Molecular dissection of haustorium development in Orobanchaceae parasitic plants

Kaori Miyashima Furuta, Lei Xiang, Songkui Cui and Satoko Yoshida

1 Graduate School of Science and Technology, Nara Institute of Science and Technology, Ikoma, Nara 630-0192, Japan
2 JST, PRESTO, Kawaguchi, Saitama 332-0012, Japan

*Author for communication: satokoy@bs.naist.jp
†Senior author.
K.M.F., L.X., S.C., and S.Y. conceived and wrote the manuscript. K.M.F. and S.C. drew the figures. S.C. and S.Y. finalized the manuscript.
The author responsible for distribution of materials integral to the findings presented in this article in accordance with the policy described in the Instructions for Authors (https://academic.oup.com/plphys/pages/general-instructions) is: Satoko Yoshida (satokoy@bs.naist.jp).

Nutrient availability is one of the critical factors for plant survival and is mediated mainly by the root system. In addition to the roots, some species have evolved novel organs specialized for the acquisition of organic and inorganic nutrients. For example, most legume species form root nodules that accommodate nitrogen-fixing bacteria to acquire fixed nitrogen, whereas carnivorous plants have developed digestive leaves that trap and kill prey to absorb additional nutrients (Markmann and Parniske, 2009; Thorogood et al., 2018). Parasitic plants form a multicellular organ, the haustorium, emanating from either their shoots or roots, to parasitize other plants in order to acquire water and nutrients (Yoshida et al., 2016). Plant parasitism has independently evolved at least 12 times among angiosperms (Westwood et al., 2010). The Orobanchaceae family includes the largest number of parasitic species and all, except the genus Lindenbergia, Rehmannia, and Triaenophora, are root parasitic plants (Angiosperm Phylogeny Group, 2016; Li et al., 2019). Haustorium development proceeds in stages, including initiation, host penetration, and the formation of vascular connections. Recent progress in molecular and cellular biology has revealed that each phase is modulated by specific plant hormones, cellular programs, and signal exchanges between the host and parasite. In this review, we discuss recent updates on the molecular details of haustorium organogenesis in the Orobanchaceae family by focusing on genetic components and signaling molecules that function at each stage of haustorium development.

Molecular actors functioning at different stages of haustorium development have been identified, including quinone receptors, ethylene signaling components, and auxin transporters. Haustorial cells change their identities throughout multiple developmental stages of the haustorium in response to host signals. Genes involved in normal plant growth and development were co-opted for haustorium organogenesis by parasitic plants during their evolution.

Haustorium development in Orobanchaceae parasitic plants

The Orobanchaceae, with approximately 90 genera and 2,000 species, is the largest family of parasitic angiosperms and exhibits the entire spectrum of parasitism, from facultative (host-independent) to obligate (host-dependent), and from hemiparasitic (photosynthetic) to holoparasitic (nonphotosynthetic). Members of the Orobanchaceae family include notorious parasitic weeds, including Striga spp., Orobanche spp., Phelipanche spp., Rhamphicarpa fistulosa...
intrusive cells, slender-shaped cells capable of penetrating the epidermal cells at the host contact site differentiate into host tissue reaches the host roots, host penetration begins; established xylem bridges to form a mature haustorium. The term haustorium is defined as "the special organ of parasitic plants, which invades host tissues and serves as the structural and physiological bridge that allows the parasites to withdraw water and nutrients from the conductive systems of living host plants" (Joel, 2013). In all cases, the hemispherical structures induced either by HIFs or host exudates/extracts lack internal cell components for nutrient absorption and host invasion, such as xylem bridges and intrusive cells, and therefore are distinguished from “haustoria” in the context of the tissue structure. In this regard, these early structures were referred to as an “early haustorial structure” (Goyet et al., 2019), “proto-haustorium” (Spallek et al., 2017), “pre-attachment haustorium” (Zhang et al., 2015), or “prehaustorium” (Ranjan et al., 2014; Goyet et al., 2019). Nevertheless, a majority of studies to date have not specified the term “haustorium,” sometimes leading to confusion, especially in nonparasitic plant spheres. In the stem parasite *Cuscuta* spp., the term “prehaustorium” was proposed by Peirce (1893) to describe the central cells behind meristematic tissue, and a similar structure was observed in *Striga* (Okwonkwo, 1967; Kuijt, 1969, 1977). Currently, the term “prehautoriaum” in *Cuscuta* spp. is widely used to distinguish mechanically induced (immature) haustoria from host-infected (mature) haustoria (Ranjan et al., 2014; Costea and Tardif, 2006). In this review, we use “prehautriaum” to describe a haustorium induced in vitro or at the stage before host attachment, “invading haustoria” for that at the penetration stage bearing intrusive cells, and “haustoria” for that with a successfully established vascular connection to the host characterized by the presence of a xylem bridge (Figure 1A).

