The Haustorium, a Specialized Invasive Organ in Parasitic Plants

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Abstract

Parasitic plants thrive by infecting other plants. Flowering plants evolved parasitism independently at least 12 times, in all cases developing a unique multicellular organ called the haustorium that forms upon detection of haustorium-inducing factors derived from the host plant. This organ penetrates into the host stem or root and connects to its vasculature, allowing exchange of materials such as water, nutrients, proteins, nucleotides, pathogens, and retrotransposons between the host and the parasite. In this review, we focus on the formation and function of the haustorium in parasitic plants, with a specific emphasis on recent advances in molecular studies of root parasites in the Orobanchaceae and stem parasites in the Convolvulaceae.

Contents

INTRODUCTION

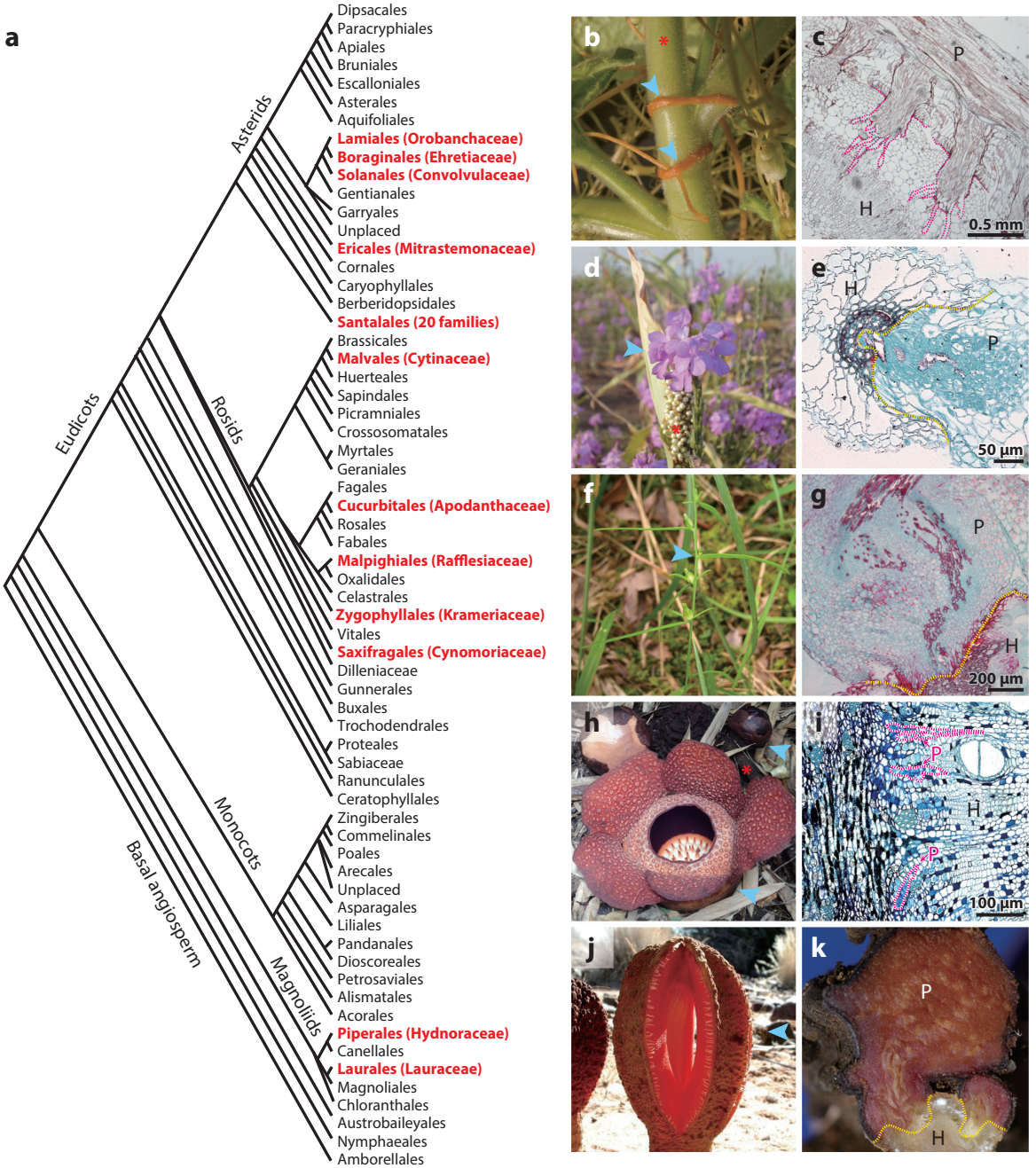
Unlike green autotrophic plants, which acquire carbohydrates by photosynthesis, parasitic plants have developed a unique heterotrophic lifestyle in which they benefit from water and nutrients supplied by their hosts. Approximately 4,500 parasitic species belonging to 28 families, representing 1% of the dicotyledonous angiosperm species, have been reported (53). These parasitic species derived from 12 or 13 independent evolutionary events (143) and therefore show taxonomic diversity and morphological variation (**Figure 1**).

Parasitic plants can be classified as either stem or root parasites, depending on the attachment site in the host plants. They can be further classified by their degree of host dependency as hemiparasites or holoparasites based on whether they have retained or completely lost photosynthetic activity. Parasites are also either facultative or obligate; the former can complete their life cycles without a host, but the latter cannot. For example, mistletoes (*Viscum* spp.) and dodders (*Cuscuta* spp.) are obligate stem hemiparasites, whereas the Orobanchaceae plants *Orobanche* spp. and *Striga* spp. are obligate root holoparasites and hemiparasites, respectively. Some other Orobanchaceae plants, such as *Triphysaria* spp. and *Phtheirospermum* spp., are facultative root hemiparasites (53). At

Figure 1

Parasitic plants in the angiosperm phylogenetic tree. (*a*) The phylogenetic tree of angiosperm orders and families. The tree was adapted from the Angiosperm Phylogeny Website (**http://www.mobot.org/MOBOT/research/APweb**) and the APG III tree (8). Orders that include parasitic genera are shown in red, and the names of parasitic families are in parentheses. (*b–k*) Macro (*left column*) and section (*right column*) photos of parasitic plants and haustoria in various families: (*b*,*c*) *Cuscuta pentagona* (Convolvulaceae), (*d*,*e*) *Striga hermonthica* (Orobanchaceae), (*f*,*g*) *Thesium chinense* Turcz. (Santalaceae in Santalales), (*h*) *Rafflesia keithii* (Rafflesiaceae), (*i*) *Rhizanthes lowii* (Rafflesiaceae), (*j*) *Hydnora africana* (Hydnoraceae), and (*k*) *Hydnora triceps* (Hydnoraceae). In panels *b*, *d*, *f*, *h*, and *j*, the arrowheads and red asterisks indicate the parasitic plants and their hosts, respectively. In panels *c*, *e*, *g*, *i*, and *k*, the dotted lines indicate parasite-host interfaces. Abbreviations: H, host plant; P, parasitic plant. Photos courtesy of Drs. Moran Farhi and Neelima Sinha (panels *b* and *c*), Kenji Suetsugu (panel *f*), Takanori Wakatake (panel *g*), Lachezar A. Nikolov and Charles C. Davis (panel *i*), and Lytton Mussleman (panels *j* and *k*).

first look, facultative parasites are almost indistinguishable from autotrophic plants, whereas some obligate parasitic plants are distinct because of their complete loss of fundamental plant structures such as leaves and roots, as they do not need to photosynthesize or absorb water from soil. For example, the root holoparasite *Rafflesia* spp., which parasitize grape family trees, completely lack leaves and roots but have giant flowers (96, 97). Similarly, *Hydnora* spp.—members of the



Hydnoraceae, which have been referred to as "the strangest plants in the world"—obtain all of their nutrients from their host Euphorbiaceae species and lack leaf and photosynthetic activities (93).

Despite the taxonomic divergence of parasitic species, all parasitic plants share a common feature: the haustorium, a specialized organ for host attachment, invasion, vasculature connection, and material transfer between the host and the parasite (**Figure 1**). The word haustorium comes from the Latin *haustor* or *haurire*, which means "water drawer." Although the term is also commonly used for an invasive organ of biotrophic plant-pathogenic fungi, the structures and functions of these two organs differ in several respects (44, 88). First, the fungal haustorium is a unicellular hypha, whereas the parasitic plant haustorium is a multicellular organ. Second, the fungal haustorium is an intracellular structure surrounded by a host-derived extrahaustorial membrane, whereas the parasitic plant haustorium is an intercellular structure that penetrates between the host cells.

