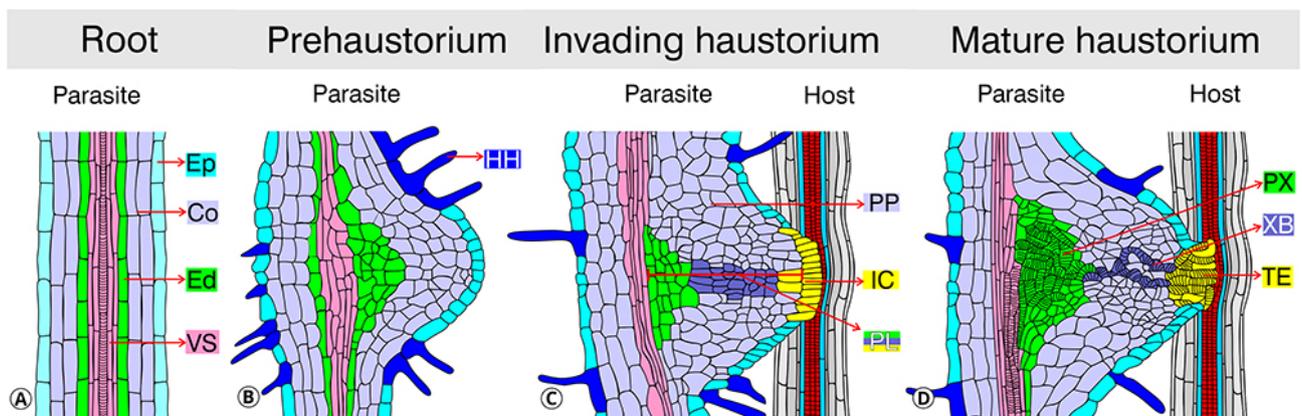
including *INTRUSIVE CELL-SPECIFIC LEUCINERICH REPEAT RECEPTOR-LIKE KINASE 1 (ICSL1)*, *GERMIN-LIKE PROTEIN 1 (GLP1)*, and several Subtilase encoding genes (*SBTs*) (Ogawa *et al.*, 2021). The Subtilase activity may be important for intrusive cell formation and later haustorium development. In addition, the ethylene signaling genes *ETHYLENE INSENSITIVE 2 (EIN2)* and *ETHYLENE RESPONSE 1 (ETR1)* are also involved in host invasion by regulating cell division and differentiation of the intrusive cells within the haustorial apical region (Cui *et al.*, 2020). The invasion of the host tissues by the intrusive cells is thought to depend on the secretion activities of cell-wall-modifying enzymes such as pectin methylsterases (PME) and their inhibitors (PMEI), as well as proteases, glycosidases involved in the loosening and degradation of the cell walls (Mitsumasu *et al.*, 2015). Currently, have been demonstrated that several *PjPME* and *PjPMEI* genes are upregulated specifically during haustorium development, which promotes the high PME activity and the low methyl esterification of homogalacturonans in the intrusive cell walls during invasion of the *Arabidopsis thaliana* host tissues (Leso *et al.*, 2023). When the intrusive cells reach the host vasculature, some intrusive cells, the endodermis, and outmost cortical cells lose their identities, differentiating into procambium-like cells (Wakatake *et al.*, 2018) (Figure 4). The ultrastructural features have been demonstrated in two distinct groups of procambium-like cells (Figure 4). Those at the base and middle of the haustorium are highly vacuolated.

In contrast, those next to the host plant (originates of the intrusive cells) contain large cytosols with many atypical membrane structures (Figure 4). The peculiar differences also exist in terms of marker procambium gene expressions, such as *P. japonicum* orthologous, the *HOMEOBOX PROTEIN 15a (PjHB15a)*, *PjHB8*, and *WUSCHEL-RELATED HOMEOBOX 4 (PjWOX4)* are expressed widely in all regions of the procambium-like cells. Still, the expression of *PjHB15b* is restricted to the middle and basal regions (Wakatake *et al.*, 2018). Procambium-like cells originate from the intrusive cells

that differentiate into tracheary elements. The procambium-like cells on the basal regions of the haustorium near the parasite's root xylem develop a mass of tracheary elements called plate xylem (Wakatake *et al.*, 2020) (Figure 4). Around the procambium-like cells in the middle region, the paratracheal parenchyma originated from the cortical cells of the parasite root and has cells with dense cytosol, several organelles, and thin primary cell walls (Masumoto *et al.*, 2021). Moreover, its function is not clear yet.

In the mature development stage, the procambium-like cells of the middle region of the haustorium differentiate into tracheal elements, establishing a xylem bridge between the parasite and the host (Yoshida *et al.*, 2016). The expression of the procambial markers is retained in actively dividing cells surrounding the xylem bridge, indicating that these cells maintain meristemic activity for tracheary element differentiation (Wakatake *et al.*, 2018). The formation of the xylem bridge has been confirmed by marker gene expression *PjHB15a* and *CELLULOSE SYNTHASE CATALYTIC SUBUNIT 7 (PjCESA7)* that encodes a xylem-specific hemicellulose synthase for secondary cell wall synthesis (Wakatake *et al.*, 2018). In addition, the co-expression of *PjCESA7* and *DR5* suggests that auxin concentration is associated with tracheary element differentiation regulated by auxin transporters, PINs, and LAXs (Wakatake *et al.*, 2020). In this case, the expression of *PjPIN1*, *PjLAX1*, and *PjLAX5* directs the auxin flow from the haustorium apex toward the plate xylem formation site.

In contrast, the expression of *PjPIN9* and *PjLAX2* promotes auxin flow from the plate xylem formation site toward the haustorium apex, maintaining a high auxin gradient in the middle region (Wakatake *et al.*, 2020). The xylem bridge, including cytokinins, is essential in transporting molecules from the host to the parasite (Spallek *et al.*, 2017). Although the *P. japonicum* haustorium does not form the phloem connection to the host, the sieve element differentiation marker *ALTERED PHLOEM DEVELOPMENT (APL)* is expressed next to the plate xylem, suggesting that haustorium lacks characteristic phloem cells (Wakatake *et al.*, 2018).