Initiation phase: converting a root into a prehaustorium

**Hautoriaum-inducing factors**

Prehaustorium induction in a majority of Orobanchaceae members requires HIFs, host-derived signaling molecules. Various chemicals, mainly phenolic compounds, and quinones, have been reported to be capable of inducing prehaustorium development in vitro (Albrecht et al., 1999; Goyet et al., 2019). Among them, 2,6-dimethoxybenzoquinone (DMBQ), a quinone isolated from sorghum root exudates (Chang and Lynn, 1985; Lynn and Chang, 1990) has the widest range of activity against numerous parasitic species, including the facultative parasites *Agalinis purpurea*, *Tryphisaria* spp., and *Phtheirospermum japonicum*, and the obligate hemiparasite *Striga* spp., but not for holoparasites such as *Phelipanche* or *Orobanche* spp. In *Phelipanche ramosa*, cytokinin plant hormones serve as HIFs; analysis of root exudates of the host plant *Brassica napus* identified cytokinin-like compounds responsible for prehaustorium induction (Goyet et al., 2017). Cytokinins were also reported to induce prehaustoria in *Striga asiatica* (Keyes et al., 2000). Sphaeropinones, the phytotoxic cyclohexene oxides isolated from fungi, can induce prehaustoria in *Orobanche crenata* and *O. cumana* as well as in *S. hermonthica* (Fernandez-Aparicio et al., 2016).

---

**Haustorium or prehaustorium?**

The term haustorium is defined as “the special organ of parasitic plants, which invades host tissues and serves as the structural and physiological bridge that allows the parasites to withdraw water and nutrients from the conductive systems of living host plants” (Joel, 2013). In all cases, the hemispherical structures induced either by HIFs or host exudates/extracts lack internal cell components for nutrient absorption and host invasion, such as xylem bridges and intrusive cells, and therefore are distinguished from “haustoria” in the context of the tissue structure. In this regard, these early structures were referred to as an “early haustorial structure” (Goyet et al., 2019), “proto-haustorium” (Spallek et al., 2017), “pre-attachment haustorium” (Zhang et al., 2015), or “prehautoriaum” (Ranjan et al., 2014; Goyet et al., 2019). Nevertheless, a majority of studies to date have not specified the term “haustorium,” sometimes leading to confusion, especially in nonparasitic plant spheres. In the stem parasite *Cuscuta* spp., the term “prehautoriaum” was proposed by Peirce (1893) to describe the central cells behind meristematic tissue, and a similar structure was observed in *Striga* (Okwonkwo, 1967; Kuijt, 1969, 1977). Currently, the term “prehautoriaum” in *Cuscuta* spp. is widely used to distinguish mechanically induced (immature) haustoria from host-infected (mature) haustoria (Ranjan et al., 2014; Costea and Tardif, 2006). In this review, we use “prehautoriaum” to describe a haustorium induced in vitro or at the stage before host attachment, “invading haustoria” for that at the penetration stage bearing intrusive cells, and “haustoria” for that with a successfully established vascular connection to the host characterized by the presence of a xylem bridge (Figure 1A).