Several parasitic plants are among the most devastating agricultural weed pests worldwide. In particular, the obligate root parasitic Orobanchaceae plants *Striga*, *Orobanche*, and *Phelipanche* spp. parasitize economically important crops, vegetables, and oil plants, including sorghum, maize, cowpea, tomato, and sunflower, and cause serious economic losses annually (104, 123). Those species have exploited highly sophisticated strategies for their parasitism. For instance, they produce small seeds that are easily spread by winds and remain highly dormant until they recognize the host-derived germination stimulants known as strigolactones. Strigolactones were originally identified as inducers of seed germination in *Striga* spp. and were later rediscovered as phytohormones that regulate plant architectures as well as rhizosphere interactions with symbiotic arbuscular mycorrhizal fungi (2, 47, 136). The strigolactone receptors were also recently identified in *Striga* spp. (28, 131, 135, 149). As excellent reviews on strigolactones have recently been published (3, 77), we do not discuss them in detail in this review. After germination, *Striga*, *Orobanche*, and *Phelipanche* spp. form a haustorium on their radicle tip, which attaches itself to the host roots to initiate the parasitic lifestyle (152). Because of the limited amount of stored nutrients in the small seeds, it is critical that obligate parasites attach to a host plant as soon as possible. In addition, because of the likely delivery of toxins by the parasites, host damage by infection is apparent soon after infection in some cases (118). Therefore, preventing the early parasitism processes will be critical for controlling parasitic weeds; however, efficient control methods have not been established to date.

Cuscuta, a genus in the Convolvulaceae family, includes approximately 200 obligate stem parasite species. *Cuscuta* spp. parasitize numerous species of dicotyledons, including cultivated crops such as tomato, tobacco, and forage legumes, resulting in serious agricultural problems (33, 70). *Cuscuta* spp. attack hosts nonspecifically, and one plant often serves as a host for multiple *Cuscuta* spp. (70). Because of their seeds' small size and hard, rough coats, which allow the seeds to remain viable in soil for many years, it is very difficult to get rid of *Cuscuta* plants once they have infested a field. The seeds can also be easily spread by humans and animals and can germinate under favorable temperatures and moisture conditions (33). Although the germination of *Cuscuta* spp. is not dependent on host plants, the parasites find their hosts by recognizing chemoattractants after germination (115, 116) and develop the haustorium to attach and invade the host, thereby establishing parasitism. Thus, the elucidation of the haustorial formation processes may provide an important basis for agricultural methods to control these parasites.

The haustorium is "the essence of parasitism" (78). The haustorium in parasitic plants dynamically changes its structures and functions during host interaction. Early in this process, the haustorium aids in host attachment and invasion, and later it helps establish nutrient absorption. The resultant symplastic continuity enables macromolecules or genetic materials such as RNA to be abundantly transferred between the hosts and the parasites. Microscopic observations and recent molecular studies have begun to highlight the biological and evolutionary importance of

haustoria. In this review, we focus on the dynamic shifts in the structure and functions of the haustorium in parasitic plants, particularly recent advances in the root parasitic Orobanchaceae plants and the stem parasitic *Cuscuta* spp. in the Convolvulaceae family.

HAUSTORIUM STRUCTURES

The haustoria in the parasitic Orobanchaceae, Santalaceae, and Convolvulaceae and those of many other families are hemispherical. The haustorium undergoes elaborate differentiation before host penetration, and this prepenetration structure is called a prehaustorium in some species. Two distinct types of haustoria are known: terminal haustoria and lateral haustoria (**Figure 2*a–e***). Although both types enable parasitic behavior, several features differentiate them. First, the lateral haustorium is present in all facultative parasites and some obligate parasites, whereas the terminal haustorium is observed only in obligate parasites. Second, the lateral haustorium can form laterally on stem or root tissues, whereas the terminal haustorium forms only at the apical meristem of the root radicle tip.

Haustorium Structures in the Orobanchaceae Family

The Orobanchaceae family contains the largest number of parasitic species that form haustoria in roots. The facultative parasites in this family, such as *Triphysaria* and *Phtheirospermum* spp., usually form lateral haustoria at the root elongation zone, and do so much less often at the maturation zone (62, 86). Because lateral haustoria do not interfere with the meristematic activity of the root apex and allow the root tips to elongate continuously, the parasites can generate multiple lateral haustoria along a single root (16, 141). By contrast, the terminal haustoria of the obligate parasites in the Orobanchaceae are normally larger and more anatomically complex. For example, some Orobanchaceae plants, such as *Orobanche*, *Phelipanche*, and *Alectra* spp. as well as *Striga gesnerioides*, develop a tubercle, which can grow up to 2–3 cm in diameter (40, 155). The tubercle accumulates starch to support the parasite's growth, flowering, and seed development (26, 69). Eventually, the apical meristems and nongeotropic adventitious roots, called crown roots or haustorial roots, also emerge from the tubercle (67).

Haustorium development starts a few hours after the exposure of the parasite to the host roots or host root exudates (14, 18). The earliest morphological event is swelling of the haustorium-forming site of the root (**Figure 3*a*,*b***). In the case of the facultative hemiparasitic Orobanchaceae plant *Agalinis purpurea*, the vacuolization and radial cellular enlargement of the cortical cells occur within 6 h of exposure to the host roots or exudates, and the anticlinal cell division of a subset of epidermal cells occurs as soon as 10 h after exposure (14, 18). These particular epidermal cells become the host interface during host penetration. Later, periclinal cell division begins from the innermost cortex and subsequently progresses to the outer cortex and pericycle layers. A similar pattern of haustorium formation occurs in the facultative parasites *Triphysaria versicolor* and *Phtheirospermum japonicum* (18, 62). A cell division marker construct was expressed in all cell layers in the haustorium within 24 h of exposure to haustorium-inducing chemicals (62).

Concomitant with the initiation of root swelling, the epidermal cells at the peripheral region of the haustorium start to form haustorial hairs, the polar outgrowths of epidermal cells, which are morphologically similar to root hairs (**Figures 2*b*** and **3**). The haustorial hairs appear in various Orobanchaceae parasites, including *Agalinis*, *Aureolaria*, *Buchnera*, *Rhamphicarpa*, *Triphysaria*, *Striga*, and *Phtheirospermum* spp. (13, 15, 62, 86, 103, 151). However, some parasitic plants, such as *Orobanche*, *Phelipanche*, and *Buchnera* spp., develop short extensions of the haustorial epidermis that result in papillae instead of haustorial hairs (69, 95). Unlike root hairs, both haustorial hairs