**Figure 4** – The progression of haustoria formation in *P. japonicum* (A) Initially, the figure on the left illustrates the root's anatomical layers without a host, highlighting its independent structure. (B) The prehaustorium phase marks the beginning of haustorial development. (C) This phase transitions into the invading haustorium stage, where the haustorium starts to penetrate the host tissue. (D) The process culminates in the mature haustorium stage, establishing a vascular connection with the host and facilitating nutrient exchange. The diagram labels various anatomical features, including the epidermis (Ep), cortex (Co), endodermis (Ed), vascular system (VS), haustorial hairs (HH), paratracheal parenchyma (PP), procambium-like cells (PL), intrusive cells (IC), tracheary elements (TE), xylem bridge (XB), and plate xylem (PX), to illustrate the complex interactions and transformations involved in haustoria development.

## Impact of Environmental Factors on Plant Parasitism

In the twenty-first century, climate change emerges as one of the foremost threats to global food security, inducing challenges such as drought, desertification, salinization, flooding, and elevated temperatures. The repercussions are more pronounced in economically and socially vulnerable regions, particularly those susceptible to desertification and higher temperatures. This is notably evident in areas where parasitic weed infestations are prevalent, specifically within the genera *Cuscuta*, *Striga*, *Orobanche*, and *Phelipanche*. Consequently, parasitic plants are a significant threat to global food security. Nevertheless, there is limited knowledge regarding the impact of environmental factors on plant parasitism, raising concerns in the context of evolving global conditions and their potential effects on economically vital crops (Samejima and Sugimoto, 2018; Fernández-Aparicio *et al.*, 2020). This predicament is exacerbated by parasitic infestations in regions characterized by poor soil fertility, recurrent droughts, and soil nutrient depletion.

Additionally, low soil fertility is thought to impede host defenses and exacerbate the damaging effects of parasitism. For instance, Kokla *et al.* (2022) described the influence of nutrient availability on haustorium formation in the parasitic plant *P. japonicum*, highlighting the role of nitrogen in repressing parasitism. Furthermore, the study by Miller *et al.* (2003) found that the infection by the parasitic mistletoe *Amyema miquelii* increased as water and salinity stress in the host plant *Eucalyptus largiflorens* decreased, while Evans and Borowicz (2013) reported that drought stress enhanced damage of the parasitic plant *Cuscuta gronovii* on its host *Verbesina alternifolia*, underscoring the diverse effects of stressors on parasitism and host tolerance. Moreover, the research by Rodenburg *et al.* (2023) revealed that fertilization benefits the facultative parasitic plant *Rhamphicarpa fistulosa*, while gains by the infected host *Oryza sativa* are marginalized, emphasizing the differential responses of parasitic plants and their hosts to nutrient availability. Thus, the available literature indicates that nutrient availability can significantly influence the dynamics of parasitic plant-host interactions, impacting plant growth, defense mechanisms, and the prevalence of parasitism. However, the specific effects of resource availability on the tolerance of host plants to parasitism remain an area that requires further investigation, particularly concerning the interactive effects of parasitism intensity with water and nutrient availability on the growth and defense of host plants.

The relationship between temperature and plant parasitism highlights the intricate interplay between climate factors and the prevalence of parasitic infections in plants (Phoenix and Press, 2005; Rafferty *et al.*, 2019). Examining how warming impacts the hemiparasite *Castilleja sulphurea* and its host, *Bouteloua gracilis*, reveals that climate change uniquely affects species interactions (Rafferty *et al.*, 2019). Warming led hosts to produce more below-ground biomass, yet the parasite's presence curtailed this subterranean growth in the host. Moreover, the parasite experienced a more significant boost in above-ground biomass when attached to the warmed

host, alongside a rise in the count of haustoria under elevated temperatures (Rafferty *et al.*, 2019). Over 13 years, David Bell and colleagues analyzed 84 locations throughout the USA, monitoring the characteristics of almost 1,400 individual trees. They discovered that warmer and drier conditions amplify mistletoe's impact (*Arceuthobium tsugense*) on the growth of its host, *Tsuga heterophylla*, and contribute to higher mortality rates (Bell *et al.*, 2020). The research indicates that parasitic plants could amplify the adverse effects of climatic stress, heightening ecosystem vulnerability to the losses in productivity and increased mortality triggered by climate change. A key factor for this intensified impact on hosts might be that elevated temperatures influence plant physiology, compromising their defense capabilities and making them more prone to pathogen invasions (Dropkin, 1969; Wang *et al.*, 2009; Cohen and Leach, 2020). Additionally, temperature fluctuations and changes in precipitation patterns may offer optimal conditions for spreading specific plant parasites, thus increasing the stress on plant health (Watson *et al.*, 2022).

## Conclusion

To understand how the climate will affect biodiversity in the future, we need to investigate more than just the direct effects of global warming. We also need to investigate the complex indirect effects of species interacting with each other. This method should include in-depth studies of ecophysiological traits like heterotrophy, autotrophic carbon gain, and how efficiently hosts and parasites use water. These are important for understanding how hosts and parasites adjust to changing climate conditions. However, understanding the molecular process behind the parasitism emergency in flowering plants is crucial to learn more about how environmental factors affect plant parasites. The large amount of OMICS data provides us with helpful information. One example is how nucleic acid molecules move between parasite plants and their hosts. It illustrates how little we know about how stable transferred sequences are in genomes, how well they integrate into germline cells, and how this affects evolutionary patterns and genomic architecture. Many studies have been done on plastid genomes, but not many have been done on the mitochondrial genomes (mitogenomes) of plants that live on other plants. The development of long-read sequencing technologies is a bright spot because they could shed light on the complicated processes of mitogenome evolution and help us learn more about the complex biological and evolutionary processes that control the life cycles of parasitic plants. This multifaceted method of studying how climate change and plant parasitism affect each other is essential for scientific progress and for developing good conservation plans to protect our planet's biodiversity in the face of ongoing environmental problems. It also helps answer critical biological questions about the evolution of parasitic plants and their interactions with their hosts.