Initiation phase: converting a root into a prehaustorium

**Hautoriaum-inducing factors**

Prehaustorium induction in a majority of Orobanchaceae members requires HIFs, host-derived signaling molecules. Various chemicals, mainly phenolic compounds, and quinones, have been reported to be capable of inducing prehaustorium development in vitro (Albrecht et al., 1999; Goyet et al., 2019). Among them, 2,6-dimethoxybenzoquinone (DMBQ), a quinone isolated from sorghum root exudates (Chang and Lynn, 1985; Lynn and Chang, 1990) has the widest range of activity against numerous parasitic species, including the facultative parasites *Agalinis purpurea*, *Tryphisaria* spp., and *Phtheirospermum japonicum*, and the obligate hemiparasite *Striga* spp., but not for holoparasites such as *Phelipanche* or *Orobanche* spp. In *Phelipanche ramosa*, cytokinin plant hormones serve as HIFs; analysis of root exudates of the host plant *Brassica napus* identified cytokinin-like compounds responsible for prehaustorium induction (Goyet et al., 2017). Cytokinins were also reported to induce prehaustoria in *Striga asiatica* (Keyes et al., 2000). Sphaeropinones, the phytotoxic cyclohexene oxides isolated from fungi, can induce prehaustoria in *Orobanche crenata* and *O. cumana* as well as in *S. hermonthica* (Fernandez-Aparicio et al., 2016).
Figure 1  Developmental stages of a facultative parasite haustorium. A. A schematic diagram of the three phases of haustorium formation. Signals and genes involved in each developmental phase are indicated in the figure. Quinone-type HIFs may be perceived by the orthologs of Arabidopsis CARD1 (CANNOT RESPOND TO DMBQ 1), named CARD-like proteins (CADLs), which drive expression of the auxin biosynthesis gene YUCCA3 (YUCCA-flavin monooxygenase 3) at the tip of the prehaustorium. During the host invasion stage, ethylene signaling driven by ETR1 and EIN2 is required. Directional localization of the auxin efflux transporter PIN (PIN-FORMED auxin transporter family proteins) and the auxin influx
Although DMBQ was identified from abraded sorghum roots, the origin of HIFs in host exudates remains obscure. The lack of any host mutant impaired in prehaustorium induction also hampers a complete understanding of the HIF generation pathway. A recent study demonstrates that HIFs are partially derived from the lignin biosynthetic pathway (Cui et al., 2018b). Several lignin monomers can induce prehaustoria in *P. japonicum* and *S. hermonthica*. Arabidopsis and rice mutants with altered lignin compositions are partially impeded in their abilities to induce prehaustoriation formation in these parasites (Cui et al., 2018b). Chemical reactions during lignin degradation or polymerization, processes that require oxidative enzymes such as peroxidases and/or laccases, can produce DMBQ (Kamaya et al., 1981; Umezawa et al., 1982). Therefore, lignin, a highly conserved polymer in land plants, seems to be an important player in HIFs production. Notably, some parasites, including *P. japonicum*, *S. hermonthica*, and *T. versicolor*, do not induce prehaustoriation against their own species or closely related species (Yoder, 1997; Yoshida and Shirasu, 2009). A recent report showed that peroxidase or laccase treatments on *T. versicolor* roots can produce HIFs, implying that parasitic plant roots may contain the substrates for HIFs (Wang et al., 2020). Interestingly, however, DMBQ was not detected in such oxidative enzyme-treated root extracts obtained from *T. versicolor*. Together with the fact that the DMBQ content in the host root exudates was three orders of magnitude lower than the concentration required to produce prehaustoriation, there may be additional HIFs or HIF enhancers present in host plant root exudates (Wang et al., 2020). Deciphering the mechanisms for parasites to avoid self-haustorium development requires a systematic comparison of root exudates between hosts and parasites and will open innovative methods for generating crops resistant to parasitic weeds.

**HIF perception**

Functional genes directly regulating haustorium initiation have not been identified. Recently, a plasma membrane-localized leucine-rich-repeat receptor kinase (LRR-RK), named CANNOT RESPOND TO DMBQ 1 (CARD1), was identified as a molecule mediating quinone perception in Arabidopsis (Laohavisit et al., 2020). Wild-type Arabidopsis responds to DMBQ with an elevated cytosolic Ca\(^{2+}\) level and MAPK activation as outputs, whereas the *card1* mutants are impaired in these responses. With the identification of CARD1, the study further uncovered the positive role of DMBQ signaling in the control of stomatal closure and plant immunity (Figure 2). Introduction of the *P. japonicum* and *S. asiatica* orthologs of CARD1 (CADLs) into the *Arabidopsis* *card1* mutant restored DMBQ responses, indicating the functional conservation of CARD1 in quinone perception in these parasites. Importantly, DMBQ treatment induces the elevation of cytosolic Ca\(^{2+}\) only in the root elongation zone in *P. japonicum* where prehaustoriation emerge, suggesting that the functional site of PjCADLs when the root is exposed to DMBQ is at the root tip. In *P. japonicum*, PjCADL1 is consistently expressed throughout the root, whereas PjCADL2 and PjCADL3 are expressed within the root epidermis; however, knockdown of individual PjCADL genes results in normal prehaustoriation induction. Either these PjCADLs function redundantly or other genes are responsible. Note that because no direct interaction was observed between CARD1 and DMBQ, quinone signaling mediated by CARD1 may require genuine quinone receptor(s) and/or an additional co-receptor(s). A pair of cysteine residues in the extracellular domain of CARD1 was shown to be crucial for the signaling output (Laohavisit et al., 2020). The sulfur-containing amino acids cysteine are often the oxidation target of reactive oxygen species (ROS) that modulate protein conformation and/or activity via disulfide bond formation. It is conceivable that CARD1 may sense DMBQ in the form of extracellular redox changes, provided that quinones are redox-active molecules. Interestingly, CARD1 was also reported to be an H₂O₂ sensor in Arabidopsis (also designated as HYDROGEN-PEROXIDE-INDUCED Ca\(^{2+}\) INCREASE 1 (HPCA1); Wu et al., transportation LAX (LIKE-AUX1 transporter family proteins) define auxin flow at the center of haustoria where xylem bridges and plate xylem develop. B–E, Schematic diagrams of the expression patterns of select genes during haustorium development. B, Expression patterns (purple) of the auxin biosynthesis gene *PjYUCCA3*. C, Expression patterns (aqua) of intrusive cell marker genes. D, Expression patterns (pink) of procambium marker genes. E, Expression patterns of auxin transporters and local auxin maxima. Areas highlighted in yellow indicate the sites of localized auxin responses, and yellow arrows indicate direction of auxin flow. Dark and light green lines indicate the localization sites for the auxin transporters PIN and LAX, respectively.