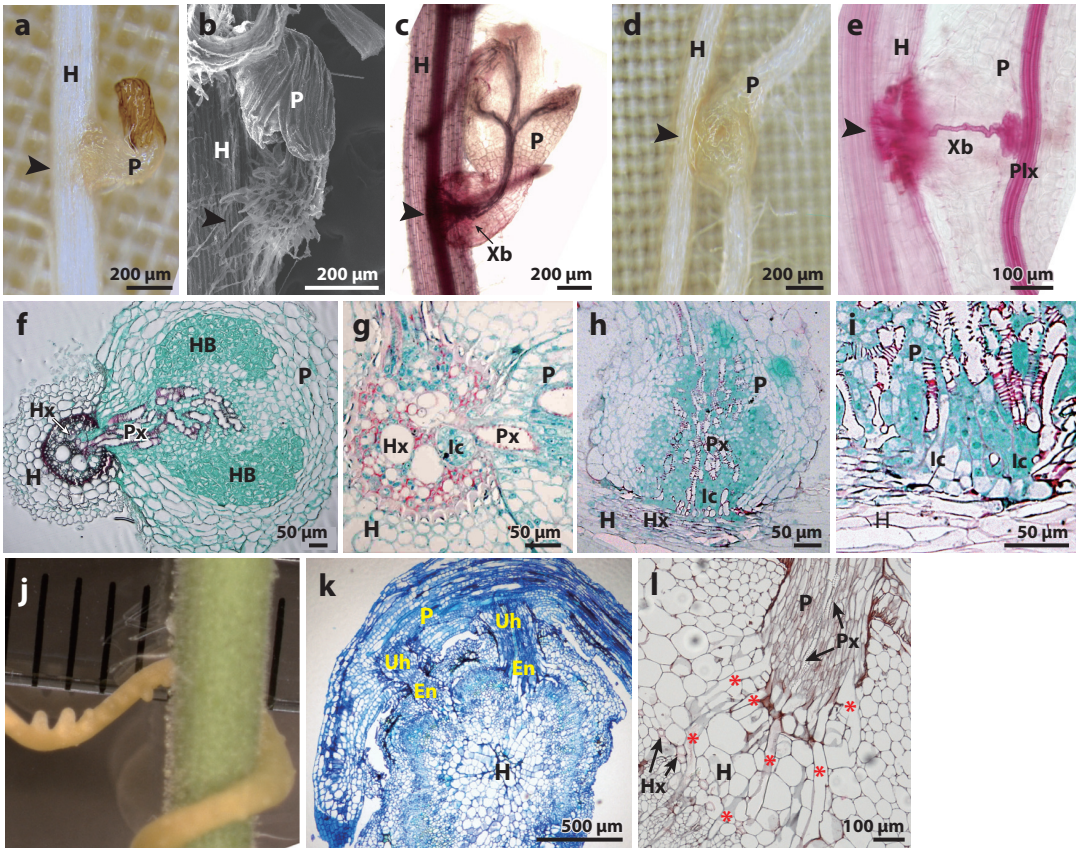


Figure 2

Haustorium structures in the Orobanchaceae and Convolvulaceae. (*a–c*) *Striga hermonthica* (Orobanchaceae) infecting rice. Panel *a* shows a macro photo of the host and parasite, panel *b* shows a scanning electron microscopy photo of haustorial hair development, and panel *c* shows a safranin O–stained *S. hermonthica* seedling forming a xylem bridge connection with rice roots. Arrowheads indicate the connecting points between the host and parasite. (*d*,*e*) The facultative parasite *Phtheirospermum japonicum* (Orobanchaceae) infecting rice. Panel *d* shows a macro photo of the host and parasite, and panel *e* shows a safranin O–stained *P. japonicum* haustorium. Arrowheads indicate the host-parasite connecting points; the xylem bridge and plate xylem are also indicated. (*f*,*g*) Cross sections of *S. hermonthica* infecting maize double stained by safranin O and fast green. Panel *f* shows the parasite xylem connected with the host xylem and the development of a hyaline body, and panel *g* shows a magnified photo of the host xylem filled with parasitic intrusive cells. (*h*,*i*) An *S. hermonthica* haustorium infecting rice. Panel *h* shows a longitudinal section of the infected tissue, and panel *i* shows a magnified photo of the *S. hermonthica* intrusive cells. (*j–l*) *Cuscuta pentagona* (Convolvulaceae) infecting a tomato stem. Panel *j* shows a macro photo of the *C. pentagona* haustoria, panel *k* shows a cross section of the *C. pentagona* haustoria, and panel *l* shows a close-up view of an endophyte. The red asterisks indicate the elongation of searching hyphae. Abbreviations: En, endophyte; H, host; HB, hyaline body; Hx, host xylem; Ic, intrusive cells; P, parasite; Plx, plate xylem; Px, parasite xylem; Uh, upper haustorium; Xb, xylem bridge. Photos of *C. pentagona* (panels *j–l*) courtesy of Drs. Moran Farhi and Neelima Sinha.

and papillae in the parasites secrete adhesive glues to anchor their haustoria to the host roots and to assist in penetration by providing mechanical forces toward the host tissue (13, 15).

After contact with the host, the epidermal cells at the apex of the haustorium become densely protoplasmic with enlarged nuclei, which is followed by rapid elongation of the cells, resulting in special cells called intrusive cells or palisade cells (55, 78, 90, 94) (**Figure 2*f–i***). The elongated intrusive cells constitute most of the parasite-host interface (54, 55) and extend between the