## Conflict of Interest

The authors declare that no conflict of interest could be perceived as prejudicial to the impartiality of the reported research.

## Authors Contributions

JKI and ECC wrote the manuscript. All authors read and approved the final version.

## References

- Ackroyd RD and Graves JD (1997) The regulation of the water potential gradient in the host and parasite relationship between *Sorghum bicolor* and *Striga hermonthica*. *Ann Bot* 80:649-656.
- Alaba OA, Bredeson JV, Egesi CN, Esuma W, Ezenwaka L, Ferguson ME, Ha CM, Hall M, Herselman L, Ikpan A *et al.* (2014) High-resolution linkage map and chromosome-scale genome assembly for cassava (*Manihot esculenta* Crantz) from 10 populations. *G3 (Bethesda)* 5:133-144.
- Alexander WG, Wisecaver JH, Rokas A and Hittinger CT (2016) Horizontally acquired genes in early-diverging pathogenic fungi enable the use of host nucleosides and nucleotides. *Proc Natl Acad Sci U S A* 113:4116-4121.
- Amutenya A, Kwembeya E, Shikangalah R and Tsvuura Z (2023) Photosynthesis, chlorophyll content and water potential of a mistletoe-host pair in a semi-arid savanna. *S Afr J Bot* 163:311-315.
- Anderson BM, Krause K and Petersen G (2021) Mitochondrial genomes of two parasitic *Cuscuta* species lack clear evidence of horizontal gene transfer and retain unusually fragmented ccmFC genes. *BMC Genomics* 22:816.
- Arias-Agudelo LM, González F, Isaza JP, Alzate JF and Pabón-Mora N (2019) Plastome reduction and gene content in new world *Pilosyles* (Apodanthaceae) unveils high similarities to African and Australian congeners. *Mol Phylogenet Evol* 135:193-202.
- Backert S, Dörfel P, Lurz R and Börner T (1996) Rolling-circle replication of mitochondrial DNA in the higher plant *Chenopodium album* (L.). *Mol Cell Biol* 16:6285-6294.
- Backert S (2002) R-loop-dependent rolling-circle replication and a new model for DNA concatemer resolution by mitochondrial plasmid *mpl1*. *EMBO J* 21:3128-3136.
- Banerjee A and Stefanović S (2020) Reconstructing plastome evolution across the phylogenetic backbone of the parasitic plant genus *Cuscuta* (Convolvulaceae). *Bot J Linn Soc* 194:423-438.
- Banerjee A and Stefanović S (2023) A comparative study across the parasitic plants of *Cuscuta* subgenus *Grammica* (Convolvulaceae) reveals a possible loss of the plastid genome in its section *Subulatae*. *Planta* 257:66.
- Bell DM, Pabst RJ and Shaw DC (2020) Tree growth declines and mortality were associated with a parasitic plant during warm and dry climatic conditions in a temperate coniferous forest ecosystem. *Glob Chang Biol* 26:1714-1724.
- Bell TL, Adams MA and Rennenberg H (2011) Attack on all fronts: functional relationships between aerial and root parasitic plants and their woody hosts and consequences for ecosystems. *Tree Physiol* 31:3-15.
- Bellot S, Cusimano N, Luo S, Sun G, Zarre S, Gröger A, Tensch E and Renner SS (2016) Assembled plastid and mitochondrial genomes, as well as nuclear genes, place the parasite family *Cynomoriaceae* in the Saxifragales. *Genome Biol Evol* 8:2214-2230.
- Bi C, Qu Y, Hou J, Wu K, Ye N and Yin T (2022) Deciphering the multi-chromosomal mitochondrial genome of *Populus simonii*. *Front Plant Sci* 13:914635.
- Bowers JE, Tang H, Burke JM and Paterson AH (2022) GC content of plant genes are linked to past gene duplications. *PLoS One* 17:e0261748.
- Braukmann T, Kuzmina M and Stefanović S (2013) Plastid genome evolution across the genus *Cuscuta* (Convolvulaceae): Two clades within subgenus *Grammica* exhibit extensive gene loss. *J Exp Bot* 64:977-989.
- Braun HP (2020) The Oxidative Phosphorylation system of the mitochondria in plants. *Mitochondrion* 53:66-75.
- Bromham L, Cowman PF and Lanfear R (2013) Parasitic plants have increased rates of molecular evolution across all three genomes. *BMC Evol Biol* 13:126.
- Cai L, Arnold BJ, Xi Z, Khost DE, Patel N, Hartmann CB, Manickam S, Sasirat S, Nikolov LA, Mathews S *et al.* (2021) Deeply altered genome architecture in the endoparasitic flowering plant *Sapria himalayana* Griff. (Rafflesiaceae). *Curr Biol* 31:1002-1011.e9.
- Chase MW, Christenhusz MJM, Fay MF, Byng JW, Judd WS, Soltis DE, Mabberley DJ, Sennikov AN, Soltis PS, Stevens PF *et al.* (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Bot J Linn Soc* 181:1-20.
- Chen J, Yu R, Dai J, Liu Y and Zhou R (2020) The loss of photosynthesis pathway and genomic locations of the lost plastid genes in a holoparasitic plant *Aeginetia indica*. *BMC Plant Biol* 20:199.
- Chen LQ, Li X, Yao X, Li DZ, Barrett C, de Pamphilis CW and Yu W Bin (2024) Variations and reduction of plastome are associated with the evolution of parasitism in Convolvulaceae. *Plant Mol Biol* 114:40.
- Chen X, Fang D, Xu Y, Duan K, Yoshida S, Yang S, Sahu SK, Fu H, Guang X, Liu M *et al.* (2023) *Balanophora* genomes display massively convergent evolution with other extreme holoparasites and provide novel insights into parasite-host interactions. *Nature Plants* 9:1627-1642.
- Coghlan A, Tyagi R, Cotton JA, Holroyd N, Rosa BA, Tsai IJ, Laetsch DR, Beech RN, Day TA, Hallsworth-Pepin K *et al.* (2018) Comparative genomics of the major parasitic worms. *Nature Genetics* 51:163-174.
- Cohen SP and Leach JE (2020) High temperature-induced plant disease susceptibility: More than the sum of its parts. *Curr Opin Plant Biol* 56:235-241.
- Cui H, Ding Z, Zhu Q, Wu Y, Qiu B and Gao P (2021) Comparative analysis of nuclear, chloroplast, and mitochondrial genomes of watermelon and melon provides evidence of gene transfer. *Sci Rep* 11:1595.
- Cui S, Wakatake T, Hashimoto K, Saucet SB, Toyooka K, Yoshida S and Shirasu K (2016) Haustorial hairs are specialized root hairs that support parasitism in the facultative parasitic plant *Phtheirospermum japonicum*. *Plant Physiol* 170:1492-1503.
- Cui S, Wada S, Tobimatsu Y, Takeda Y, Saucet SB, Takano T, Umezawa T, Shirasu K and Yoshida S (2018) Host lignin composition affects haustorium induction in the parasitic plants *Phtheirospermum japonicum* and *Striga hermonthica*. *New Phytologist* 218:710-723.
- Cui S, Kubota T, Nishiyama T, Juliane K, Shigenobu S, Shibata TF, Toyoda A, Hasebe M, Shirasu K and Yoshida S (2020) Ethylene signaling mediates host invasion by parasitic plants. *Sci Adv* 6:eabc2385.
- Cusimano N and Renner SS (2019) Sequential horizontal gene transfers from different hosts in a widespread Eurasian parasitic plant, *Cynomorium coccineum*. *Am J Bot* 106:679-689.
- Davis CC and Xi Z (2015) Horizontal gene transfer in parasitic plants. *Curr Opin Plant Biol* 26:14-19.
- Ding Y, Zhou Q and Wang W (2012) Origins of new genes and evolution of their novel functions. *Annu Rev Ecol Evol Syst* 43:345-363.
- Dropkin VH (1969) The necrotic reaction of tomatoes and other hosts resistant to *Meloidogyne*: Reversal by temperature. *Phytopathology* 59:1632-1637.