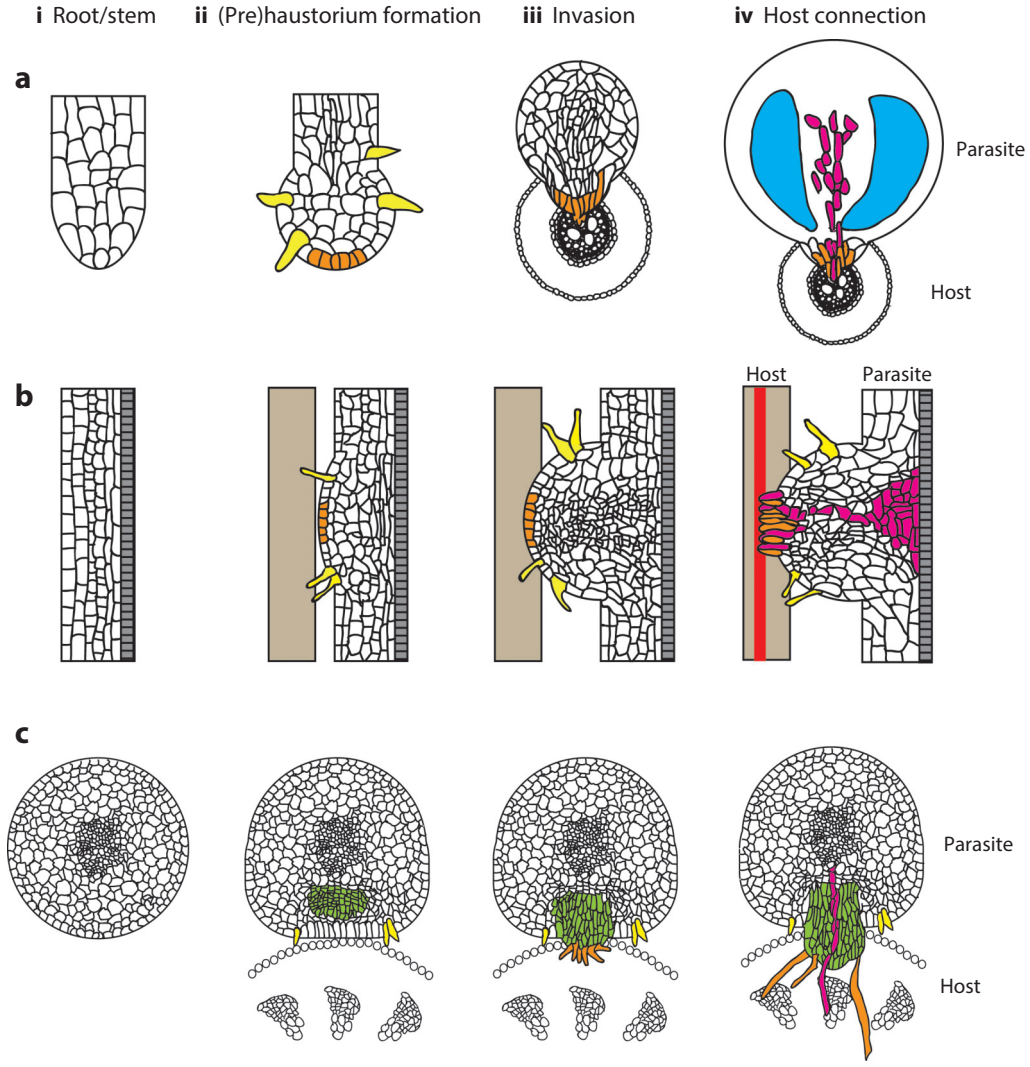


Figure 3

Schematic illustrations of haustorium development. (*a*) Development of a terminal haustorium in *Striga* spp. The radicle tip of *Striga* lacks a proper root cap structure (*i*) and starts to swell after haustorium-inducing-factor perception (*ii*). Swelling of cortical cells, division of epidermal cells (*orange*), and proliferation of haustorial hairs (*yellow*) occur in early haustorium formation (*ii*). The elongated intrusive cells derived from the epidermis are obvious during host invasion (*iii*). After reaching the host vasculature, some of the intrusive cells turn into xylem cells (*pink*) (*iv*). Haustorium cell structures drawn based on previous work (72) and our own observations. (*b*) Development of a lateral haustorium in *Phtheirospermum japonicum*. At the early stage of haustorium formation, expansion of cortical cells, cell division of the epidermis (*orange*) and inner cortex, and elongation of haustorial hairs (*yellow*) occur (*ii*). During host invasion, cell division spreads to other cell layers from the epidermis to the pericycle (*iii*). After reaching a host stele (*red bar*), some of the intrusive cells (*orange*) turn into xylem cells (*pink*) to form a xylem connection (*iv*). Gray striped boxes represent the parasite vasculature. Cell structures drawn based on observations of longitudinal sections of a *P. japonicum* haustorium with modifications. (*c*) Development of a haustorium in *Cuscuta* spp. The disc-like meristem appears in the *Cuscuta* prehaustorium (*green*) (*ii*), and the epidermal cells divide and form trichome-like elongated cells (*yellow*). The cortex-derived haustorium (*green*) penetrates the host tissue (*iii*). During this process, the outside layers of the haustorial meristem are compressed and detached, similar to root cap cells. Inside host tissues, the elongated searching hyphae (*orange*) grow toward the host vasculature (*iv*). The searching hyphae that come into contact with the host xylem become xylem cells (*pink*) to establish the xylem bridge (*iv*). Cell structures drawn based on photos in References 33 and 82 with some modifications.

host cells toward the host vasculature. After reaching the host xylem, some of the intrusive cells penetrate host vessel elements, perforate their tips to form tube-like structures, and turn into vessel elements known as oscula in *S. hermonthica* (36) (**Figure 2*f*,*g***). Subsequently, cells at the center of the haustorium differentiate into vessels or tracheary elements to form a xylem bridge, establishing the host-parasite xylem continuity (54, 94, 151, 152, 155) (**Figure 2*c*,*e***). In lateral haustoria, periclinally divided haustorial cells close to the parasite vasculature differentiate into xylem cells and form a stack of tracheid cells called plate xylem (55) (**Figures 2*e*** and **3*b***). In addition to the xylem continuity, some obligate parasites in the Orobanchaceae, including *Orobanche crenata* and *Alectra vogelii*, develop phloem cells inside the haustorium to connect to the host vascular system (38, 155). Symplastic continuity through plasmodesmata has also been observed at the interface between the neighboring cells of *O. crenata* and its host (11, 37, 101).

As the host-parasite vascular connection is established, a cluster of secondary parenchyma cells called the hyaline body—also referred to as the hyaline tissue, central parenchyma core, or haustorial nucleus—forms around the central xylem strand of the haustorium (90, 99, 149) (**Figures 2*f*** and **3*a***). The hyaline body appears in both lateral and terminal haustoria and is prominent in major genera within the Orobanchaceae, including *Alectra*, *Striga*, *Buchnera*, *Lathraea*, *Rhinanthus*, *Odontites*, and *Melampyrum* (48, 56, 78, 95, 108, 140). Other parasites, such as *Rhamphicarpa* and *Triphysaria* spp., do not contain the cells that structurally resemble hyaline bodies (55, 94). Hyaline bodies have also been reported in parasitic plants outside of the Orobanchaceae, such as *Thesium chinense* and *Santalum album* (125, 128). The presence of abundant mitochondria, endoplasmic reticulum, and large nuclei suggests that hyaline bodies are highly active in metabolism (140). Indeed, a large amount of carbohydrate deposits in the intercellular space is a characteristic feature of the hyaline body (140). The proposed function of these accumulations is to provide osmotic gradients that favor the nutrient flow toward the parasites (108). Histochemical studies in three genera of the Orobanchaceae revealed that the cell walls of hyaline bodies are particularly enriched in arabinogalactan proteins, which might increase the haustorium's water-holding ability (108).

Haustorium Structures in the Convolvulaceae Family

Cuscuta spp. in the Convolvulaceae form haustoria from stem tissues (4, 52) (**Figures 1*b*,*c*** and **2*j***). These parasites have lost their roots and leaves in conjunction with a reduction in their rate of photosynthesis, and thus their main body consists only of stems that twine around the host (27, 42). The cone-like haustoria with wedge-shaped tips develop along the inner side of the twined coil of *Cuscuta* spp. Similar to the facultative root parasites, a single *Cuscuta* plant produces a large number of lateral haustoria (4). The prehaustorium of *Cuscuta japonica* forms within 24 h of host contact (60). The first changes in haustorium formation are starch accumulation and nuclei enlargement in the cortex, leading to the formation of haustorium initials accompanied by cell divisions of the epidermal cells (33, 82). The prehaustorium—also called the adhesive disk or upper haustorium—is an external part of the haustorium that remains outside of host tissues. The epidermal cells of the prehaustorium dedifferentiate, divide anticlinally, and form cytoplasm-rich cells. Some of these cells become elongated and form trichome-like cells that secrete pectinaceous substances that seal the space between the host and the parasite (137) (**Figure 3*c***).

The inner part of the haustorium that penetrates host tissues is called the endophyte or inner haustorium in *Cuscuta* spp. The endophyte primordia appear from the disc-like meristem formed by the activation of cortical cell division in the prehaustoria (33, 82). In *C. japonica* and *Cuscuta pentagona*, the endophyte primordia consist of two cell types: digitate cells and file cells (4, 82). The digitate cells are located at the distal region and have elongated shapes with large nuclei and dense cytoplasm, whereas file cells are located at the proximal region and are small and have

conspicuous nuclei (82). The endophyte primordia continue to grow through the peripheral cells in stems to form wedge-shaped haustoria that penetrate the host tissues (33) (**Figures 2*k*** and **3*c***).

One or two days after host attachment, the tip of the endophyte begins to elongate and forms searching hyphae. Searching hyphae are tip-growing cells and extend as far as 2 mm into compatible hosts (30, 33, 138) (**Figures 2*l*** and **3*c***). The growing end of the searching hyphae is rich in Golgi-derived vesicles and organelles and contains a large nucleus (138). The searching hyphae elongate toward the host vasculature, with the hyphal tip ends contacting the host phloem or xylem cells. Interspecies plasmodesmata connections form along the walls of developing searching hyphae, especially near the tip region (138).

When the searching hyphae reach the host xylem or phloem, the hyphal cells transform to resemble the host cells that they contact. For example, the searching hyphae that contact the host xylem differentiate into xylem elements. The xylic hyphae directly connect host and parasite xylems and form xylem bridges. By contrast, the searching hyphae that contact sieve elements of phloem differentiate into phloem cells, also called absorbing hyphae (35). Absorbing hyphae form finger-like protrusions surrounding the host sieve elements (33). The absorbing hyphae represent highly specialized sieve elements characterized by an abundance of smooth-surfaced endoplasmic reticulum that facilitates apoplastic transfer of saccharides (139).

HAUSTORIUM-INDUCING FACTORS

The initiation of haustorium formation is the critical step for the transition from the autotrophic to heterotrophic lifestyle. Although many parasitic plants form haustoria on nonbiological materials (78), chemical and/or physical cues are known to stimulate haustorium initiation. The chemical compounds that induce haustoria in the Orobanchaceae are called haustorium-inducing factors (HIFs) (25, 112). The first HIF identified directly from host root extracts was 2,6-dimethoxy-*p*-benzoquinone (DMBQ) (25). After the identification of DMBQ, many structural analogs of DMBQ were found to exhibit similar haustorium-inducing activities. These active analogs fall into a certain range of electromotive potential, whereas the inactive analogs fall out of this range, implying that the redox range is important for the haustorium-inducing activity (120).

The exact biosynthetic pathway of DMBQ is not well defined, but it can be derived from the oxidation of syringic acid, a phenolic acid that originates from cell wall lignin (25). Various phenolic acids, including syringic acids, *p*-coumaric acids, and vanilic acids, induce haustorium formation in *T. versicolor* roots at different concentrations (5). For example, *p*-coumaric acid displayed significantly higher activity than syringic acids in *T. versicolor* but failed to induce haustoria in *A. purpurea* (5), suggesting that the recognition of phenolic acids for haustorium formation varies across parasite species. Conversion from phenolic acids to quinones requires an enzymatic reaction through H_2O_2 and other peroxidases (65, 73). When Kim et al. (73) applied syringic acid to *Striga asiatica*, they detected DMBQ in the media. The addition of catalase, an H_2O_2-scavenging enzyme, inhibited haustorium induction by syringic acid but not induction by DMBQ, suggesting the importance of H_2O_2 in the haustorium-inducing activity of syringic acid (73). This supports the proposed model that the host-released phenolic acids are converted into quinones by peroxidase and H_2O_2 secreted from parasite radicle tips, and haustorium initiation is then triggered by quinones. Indeed, *S. asiatica* produces H_2O_2 abundantly in the cytoplasm and the apoplastic region of the radicle tip (71). However, it remains unclear whether host roots release phenolic acids without mechanical wounds and why the parasite roots do not induce haustorium formation. In addition, flavonoids, which often serve as signaling compounds in plant-microbe interactions, such as the symbiotic rhizobium-legume relationship (106), also induce haustorium formation in the Orobanchaceae. For example, the flavonoid peonidin shows haustorium-inducing activities

similar to those of DMBQ in *T. versicolor* (5), implying that host root exudates may contain HIFs other than DMBQ.

The identification of key genes for haustorium formation may contribute greatly to the elucidation of haustorium-inducing signal components. Transcriptome analyses in *T. versicolor* found that DMBQ exposure substantially upregulates the quinone oxidoreductase–encoding genes *TvQR1* and *TvQR2* at the root tip (86, 87). TvQR1 mediates a single-electron reduction of DMBQ, leading to the generation of a semiquinone, an intermediate product during DMBQ conversion to hydroquinone (124); TvQR2, which catalyzes two-electron reduction, directly mediates the production of hydroquinone. Interestingly, knockdown of *TvQR1*, but not of *TvQR2*, reduces the number of haustoria (16). Semiquinone is a highly reactive free radical and can react with oxygen to produce superoxide anion radicals, leading to the hypothesis that either the reactive oxygen species itself or the reduced semiquinone intermediate acts as a signal to initiate haustorium development. However, the *TvQR1* ortholog was not upregulated in the closely related facultative parasite *P. japonicum*, indicating that the signaling pathway may vary across species (63). Another early-induced gene that positively regulates haustorium formation is *TvPirin*, which encodes a transcription regulator whose homologs are generally involved in environmental sensing in nonparasitic plants (17). The functional analyses of these genes may validate their involvement in haustorium formation.

Unlike several Orobanchaceae species, *Orobanche* and *Phelipanche* spp. do not respond to DMBQ, phenolic acids, or flavonoids with haustorium initiation (69, 142). In addition, some *Triphysaria* spp. form haustoria in response to host root exudates but rarely in response to DMBQ (64). Thus, chemical compounds that may have different structural features from known HIFs can still act as HIFs. Another important point is that the haustoria induced by HIFs do not fully develop internal structures, such as intrusive cells or xylem bridges, indicating that other host signals are necessary to establish the parasite-host connection (39).

HAUSTORIUM FUNCTIONS

Immediately after the perception of haustorium-inducing signals, parasitic plants initiate the developmental program of haustorium formation. The haustorium has four main sequential functions: to attach to the host, to penetrate the host tissues, to avoid the host immunity system, and to develop a vascular connection between the host and parasite to absorb water and nutrients. Because present sequencing technologies allow comprehensive surveys of gene expression in nonmodel organisms, transcriptome analyses have been conducted in several parasitic plants, and genes expressed in haustoria have been successfully identified in order to describe these functions in molecular terms (59, 149) (**Figure 4**).

Host Attachment

The first step in the attack by parasitic plants is host attachment, which is facilitated by haustorial hairs (105). The development of haustorial hairs at the periphery of the attachment site is a common feature of many root parasitic plants. Because these hairs play a role in anchoring to the host, their surface is covered by sticky secreted materials, such as the hemicelluloses on the haustorium hairs in *A. purpurea* (13) and the pectinaceous mucilage-like material in *Triphysaria* spp. (55). These secretion materials allow haustorial hairs to establish a structural bond with the host surface. Similar to the haustorial hairs, the epidermal cells of the prehaustorium in *Cuscuta* spp. elongate and form secretory trichome-like structures, which secrete materials that are highly enriched with de-esterified pectin (137). Thus, the trichome-like cells ensure tight contact and adhesion of the parasite to the host surface. However, the precise role of these trichome-like cells

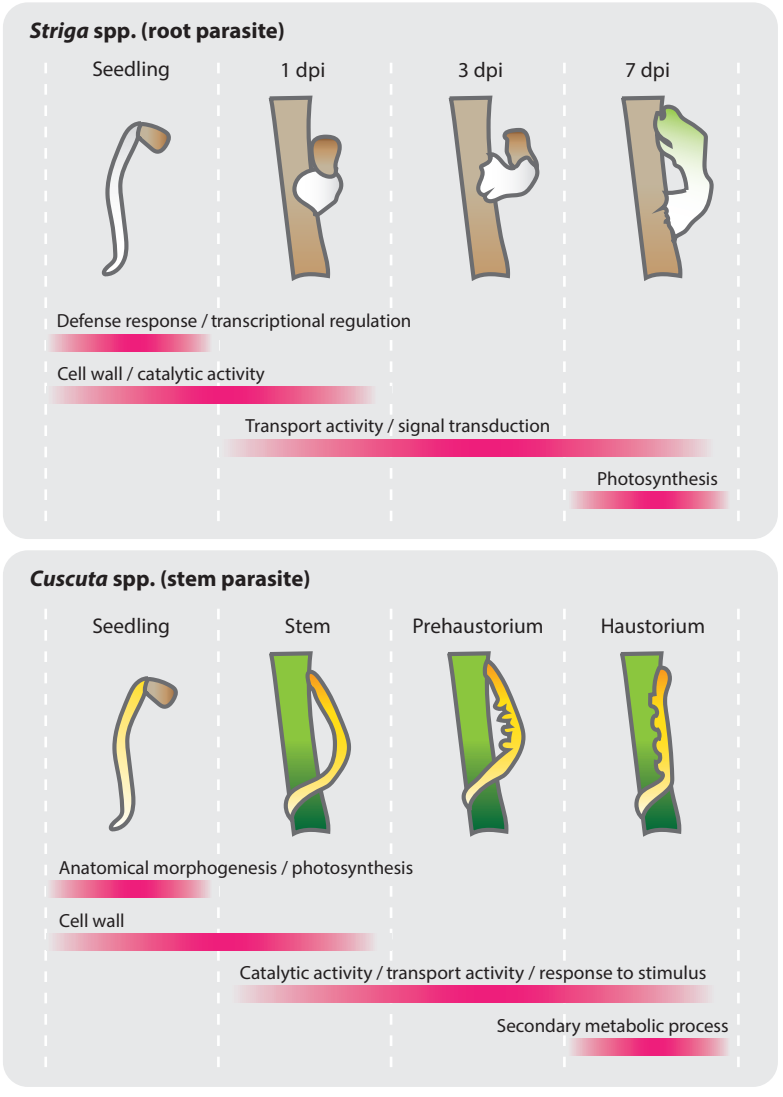


Figure 4

Representative Gene Ontology categories enriched at the indicated developmental stages. Although *Striga* spp. and *Cuscuta* spp. are phylogenetically independent and show different parasitic modes, they share common functional aspects in gene expression patterns. The Gene Ontology categories are adapted from References 109 and 149. Abbreviation: dpi, days post-infection.

in host invasion is still unclear (30, 33). Detailed characterization of secondary products secreted from either haustorium hairs or the trichome-like structures is necessary for further understanding of the haustorium function.

Host Invasion

Enzymatic activities are important after host attachment, when the intrusive cells in the Orobanchaceae penetrate between host cells (34, 79, 89). This idea is supported by the fact that host

cortical cells and their cell walls appear to be fragmented or dissolved rather than crushed by the intrusive cells during the penetration process (95, 102). In addition to the dissolution of host cells and walls, the mechanical pressure by the penetrating intrusive cells pushes host cells aside so that the shapes of the host cells change and the space between them is fully occupied by the parasite cells (105). An interesting aspect of the invasion process is that the intrusive parasite cells can overcome the endodermis, including the Casparian strips, where lignin polymers create an apoplastic diffusion barrier (43, 92). For example, the *Striga hermonthica* haustorium advances into intercellular spaces of the host endodermis by dissolving the Casparian strips without damaging the host endodermal cells (95). Interestingly, several resistance cultivars exhibit post-attachment resistance to parasites by blocking them at the root endodermal layer (46, 49). Similar to intrusive cells in the Orobanchaceae, searching hyphae in *Cuscuta* spp. invade host tissues. Unlike intrusive cells, which generally penetrate the apoplastic spaces of host tissues, searching hyphae can penetrate intracellular spaces (138).