- Evans B and Borowicz V (2013) *Verbescina alternifolia* tolerance to the holoparasite *Cuscuta groenovii* and the impact of drought. *Plants (Basel)* 2:635-649.
- Fernández-Aparicio M, Delavault P and Timko MP (2020) Management of infection by parasitic weeds: A Review. *Plants* 9:1184.
- Garron ML and Henrissat B (2019) The continuing expansion of CAZymes and their families. *Curr Opin Chem Biol* 53:82-87.
- Goyet V, Wada S, Cui S, Wakatake T, Shirasu K, Montiel G, Simier P and Yoshida S (2019) Haustorium inducing factors for parasitic Orobanchaceae. *Front Plant Sci* 10:1056.
- Haegeman A, Jones JT and Danchin EGJ (2011) Horizontal gene transfer in nematodes: A catalyst for plant parasitism? *Mol Plant Microbe Interact* 24:879-887.
- Hellsten U, Wright KM, Jenkins J, Shu S, Yuan Y, Wessler SR, Schmutz J, Willis JH and Rokhsar DS (2013) Fine-scale variation in meiotic recombination in *Mimulus* inferred from population shotgun sequencing. *Proc Natl Acad Sci U S A* 110:19478-19482.
- Hershey DR (1999) Myco-heterophytes & parasitic plants in food chains. *Am Biol Teach* 61:575-578.
- Hoshino A, Jayakumar V, Nitasaka E, Toyoda A, Noguchi H, Itoh T, Shin T, Minakuchi Y, Koda Y, Nagano AJ *et al.* (2016) Genome sequence and analysis of the Japanese morning glory *Ipomoea nil*. *Nat Commun* 7:13295.
- Ichihashi Y, Mutuku JM, Yoshida S and Shirasu K (2015) Transcriptomics exposes the uniqueness of parasitic plants. *Brief Funct Genomics* 14:275-282.
- Ishida JK, Wakatake T, Yoshida S, Takebayashi Y, Kasahara H, Wafula E, Depamphilis CW, Namba S and Shirasu K (2016) Local auxin biosynthesis mediated by a yucca flavin monooxygenase regulates haustorium development in the parasitic plant *Phtheirospermum japonicum*. *Plant Cell* 28:795-814.
- Ishida JK, Yoshida S and Shirasu K (2017a) Haustorium Induction assay of the parasitic plant *Phtheirospermum japonicum*. *Bio Protoc* 9:e2260.
- Ishida JK, Yoshida S and Shirasu K (2017b) Quinone oxidoreductase 2 is involved in haustorium development of the parasitic plant *Phtheirospermum japonicum*. *Plant Signal Behav* 12:1319029.
- Ishida JKK, Yoshida S, Ito M, Namba S and Shirasu K (2011) *Agrobacterium rhizogenes*-mediated transformation of the parasitic plant *Phtheirospermum japonicum*. *PLoS One* 6:e25802.
- Jiang F, Jeschke WD and Hartung W (2003) Water flows in the parasitic association *Rhinanthus minor*/*Hordeum vulgare*. *J Exp Bot* 54:1985-1993.
- Jiang F, Timergalina L, Kudoyarova G, Jeschke WD and Hartung W (2007) Growth and development of the facultative root hemiparasite *Rhinanthus minor* after removal of its host. *Funct Plant Biol* 34:237-245.
- Kado T and Innan H (2018) Horizontal gene transfer in five parasitic plant species in Orobanchaceae. *Genome Biol Evol* 10:3196-3210.
- Kaga Y, Yokoyama R, Sano R, Ohtani M, Demura T, Kuroha T, Shinohara N and Nishitani K (2020) Interspecific signaling between the parasitic plant and the host plants regulate xylem vessel cell differentiation in haustoria of *Cuscuta campestris*. *Front Plant Sci* 11:524693.
- Kfoury B, Rodrigues WFC, Kim SJ, Brandizzi F and Del-Bem LE (2024) Multiple horizontal gene transfer events have shaped plant glycosyl hydrolase diversity and function. *New Phytol* 242:809-824.
- Kianian PMA and Kianian SF (2014) Mitochondrial dynamics and the cell cycle. *Front Plant Sci* 5:222.
- Kim G, LeBlanc ML, Wafula EK, DePamphilis CW and Westwood JH (2014) Plant science. Genomic-scale exchange of mRNA between a parasitic plant and its hosts. *Science* 345:808-811.
- Kim W, Lautenschläger T, Bolin JF, Rees M, Nzuzi A, Zhou R, Wanke S and Jost M (2023) Extreme plastomes in holoparasitic Balanophoraceae are not the norm. *BMC Genomics* 24:330.
- Kokla A and Melnyk CW (2018) Developing a thief: Haustoria formation in parasitic plants. *Dev Biol* 442:53-59.
- Kokla A, Leso M, Zhang X, Simura J, Serivichyaswat PT, Cui S, Ljung K, Yoshida S and Melnyk CW (2022) Nitrogen represses haustoria formation through abscisic acid in the parasitic plant *Phtheirospermum japonicum*. *Nat Commun* 13:2976.
- Kurotani Kichi, Wakatake T, Ichihashi Y, Okayasu K, Sawai Y, Ogawa S, Cui S, Suzuki T, Shirasu K and Notaguchi M (2020) Host-parasite tissue adhesion by a secreted type of  $\beta$ -1,4-glucanase in the parasitic plant *Phtheirospermum japonicum*. *Commun Biol* 2020 3:407.
- Lamesch P, Berardini TZ, Li D, Swarbreck D, Wilks C, Sasidharan R, Muller R, Dreher K, Alexander DL, Garcia-Hernandez M *et al.* (2012) The *Arabidopsis* Information Resource (TAIR): Improved gene annotation and new tools. *Nucleic Acids Res* 40:D1202-D1210.
- Leblanc M, Kim G and Westwood JH (2012) RNA trafficking in parasitic plant systems. *Front Plant Sci* 3:203.
- Leso M, Kokla A, Feng M and Melnyk CW (2023) Pectin modifications promote haustoria development in the parasitic plant *Phtheirospermum japonicum*. *Plant Physiol* 194:229-242.
- Lewis SC, Joers P, Willcox S, Griffith JD, Jacobs HT and Hyman BC (2015) A rolling circle replication mechanism produces multimeric lariats of mitochondrial DNA in *Caenorhabditis elegans*. *PLoS Genet* 11:e1004985.
- Li X, Yang JB, Wang H, Song Y, Corlett RT, Yao X, Li DZ and Yu W Bin (2021) Plastid NDH pseudogenization and gene loss in a recently derived lineage from the largest hemiparasitic plant genus *Pedicularis* (Orobanchaceae). *Plant Cell Physiol* 62:971-984.
- Lin Y, Li P, Zhang Y, Akhter D, Pan R, Fu Z, Huang M, Li X and Feng Y (2022) Unprecedented organelle genomic variations in morning glories reveal independent evolutionary scenarios of parasitic plants and the diversification of plant mitochondrial complexes. *BMC Biol* 20:49.
- Logan DC (2006) Plant mitochondrial dynamics. *Biochim Biophys Acta Mol Cell Res* 1763:430-441.
- Lyko P and Wicke S (2021) Genomic reconfiguration in parasitic plants involves considerable gene losses alongside global genome size inflation and gene births. *Plant Physiol* 186:1412.
- Ma J, Wang S, Zhu X, Sun G, Chang G, Li L, Hu X, Zhang S, Zhou Y, Song C-P *et al.* (2022) Major episodes of horizontal gene transfer drove the evolution of land plants. *Mol Plant* 15:857-871.
- Ma M, Liu Y, Bai C and Yong JWH (2021) The significance of chloroplast NAD(P)H dehydrogenase complex and its dependent cyclic electron transport in photosynthesis. *Front Plant Sci* 12:661863.
- Maclean AE, Hertle AP, Ligas J, Bock R, Balk J and Meyer EH (2018) Absence of complex I is associated with diminished respiratory chain function in *European mistletoe*. *Curr Biol* 28:1614-1619.e3.
- Masumoto N, Suzuki Y, Cui S, Wakazaki M, Sato M, Kumaishi K, Shibata A, Furuta KM, Ichihashi Y, Shirasu K *et al.* (2021) Three-dimensional reconstructions of haustoria in two parasitic plant species in the Orobanchaceae. *Plant Physiol* 185:1429-1442.
- Merckx V, Bidartondo MI and Hynson NA (2009) Myco-heterotrophy: When fungi host plants. *Ann Bot* 104:1255.