Several enzymes are considered to be involved in the host invasion. Gene Ontology categories related to cell walls or hydrolases include many genes that are highly expressed in the host-invading haustoria of species in both the Orobanchaceae and Convolvulaceae families (60, 109, 148, 149) (**Figure 4**). Pectin methylesterase is secreted on the host cell walls adjacent to the parasite and is associated with the appearance of demethylated pectins (85). Furthermore, several genes encoding putative pectin methylesterase inhibitors are specific to the haustorial tissue, suggesting that a combination of pectin methylesterases and pectin methylesterase inhibitors might have a role in host invasion (148). A recent *S. hermonthica* transcriptome analysis identified 1,292 genes categorized in the Carbohydrate-Active Enzymes (CAZy) database, 252 of which are differentially expressed during the invasion stages (149). These genes mainly encode pectin-degrading enzymes. In addition, many other gene families that encode cell wall–modifying enzymes such as cellulose hydrolases, glycosyl hydrolases, and peroxidase enzymes are expressed in the haustoria of Orobanchaceae spp. as well as the parasites *Viscum album* and *C. pentagona* (96, 109, 148). Expansins, which unlock the network of wall polysaccharides to loosen the cell walls (29), are also associated with host invasion (87, 100). Consistently, transcriptomic analyses combined with laser capture microdissection approaches have revealed that expansin-encoding genes are expressed specifically in the intrusive cells of *T. versicolor* (58). Further functional analysis of these cell wall–degrading or cell wall–modifying enzymes in host cell wall degradation will provide additional insights into host invasion by parasitic plants.

Host Immunity Avoidance

The attachment tissues, such as haustorium hairs and intrusive cells, allow parasitic plants to anchor and penetrate into the host, but this action is likely to activate the host immunity system (89, 91, 126). Parasitic plants may mimic the compatible intrusive growth of pollen tubes, which are able to avoid immunity activation. Interestingly, genes encoding pectate lyases, which are required for pectin degradation during pollen tube growth (145), and expansins, which loosen maternal cell walls to aid penetration of the stigma by the pollen tube (29), are expressed in the haustorium (58, 87, 100, 109, 148, 149). Recent comparative transcriptome analysis using three Orobanchaceae species also revealed adaptive changes in genes recruited from pollen tube development in parasitic lineages (148, 149). However, parasitic plants make a clear wound site in the host root tissues during invasion, and the host should therefore recognize the parasite cells as intruders (91). Thus, an active parasitic mechanism that prevents host immunity should exist. Studies using cowpea revealed that a typical nucleotide-binding site–leucine-rich repeat (NBS-LRR) immune sensor protein confers resistance against *S. gesnerioides* (83), suggesting that parasites secrete a corresponding effector that

is recognized by the NBS-LRR protein in resistant hosts but suppresses the host immunity system in hosts that lack the protein. Other plant pathogens, including bacteria, fungi, oomycetes, and nematodes, employ secreted effectors to manipulate host responses (9, 144). Sequencing of the *S. asiatica* genome indeed identified 532 genes encoding putative uncharacterized secreted proteins (149). Functional characterization of those potential effectors may provide insight into a novel strategy of immunity suppression by parasitic plants.

Nutrient Transfer

The fully functional haustorium establishes connections between the conductive tissues of its hosts to enable the transfer of water and nutrients. In this sense, haustoria share some functional characteristics with roots, which absorb water and minerals, as well as with minor leaf veins, which upload the products of photosynthesis (58). Although the haustoria of certain holoparasites, such as *Orobanche* and *Cuscuta* spp., make both xylem and phloem connections to the host, some hemiparasites, such as *Striga* and *Triphysaria* spp., form only xylem (and not phloem) connections to the host (41).

Water and mineral nutrients move from a host to a parasite through the xylem connection. A gradient of water potential between the host and parasite should drive the flow direction. Solute accumulation, open stomata, or a combination of these could allow a parasitic plant to maintain a lower water potential than the host (122). In accordance with this idea, Orobanchaceae parasites selectively accumulate certain cations, such as potassium, thereby attaining higher concentrations of these cations compared with the host tissues (24, 57, 84). Similarly, *Rhinanthus* spp. keep their own stomata open, which leads to a higher rate of transpiration that allows a directional flow from the host to the parasite (66). Interestingly, physiological experiments using isolated guard cells of *S. hermonthica* suggested that a high potassium concentration leads to anomalous stomatal responses to environmental factors (119). In other words, the accumulation of potassium ions may increase the transpiration rate by keeping stomata open, thus increasing the potassium influx. Accumulation of sugar alcohols such as mannitol also contributes to the unidirectional flow of water into the parasite. Active mannitol biosynthesis pathways have been identified in many Orobanchaceae plants (50, 113). In particular, in *Phelipanche aegyptiaca*, host-induced gene silencing to reduce the levels of mannose 6-phosphate reductase—a key enzyme that converts mannose 6-phosphate to mannitol 1-phosphate in mannitol synthesis—decreases mannitol levels in the parasite and increases the number of dead tubercles, suggesting that mannitol accumulation is important for parasitism (6).

The proportion of organic carbon and nitrogen derived from a host is directly related to the level of parasite dependency on the host as well as to the host species (58, 61). Facultative parasites such as *Rhinanthus minor*, obligate hemiparasites such as *Striga* spp., and holoparasites such as *Orobanche* spp. obtain approximately 10%, 30%, and 100% of their carbon from their hosts, respectively (61). The level of dependency on the host for carbon and nitrogen could change during a parasite's life cycle (1). In addition, parasites have less capacity for nitrate reduction than fully autotrophic plants (58). However, transcriptome data showed increased expression of genes associated with the transport of nitrate, ammonia, and amino acids in the haustorial stage of *C. pentagona* (109). Genes related to the transport of glutamate, which is the predominant form of translocated nitrogen, are upregulated in the haustoria of Orobanchaceae plants (148). Therefore, some parasites may have undergone an evolutionary reduction in nitrogen assimilation machinery and developed transporter activity in their haustoria to obtain nitrogen from their hosts. Furthermore, the genes whose functions fall under the Gene Ontology category of transporter activity are enriched in the transcriptome at the late stage of haustorium development (**Figure 4**). Detailed analysis of such

transporter characteristics may also contribute to understanding how parasitic plants evolved their nutrient acquisition systems.

TRANSFER OF GENETIC MATERIAL VIA THE HAUSTORIUM

mRNA Exchanges

The haustorium not only absorbs water and nutrients from hosts but also transfers macromolecules, such as proteins, mRNAs, and metabolites, as well as pathogens such as viruses and phytoplasma (75, 121). For instance, transgenic host plants expressing green fluorescent protein under the control of a companion cell–specific promoter demonstrated the direct movement of proteins to *Cuscuta* spp. or *P. aegyptiaca* via phloem connections (7, 22, 51). Macromolecules are also transferred through the xylem continuity, as shown by a tomato–*P. aegyptiaca* interaction that transferred fluorescent-dye-labeled dextrans of sizes up to 70 kDa (7). Importantly, the dye loaded on the parasites was also observed in the hosts, demonstrating that the xylem flow is bidirectional (7).

Intriguingly, several thousand mRNAs are bidirectionally transferred between *Cuscuta* spp. and their hosts (74, 114, 130). The amounts and variety of transferred RNAs appear to be dependent on the specific combinations of host and parasite and on the mRNA detection conditions. In the *Arabidopsis–C. pentagona* interaction, for example, approximately 1% of mRNAs are transferred from the host to the parasite and 0.6% are transferred from the parasite to the host, covering 45% and 24% of total expressed unigenes of the host and parasite, respectively (74). A similar experiment showed that more than 2,000 mRNA species are transferred from *Arabidopsis* to *Cuscuta reflexa*, and similar numbers were observed in the root-shoot mobile mRNAs after intraspecies grafting (130). The mobile mRNAs seem to have some selectivity, because the quantity of transferred mRNAs differs among RNA species (81). Remarkably, in the case of intraspecies grafting, the immobile RNAs become mobile by fusing with mobile RNAs (130). However, no specific structural features of transcripts have been found to correlate with their mobility (75). The abundance of a transcript at the region of the haustorial connection could potentially be one of the factors, but this would not entirely explain the selectivity of mobile RNAs (74).

David-Schwartz et al. (31) detected host mRNAs in parasite parenchyma cells and in phloem, suggesting that the RNAs were transferred via symplastic connections between parenchyma cells and were then loaded onto the phloem. The RNAs can be transferred across a long distance, probably through the phloem; in the case of the tomato–*C. pentagona* interaction, the host RNA was detected in the parasite stem as far as 30 cm away from the interaction point (31, 81) and for as long as 8 h after the parasite was detached from the host (81). The exact biological roles of this bidirectional bulk flow of RNAs remain to be determined, and it would be interesting to know whether it acts to maintain the parasitism, either by acquiring physiological components from hosts or by fooling the host plants. Tesitel et al. (129) detected the translational products of mobile RNAs in intraspecific grafts, suggesting that the mobile RNAs may be translated to have biological functions at their destination. The bulk flow of RNAs also suggests that plant parasitism is similar to interspecific grafting, with the host and parasite behaving like a connected single plant.

The mobility of macromolecules can be used to control parasitic weeds. Because small RNAs can move from hosts to parasites, host-induced gene silencing is becoming a practical way to control parasite genes (98). The concept of this method is that the silencing constructs for essential parasite genes are transformed to host plants and suppress the parasite's growth because of the small interfering RNA (siRNA) movement from host to parasite, where the actual silencing takes place. Tomilov et al. (133) have performed a proof-of-concept experiment with the facultative

T. versicolor system using lettuce as the host. Interestingly, the silencing signals can be transmitted from one host to another host by using the parasite as a bridge, indicating that the siRNA signals are bidirectional and can travel long distances (133). Host-induced gene silencing has been used to silence genes encoding mannose 6-phosphate reductase in *P. aegyptiaca* (as mentioned above) (6), the cytosolic acetyl–coenzyme A carboxylase (EC 6.4.12) in *T. versicolor* (19), and the KNOTTED-like homeobox transcription factor SHOOT MERISTEMLESS-like (STM) in *C. pentagona* (4), all of which successfully reduced parasite viability, confirming the usefulness of this technique for controlling parasitic plants. Finding more target genes and transforming agriculturally important host plants will be the next steps to push this technology forward.

The movement of endogenous small RNAs, such as microRNAs, has not been confirmed but is quite likely. siRNA derived from host transgenes has been detected in *T. versicolor* and *C. pentagona* (4, 19). The abundance of endogenous *C. pentagona* microRNAs differed between transgenic and nontransgenic hosts, correlating with developmental defects of the parasite (4). This result indicates that the developmental control of *C. pentagona* may be regulated by microRNA species. Endogenous microRNAs were also detected in *P. aegyptiaca*, suggesting the existence of a microRNA-dependent pathway in parasitic plants similar to that of other autotrophic plants (6). Small-RNA movement between hosts and parasites might be one of the endogenous mechanisms to control host-parasite interactions.

Horizontal Gene Transfer

The macromolecule exchanges during the intimate haustorial connection result in stable exchanges of genetic components called horizontal gene transfers (HGTs). HGT events are more common in parasitic species than in free-living angiosperms (32) and are more common in mitochondria than in plastid and nuclear genomes. Mitochondrial HGTs in both directions are recognized in 10 of 12 parasitic lineages, explaining the higher frequency of mitochondrial HGTs in host-parasite interactions (32). A genome survey of endophytic holoparasite Rafflesiaceae plants indicated that 24–41% of mitochondrial genes showed evidence of HGTs (147). Although the autotrophic and ancestral angiosperm species *Amborella trichopoda* showed remarkable contents of mitochondrial genes that originated from HGT events (likely via mitochondrial fusion), most *Amborella* transgenes are pseudogenes. By contrast, the transferred genes in the Rafflesiaceae retain their gene structures and probably their functions as well (110, 147). Therefore, the foreign genes may have contributed to the parasitic function or its evolution.

Nuclear HGT between plant species has been considered rare, but an increasing amount of evidence indicates that it occurs more frequently than expected (117). Nuclear HGT includes both protein-coding genes and retrotransposons. *S. hermonthica* obtained a functionally unknown gene from its natural hosts, sorghum and related species (150). The sequence similarity of the transferred gene to the corresponding host gene suggests that this HGT event occurred shortly after the speciation of *Striga* spp. (150). Similar HGTs have occurred for a gene encoding the albumin 1 KNOTTIN-like protein, which was transferred from a legume host to the parasite *P. aegyptiaca* (154), and a gene encoding the strictosidine synthase-like protein (153), which was transferred from a Brassicaceae host to the related parasite *Orobanche aegyptiaca*. Interestingly, both of these genes are also present in *Cuscuta* spp., and the phylogenies showed evidence of HGTs from similar hosts in separate HGT events, suggesting that there may be a preference for the horizontally transferred genes (153, 154). Alternatively, the functions of these genes may be crucial for parasitism, and therefore the genes were retained in the parasite genome.

A recent genome-scale survey revealed the frequency of nuclear HGTs. Large-scale transcriptome analysis of the holoparasite *Rafflesia cantleyi* (Rafflesiaceae) identified at least 31 genes

obtained from its hosts (146). The complete genome sequence of *S. asiatica* also identified at least 3 protein-coding genes from its monocot hosts (149). Moreover, the *S. asiatica* genome sequence identified several bidirectional HGTs of retrotransposons. Although HGTs of retrotransposons between angiosperms are commonly acknowledged, such transfers usually occur between closely related species. In fact, an analysis of 40 fully sequenced plant genomes identified only one dicot-monocot HGT event (12). By contrast, retrotransposon HGTs between hosts and parasites seem to occur more frequently (149), raising the intriguing possibility that parasitic plants act as vectors for retrotransposon transfer.

THE EVOLUTION OF THE HAUSTORIUM

Haustoria have evolved independently at least 12 times in angiosperms (21). The haustoria share common structures and functions across evolutionarily independent lineages, indicating that this organ is a key innovation that facilitates the convergent evolution of parasitism. What is the mechanism that allowed the development of haustoria across independent lineages? Although it has been hypothesized that parasites evolved through endophytic association or HGTs from microorganisms that could confer parasitic ability (10), it has commonly been assumed that haustoria originated from a mutation-based modification of the root or stem (78).

In the Orobanchaceae, haustoria and lateral roots share similar developmental and cellular events: auxin accumulation, cell proliferation, and cell wall remodeling (149). The lateral root development (LRD) program has been well studied in *Arabidopsis*, and the results have indicated that local auxin accumulation is the key to specifying the founder cells for lateral roots (107). Genes such as *SOLITARY ROOT* (*SLR*)/*INDOLE-3-ACETIC ACID INDUCIBLE 14* (*IAA14*) and *AUXIN RESPONSE FACTOR 19* (*ARF19*) function as a module to regulate expression of the auxin influx carrier gene *LIKE-AUX 3* (*LAX3*) and localized auxin accumulation at the pericycle (127). Similarly, local auxin accumulation is crucial for haustorium development in parasitic plants. In *T. versicolor* and *P. aegyptiaca*, exogenous application of auxin increases the number of haustoria, whereas disturbing auxin flux decreases the number of haustoria (20, 132). A root tip dissection experiment and characterization of the auxin-responsive *IAA2* promoter demonstrated that the auxin accumulation is involved in haustorium initiation in *T. versicolor* (132). Transcriptome analyses using the facultative parasite *P. japonicum* identified a *P. japonicum YUCCA 3* (*PjYUC3*) gene encoding an auxin biosynthesis enzyme expressed specifically at the haustorium apex in the early stage of haustorium development (63). Detailed characterization of *PjYUC3* knockdown and its promoter activity using hairy root transformation of *P. japonicum* indicated that *PjYUC3* is important for haustorium development. Observations of auxin-responsive marker *DR5* expression during haustorium formation suggest that the high auxin response at the haustorium apex is coincident with the local expression of the *PjYUC3* gene (63). In addition, a transcriptome study in *C. pentagona* revealed that genes associated with polar auxin transport are enriched at the early haustorial stage (109). A transcriptome analysis in *S. hermonthica* also showed that orthologous genes related to auxin maxima, such as *SLR/IAA14*, *ARF19*, and *LAX3*, are specifically expressed in the germinated seedling (149), suggesting that the *SLR/IAA14-ARF19-LAX3* pathway might be utilized during the early stages of *Striga* haustorial formation.