- Miller AC, Watling JR, Overton IC and Sinclair R (2003) Does water status of *Eucalyptus largiflorens* (Myrtaceae) affect infection by the mistletoe *Amyema miquelii* (Loranthaceae)? *Funct Plant Biol* 30:1239-1247.
- Mitsumasu K, Seto Y and Yoshida S (2015) Apoplastic interactions between plants and plant root intruders. *Front Plant Sci* 6:617.
- Molina J, Hazzouri KM, Nickrent D, Geisler M, Meyer RS, Pentony MM, Flowers JM, Pelsler P, Barcelona J, Inovejas SA *et al.* (2014) Possible loss of the chloroplast genome in the parasitic flowering plant *Rafflesia lagascae* (Rafflesiaceae). *Mol Biol Evol* 31:793-803.
- Mower JP, Stefanović S, Young GJ and Palmer JD (2004) Gene transfer from parasitic to host plants. *Nature* 432:165-166.
- Mower JP, Stefanović S, Hao W, Gummow JS, Jain K, Ahmed D and Palmer JD (2010) Horizontal acquisition of multiple mitochondrial genes from a parasitic plant followed by gene conversion with host mitochondrial genes. *BMC Biol* 8:150.
- Müller AE, Kamisugi Y, Grüneberg R, Niedenhof I, Hörold RJ and Meyer P (1999) Palindromic sequences and A+T-rich DNA elements promote illegitimate recombination in *Nicotiana tabacum*. *J Mol Biol* 291:29-46.
- Neumann P, Oliveira L, Čížková J, Jang TS, Klemme S, Novák P, Stelmach K, Koblížková A, Doležel J and Macas J (2021) Impact of parasitic lifestyle and different types of centromere organization on chromosome and genome evolution in the plant genus *Cuscuta*. *New Phytol* 229:2365-2377.
- Nickrent DL and Musselman LJ (2004) Introduction to parasitic flowering plants. *Plant Health Instr.* DOI: 10.1094/PHI-I-2004-0330-01.
- Nickrent DL (2020) Parasitic angiosperms: How often and how many? *Taxon* 69:5-27.
- Nickrent DL (2011) Santalales (Including Mistletoes). *Encyclopedia of Life Sciences* 689:1-6.
- Ogawa S, Wakatake T, Spallek T, Ishida JK, Sano R, Kurata T, Demura T, Yoshida S, Ichihashi Y, Schaller A *et al.* (2021) Subtilase activity in intrusive cells mediates haustorium maturation in parasitic plants. *Plant Physiol* 185:1381-1394.
- Oldenburg DJ and Bendich AJ (2015) DNA maintenance in plastids and mitochondria of plants. *Front Plant Sci* 6:164884.
- Petersen G, Cuenca A, Möller IM and Seberg O (2015) Massive gene loss in mistletoe (*Viscum*, Viscaceae) mitochondria. *Sci Rep* 5:17588.
- Phoenix GK and Press MC (2005) Effects of climate change on parasitic plants: The root hemiparasitic Orobanchaceae. *Folia Geobot* 40:205-216.
- Piednoël M, Aberer AJ, Schneeweiss GM, MacAs J, Novak P, Gundlach H, Temsch EM and Renner SS (2012) Next-generation sequencing reveals the impact of repetitive DNA across phylogenetically closely related genomes of Orobanchaceae. *Mol Biol Evol* 29:3601-3611.
- Poulin R and Randhawa HS (2015) Evolution of parasitism along convergent lines: From ecology to genomics. *Parasitology* 142:S6.
- Prasai K, Robinson LC, Scott RS, Tatchell K and Harrison L (2017) Evidence for double-strand break mediated mitochondrial DNA replication in *Saccharomyces cerevisiae*. *Nucleic Acids Res* 45:7760-7773.
- Press M and Graves J (1995) Parasitic plants. Springer Science & Business Media, Dordrecht.
- Rafferty NE, Agnew L and Nability PD (2019) Parasitism modifies the direct effects of warming on a hemiparasite and its host. *PLoS One* 14:e0224482.
- Reid N, Stafford Smith M and Yan Z (1995) Ecology and population biology of mistletoes. In: Lowman MD and Nadkarn NM (eds) *Forest canopies*, Academic Press, San Diego, pp 285-310.
- Rice DW, Alverson AJ, Richardson AO, Young GJ, Sanchez-Puerta MV, Munzinger J, Barry K, Boore JL, Zhang Y, DePamphilis CW *et al.* (2013) Horizontal transfer of entire genomes via mitochondrial fusion in the angiosperm *Amborella*. *Science* 342:1468-1473.
- Richards TA, Soanes DM, Jones MDM, Vasieva O, Leonard G, Paszkiewicz K, Foster PG, Hall N and Talbot NJ (2011) Horizontal gene transfer facilitated the evolution of plant parasitic mechanisms in the oomycetes. *Proc Natl Acad Sci U S A* 108:15258-15263.
- Rodenburg J, Dümmer R, Ho Y-H and Bastiaans L (2023) Fertilization benefits the facultative parasitic plant *Rhaphicarpa fistulosa* while gains by the infected host *Oryza sativa* are marginalized. *Ann Bot* 133:337-348.
- Roulet ME, Garcia LE, Gandini CL, Sato H, Ponce G and Sanchez-Puerta MV (2020) Multichromosomal structure and foreign tracts in the *Ombrophytum subterraneum* (Balanophoraceae) mitochondrial genome. *Plant Mol Biol* 103:623-638.
- Roy Smith D (2019) Evolution: A plant plastid genome that has forsaken guanine and cytosine. *Curr Biol* 29:R99-R101.
- Sakamoto W and Takami T (2024) Plastid inheritance revisited: Emerging role of organelle DNA degradation in Angiosperms. *Plant Cell Physiol* 65:484-492.
- Samejima H and Sugimoto Y (2018) Recent research progress in combatting root parasitic weeds. *Biotechnol Biotechnol Equip* 32:221-240.
- Sanchez-Puerta MV, Garcia LE, Wohlfeiler J and Ceriotti LF (2017) Unparalleled replacement of native mitochondrial genes by foreign homologs in a holoparasitic plant. *New Phytol* 214:376-387.
- Sanchez-Puerta MV, Edera A, Gandini CL, Williams AV, Howell KA, Nevill PG and Small I (2019) Genome-scale transfer of mitochondrial DNA from legume hosts to the holoparasite *Lophophytum mirabile* (Balanophoraceae). *Mol Phylogenet Evol* 132:243-250.
- Sanchez-Puerta MV, Ceriotti LF, Gatica-Soria LM, Roulet ME, Garcia LE and Sato HA (2023) Invited review beyond parasitic convergence: Unravelling the evolution of the organellar genomes in holoparasites. *Ann Bot* 132:909-928.
- Sato M and Sato K (2013) Maternal inheritance of mitochondrial DNA by diverse mechanisms to eliminate paternal mitochondrial DNA. *Biochim Biophys Acta* 1833:1979-1984.
- Schertl P and Braun HP (2014) Respiratory electron transfer pathways in plant mitochondria. *Front Plant Sci* 5:163.
- Schwarzländer M and Finkemeier I (2013) Mitochondrial energy and redox signaling in plants. *Antioxid Redox Signal* 18:2122.
- Scott I and Logan DC (2008) Mitochondria and cell death pathways in plants: Actions speak louder than words. *Plant Signal Behav* 3:475.
- Senkler J, Rugen N, Eubel H, Hegermann J and Braun HP (2018) Absence of complex I implicates rearrangement of the respiratory chain in *European mistletoe*. *Curr Biol* 28:1606-1613.e4.
- Shearman JR, Sonthirod C, Naktang C, Pootakham W, Yoocha T, Sangsrakru D, Jomchai N, Tragoonrun S and Tangphatsomruang S (2016) The two chromosomes of the mitochondrial genome of a sugarcane cultivar: assembly and recombination analysis using long PacBio reads. *Sci Rep* 6:31533.
- Shen J, Zhao J, Bartoszewski G, Malepszy S, Havey M and Chen J (2015) Persistence and protection of mitochondrial DNA in the generative cell of Cucumber is consistent with its paternal transmission. *Plant Cell Physiol* 56:2271-2282.
- Skippingtona E, Barkmanb TJ, Ricea DW and Palmera JD (2015) Miniaturized mitogenome of the parasitic plant *Viscum*

- scurruloideum* is extremely divergent and dynamic and has lost all nad genes. Proc Natl Acad Sci U S A 112:E3515-E3524.
- Spallek T, Melnyk CW, Wakatake T, Zhang J, Sakamoto Y, Kiba T, Yoshida S, Matsunaga S, Sakakibara H and Shirasu K (2017) Interspecies hormonal control of host root morphology by parasitic plants. Proc Natl Acad Sci U S A 114:5283-5288.
- Stegemann S and Bock R (2009) Exchange of genetic material between cells in plant tissue grafts. Science 324:649-651.
- Stegemann S, Keuthe M, Greiner S and Bock R (2012) Horizontal transfer of chloroplast genomes between plant species. Proc Natl Acad Sci U S A 109:2434-2438.
- Su HJ, Barkman TJ, Hao W, Jones SS, Naumann J, Skippington E, Wafula EK, Hu JM, Palmer JD and DePamphilis CW (2019) Novel genetic code and record-setting AT-richness in the highly reduced plastid genome of the holoparasitic plant *Balanophora*. Proc Natl Acad Sci U S A 116:934-943.
- Sun G, Xu Y, Liu H, Sun T, Zhang J, Hettenhausen C, Shen G, Qi J, Qin Y, Li J *et al.* (2018) Large-scale gene losses underlie the genome evolution of parasitic plant *Cuscuta australis*. Nat Commun 9:2683.
- Sundararajan A, Dukowicz-Schulze S, Kwicklis M, Engstrom K, Garcia N, Oviedo OJ, Ramaraj T, Gonzales MD, He Y, Wang M *et al.* (2016) Gene evolutionary trajectories and GC patterns driven by recombination in *Zea mays*. Front Plant Sci 7:220732.
- Světlíková P, Hájek T and Těšitel J (2018) Water-stress physiology of *Rhinanthus alectorolophus*, a root-hemiparasitic plant. PLoS One 13:e0200927.
- Syrenki RM, Charles S, Levings I and Shah DM (1978) Physicochemical characterization of mitochondrial DNA from soybean. Plant Physiol 61:460.
- Thorogood CJ, Teixeira-Costa L, Ceccantini G, Davis C and Hiscock SJ (2021) Endoparasitic plants and fungi show evolutionary convergence across phylogenetic divisions. New Phytol 232:1159-1167.
- Tomilov A, Tomilova N and Yoder JI (2007) *Agrobacterium tumefaciens* and *Agrobacterium rhizogenes* transformed roots of the parasitic plant *Triphysaria versicolor* retain parasitic competence. Planta 225:1059-1071.
- van Aken O (2021) Mitochondrial redox systems as central hubs in plant metabolism and signaling. Plant Physiol 186:36.
- Van G and Alamy O (2018) Parasites plant microRNAs in the host. Nat Rev Genet 19:127.
- Vidal-Russell R and Nickrent DL (2008) The first mistletoes: Origins of aerial parasitism in Santalales. Mol Phylogenet Evol 47:523-537.
- Vogel A, Schwacke R, Denton AK, Usadel B, Hollmann J, Fischer K, Bolger A, Schmidt MHW, Bolger ME, Gundlach H *et al.* (2018) Footprints of parasitism in the genome of the parasitic flowering plant *Cuscuta campestris*. Nat Commun 9:2515.
- Wakatake T, Yoshida S and Shirasu K (2018) Induced cell fate transitions at multiple cell layers configure haustorium development in parasitic plants. Development 145:dev164848.
- Wakatake T, Ogawa S, Yoshida S and Shirasu K (2020) An auxin transport network underlies xylem bridge formation between the hemi-parasitic plant *Phtheirospermum japonicum* and host *Arabidopsis*. Development 147:dev187781.
- Wang Y, Bao Z, Zhu Y and Hua J (2009) Analysis of temperature modulation of plant defense against biotrophic microbes. Mol Plant Microbe Interact 22:498-506.
- Watson DM, McLellan RC and Fonturbel FE (2022) Functional roles of parasitic plants in a warming World. Annu Rev Ecol Evol Syst 53:25-45.
- Weihe A, Apitz J, Pohlheim F, Salinas-Hartwig A and Börner T (2009) Biparental inheritance of plastidial and mitochondrial DNA and hybrid variegation in *Pelargonium*. Mol Genet Genomics 282:587-593.