Local regulation of cell proliferation is consistently shared between LRD and haustorium development. The cell cycle marker *cyclin B1* promoter is activated during the haustorium formation, indicating that the haustorial cells reenter the cell cycle (62). In *Arabidopsis*, *PUCHI* and *LOB DOMAIN–CONTAINING PROTEIN 18* (*LBD18*), which are targets of the *SLR/IAA14-ARF19* module, inhibit and activate cell proliferation, respectively, to shape lateral root formation (80). The orthologs of *PUCHI* and *LBD18* in *S. hermonthica* are highly expressed at the attachment

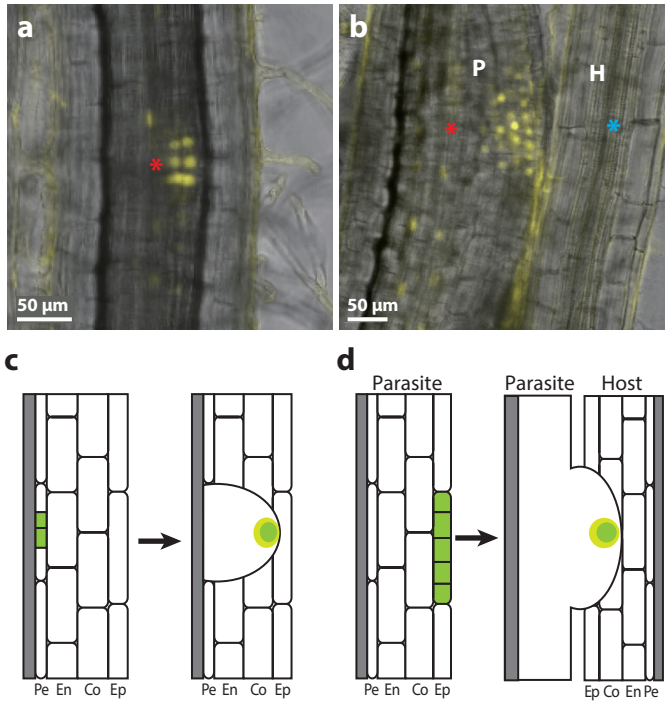


Figure 5

Local auxin accumulation during LRD and haustorium formation. (*a*,*b*) Expression of an auxin-responsive *DR5* promoter visualized by nuclear-localizing YFP fluorescence at lateral root primordia during LRD (panel *a*) and at the haustorium apex at an early stage of haustorium formation (panel *b*) in *Phtheirospermum japonicum*. Red and blue asterisks indicate the parasite and host xylems, respectively. In the lateral root primordia, auxin responses were detected at the pericycle, whereas in the haustorium, auxin responses were detected at the epidermis and outer cortex. (*c*,*d*) Schematic illustrations of LRD (panel *c*) and haustorium formation (panel *d*). During LRD, auxin responses (*green*) occur at the pericycle, and the pericycle-derived lateral root primordia grow out through the endodermal, cortical, and epidermal layers. During haustorium formation, the auxin responses occur at the epidermis, and the haustorium grows through the host epidermis, cortex, endodermis, and pericycle to reach the host stele. The gray bars in panels *c* and *d* represent the stele. Abbreviations: Co, cortex; En, endodermis; Ep, epidermis; H, host; LRD, lateral root development; P, parasite; Pe, pericycle; YFP, yellow fluorescent protein. Photos for panels *a* and *b* taken by Takanori Wakatake.

stages, and their expression occurs just after the expression of *SLR/IAA14-ARF19-LAX3* orthologs (149). In addition, the cell wall remodeling pattern shows similar developmental events for LRD and haustorium development. To emerge from the parent root, the lateral root must go through three cell layers: the endodermis, the cortex, and the epidermis. In an analogous fashion, the host invasion of the haustorium must overcome the same three cell layers of the host root to complete the vascular connection (**Figure 5**). *SHORT HYPOCOTYL 2* (*SHY2*)*/IAA3* regulates cell wall remodeling–related genes in LRD (45), whereas its *Striga* orthologs are expressed at the invasion stage of parasitic plants (149). Notably, pectate lyases, pectin methylesterase, and expansin are induced by auxin in a *LAX3*-dependent manner in *Arabidopsis* LRD (127), whereas the *Striga* orthologs of these enzymes are expressed in the host invasion stages (149).

Taken together, the findings described above indicate that the LRD genes of *S. hermonthica* are activated during haustorium formation in a manner that resembles *Arabidopsis* LRD. Interestingly,

the rootless stem parasites *Cuscuta* spp. also express the *SLR/IAA14* and *SHY2* orthologs in the seedling stage and stem (109), consistent with the idea that the haustorium might have evolved through recruitment of the LRD program (78). However, *STM*, a key regulator of shoot development, also has a function in the haustorial developmental programs in *C. pentagona* (4), suggesting that the haustorium might have co-opted the developmental programs of both the shoot and the root and therefore exhibits characteristics of both. Functional analysis of LRD and shoot developmental genes in parasitic plants might provide further insights.

Comparative transcriptomics of the Orobanchaceae and nonparasitic angiosperms identified potential parasitism genes that are upregulated during haustorial development and in response to HIFs (148). This analysis suggested that parasitism genes are derived primarily from root and floral tissues and that gene duplication was an important process in the origin of the haustorium (148). Therefore, it is also possible that parasitic functions evolved through neofunctionalization of genes encoding nonparasitic functions. However, considering that haustoria have evolved multiple times independently, the key evolutionary changes to develop haustoria should be simple to explain with this convergent phenomenon. Therefore, it would be worthwhile to investigate whether a few genes play key roles as master regulators in haustorium formation. Future comparative genomics work across phylogenetically distant species will be quite useful for this purpose.

CONCLUDING REMARKS AND FUTURE PERSPECTIVES

The haustorium is a unique organ that allows plants to parasitize other plants. Because this organ evolved independently at least 12 times in the angiosperms, a common mechanism for its development may exist. To elucidate such a mechanism, more genomic sequencing of parasitic plants combined with haustorium cell-specific transcriptome analyses should be conducted. Recent advances in sequencing technologies have already brought great progress in understanding the lifestyles of parasitic plants at the molecular level and will continue to do so. In addition to gene knockdown systems using host-induced gene silencing and virus-induced gene silencing (76), the newest genome editing technologies, such as the CRISPR/Cas9 system (23), will enable researchers to identify the genes required for parasitism and test hypotheses about how the haustorium evolved. Several parasitic plants have also been established as genetically amenable systems for functional analysis (40, 62, 134). These tools will help answer an array of interesting biological questions: How do plants recognize other plants? How was the HIF recognition system invented, and how does it work? What defines host specificity? How do resistant plants prevent haustorium invasion? How do parasites control the host to maximize water and nutrient transfers? By answering these questions, researchers may be able to build a unified view of how plants parasitize other plants.

SUMMARY POINTS

1. The haustorium of parasitic plants is a specialized invasive organ common in all parasitic plants.
2. The haustorium has unique cellular structures.
3. Haustorium induction in Orobanchaceae plants is regulated by quinones, phenolic acids, and flavonoids.
4. At different developmental stages, the haustorium functions in host attachment, host invasion, host immunity avoidance, and nutrient transfer.

5. Macromolecules, including RNAs, viruses, and proteins, are exchanged between hosts and parasitic plants, similar to interspecies grafting.
6. Horizontal transfer of mitochondrion- and nucleus-encoded genes as well as transposons occurs between hosts and parasitic plants.
7. Local biosynthesis of auxin at the haustorium apex is important for haustorium development.
8. The expression patterns of genes related to lateral root development suggest that the haustorium may have originated from lateral roots.

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148. Identified potentially common haustorium genes from the Orobanchaceae and predicted their evolutionary origin.

149. Presents the first complete genome sequencing of the parasitic plant *S. asiatica*.

150. Presented evidence of nuclear gene transfer from hosts to parasites.

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Contents

Errata

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