- Westwood JH, Roney JK, Khatibi PA and Stromberg VK (2009) RNA translocation between parasitic plants and their hosts. Pest Manag Sci 65:533-539.
- Westwood JH, Yoder JohnI, Timko MP and DePamphilis CW (2010) The evolution of parasitism in plants. Trends Plant Sci 15:227-235.
- Wicke S, Müller KF, DePamphilis CW, Quandt D, Bellot S and Schneeweiss GM (2016) Mechanistic model of evolutionary rate variation en route to a nonphotosynthetic lifestyle in plants. Proc Natl Acad Sci U S A 113:9045-9050.
- Wicke S and Naumann J (2018) Molecular evolution of plastid genomes in parasitic flowering plants. Adv Bot Res 85:315-347.
- Wickell DA and Li FW (2020) On the evolutionary significance of horizontal gene transfers in plants. New Phytol 225:113-117.
- Windsor DA (1998) Most of the species on Earth are parasites. Int J Parasitol 28:1939-1941.
- Xi Z, Bradley RK, Wurdack KJ, Wong K, Sugumaran M, Bomblies K, Rest JS and Davis CC (2012) Horizontal transfer of expressed genes in a parasitic flowering plant. BMC Genomics 13:227.
- Xi Z, Wang Y, Bradley RK, Sugumaran M, Marx CJ, Rest JS and Davis CC (2013) Massive mitochondrial gene transfer in a parasitic flowering plant clade. PLoS Genet 9:e1003265.
- Xie L, Gong X, Yang K, Huang Y, Zhang S, Shen L, Sun Y, Wu D, Ye C, Zhu QH *et al.* (2024) Technology-enabled great leap in deciphering plant genomes. Nat Plants 10:551-566.
- Xu Y, Lei Y, Su Z, Zhao M, Zhang J, Shen G, Wang L, Li J, Qi J and Wu J (2021) A chromosome-scale *Gastrodia elata* genome and large-scale comparative genomic analysis indicate convergent evolution by gene loss in mycoheterotrophic and parasitic plants. Plant J 108:1609-1623.
- Xu Y, Zhang J, Ma C, Lei Y, Shen G, Jin J, Eaton DAR and Wu J (2022) Comparative genomics of orobanchaceous species with different parasitic lifestyles reveals the origin and stepwise evolution of plant parasitism. Mol Plant 15:1384-1399.
- Yamao F, Muto A, Kawachi Y, Iwami M, Iwagami S, Azumi Y and Osawa S (1985) UGA is read as tryptophan in *Mycoplasma capricolum*. Proc Natl Acad Sci U S A 82:2306-2309.
- Yang Z, Zhang Y, Wafula EK, Honaas LA, Ralph PE, Jones S, Clarke CR, Liu S, Su C, Zhang H *et al.* (2016) Horizontal gene transfer is more frequent with increased heterotrophy and contributes to parasite adaptation. Proc Natl Acad Sci U S A 113:E7010-E7019.
- Yang Z, Wafula EK, Kim G, Shahid S, McNeal JR, Ralph PE, Timilsena PR, Yu W bin, Kelly EA, Zhang H *et al.* (2019) Convergent horizontal gene transfer and cross-talk of mobile nucleic acids in parasitic plants. Nat Plants 5:991-1001.
- Yoshida S, Maruyama S, Nozaki H and Shirasu K (2010) Horizontal gene transfer by the parasitic plant *Striga hermonthica*. Science 328:1128.
- Yoshida S, Cui S, Ichihashi Y and Shirasu K (2016) The haustorium, a specialized invasive organ in parasitic plants. Annu Rev Plant Biol 67:643-667.
- Yoshida S, Kim S, Wafula EK, Tanskanen J, Kim YM, Honaas L, Yang Z, Spallek T, Conn CE, Ichihashi Y *et al.* (2019) Genome sequence of *Striga asiatica* provides insight into the evolution of plant parasitism. Curr Biol 29:3041-3052.e4.
- Yu R, Sun C, Zhong Y, Liu Y, Sanchez-Puerta MV, Mower JP and Zhou R (2022) The minicircular and extremely heteroplasmic mitogenome of the holoparasitic plant *Rhopalocnemis phalloides*. Curr Biol 32:470-479.e5.
- Zangishei Z, Annacondia ML, Gundlach H, Didriksen A, Bruckmüller J, Salari H, Krause K and Martinez G (2022) Parasitic plant small RNA analyses unveil parasite-specific signatures of microRNA retention, loss, and gain. Plant Physiol 190:1242-1259.

- Zervas A, Petersen G and Seberg O (2019) Mitochondrial genome evolution in parasitic plants. *BMC Evol Biol* 19:87.
- Zhang D, Qi J, Yue J, Huang J, Sun T, Li S, Wen JF, Hettenhausen C, Wu J, Wang L *et al.* (2014) Root parasitic plant *Orobanchae aegyptiaca* and shoot parasitic plant *Cuscuta australis* obtained Brassicaceae-specific strictosidine synthase-like genes by horizontal gene transfer. *BMC Plant Biol* 14:19.
- Zhang GQ, Liu KW, Li Z, Lohaus R, Hsiao YY, Niu SC, Wang JY, Lin YC, Xu Q, Chen LJ *et al.* (2017) The *Apostasia* genome and the evolution of orchids. *Nature* 549:379-383.
- Zhou S, Wei N, Jost M, Wanke S, Rees M, Liu Y and Zhou R (2023) The mitochondrial genome of the holoparasitic plant *Thonningia sanguinea* provides insights into the evolution of the multichromosomal structure. *Genome Biol Evol* 15:evad155.

## Internet Resources

- Leitch IJ, Johnston E, Pellicer J, Hidalgo O and Bennett MD (2019) Plant DNA C-values Database. In: Plant DNA C-values database (release 7.1, Apr 2019). <https://cvalues.science.kew.org/search> (accessed 25 May 2024).
- U.S. DEPARTMENT OF AGRICULTURE (2024) Parasitic Plant Genera List. <https://www.aphis.usda.gov/organism-soil-import/federal-noxious-weeds/parasitic-plant-list> (accessed 25 May 2024).

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