![Figure 2](https://image-url.com)
Similar to quinone sensing, pairs of extracellular cysteine residues in CARD1/HPCA1 are crucial for H$_2$O$_2$ sensing; however, the positions of crucial residues are different for H$_2$O$_2$ and quinone sensing (Laohavisit et al., 2020, Wu et al., 2020). This may suggest that CARD1/HPCA1 has dual function for perceiving extracellular H$_2$O$_2$ and quinones, although both signals are likely to be perceived via oxidation of the extracellular domain.

Earlier studies have shown that redox potentials are associated with prehaustorium induction activity, and redox modifying chemicals inhibit prehaustorium induction in T. versicolor (Smith et al., 1996; Wang et al., 2019). Moreover, quinone oxidoreductases that are involved in the redox cycling of quinones are required in DMBQ-treated prehaustorium formation in T. versicolor and P. japonicum (Bandaranayake et al., 2010; Ishida et al., 2017). These results further suggest the involvement of redox signaling in the process from HIF perception to prehaustorium morphogenesis. ROS are also important in prehaustorium induction (Wada et al., 2019). Inhibitors of NADPH oxidases, superoxide dismutases, and peroxidases involved in ROS production or regulation block prehaustorium formation upon DMBQ treatment in S. hermonthica, suggesting that ROS are required for transducing the DMBQ signal (Figure 1A). To date, whether quinones and phenolics induce ROS in parasitic plants has not been clearly shown. In S. hermonthica, DMBQ treatment induces H$_2$O$_2$ production in prehaustoria at approximately 7-h post treatment, but not at the radical tip during the earlier initiation stage (Wada et al., 2019). Furthermore, DMBQ does not induce ROS generation in Arabidopsis seedlings (Laohavisit et al., 2020). The functional relationship between HIFs and ROS in prehaustorium formation remains to be solved.

**Auxin-biosynthesis directs prehaustorium initiation**

Auxin is known to have a central role in promoting cell division and, thus, meristematic activities in organ development. Several studies have documented the importance of the phytohormone auxin in haustorium initiation. Microarray analysis in DMBQ-treated P. japonicum revealed the upregulation of auxin-responsive genes (Ishida et al., 2016). PjYUC3, which encodes a catalytic enzyme for auxin biosynthesis, and the auxin-responsive DR5 marker are specifically expressed in the epidermis and outer cortical cells of the haustorium initiation site (Figure 1B; Ishida et al., 2016). Knockdown of PjYUC3 resulted in reduced haustorium formation levels, whereas ectopic expression of PjYUC3 in root epidermal cells induced the formation of haustorium-like structures (Ishida et al., 2016). Thus, auxin biosynthesis within epidermal cells is required and sufficient for prehaustorium formation.

In T. versicolor, an auxin-responsive marker and an ethylene-responsive marker are expressed in the root tips upon DMBQ treatment (Tomilov et al., 2005). Excess auxin application substantially increased the frequency of haustorium formation in T. versicolor, whereas disturbed auxin fluxes, either by application of an auxin efflux or auxin activity inhibitor, reduced the number of haustoria (Tomilov et al., 2005). Transcriptome analysis of Santalum album, a facultative root parasitic plant in the Santalaceae family, showed that auxin-related genes are upregulated in prehaustoria (preattached haustoria) and downregulated in postattached haustoria (Zhang et al., 2015).

**Penetration phase**

**Firm attachment to the host by haustorial hairs**

Haustorial hairs, also recognized as papillae in holoparasites, are tubular extensions from the haustorial surface and function in providing tight adhesion with the host surface by secreting mucilage (Baird and Riopel, 1983; Joel and Losner-Goshen, 1994; Heide-Jørgensen and Kuijt, 1995). Immunolabeling of cell-wall components indicates the presence of low-esterified homogalacturonan and arabinoxylan proteins at the epidermal surface of the holdfast that may act as adhesive compounds between the host and parasite cells in the stem parasite Cuscuta (Stribeny and Krause, 2015; Hozumi et al., 2017). Phtheirospermum japonicum haustorial hair defective mutants (hhd) form fewer haustoria compared with the wild-type when infecting hosts; this impairment is restored by providing external forces that allow the host and parasite to grow side-by-side, implying that haustorial hairs support parasitism by attaching to the host root (Cui et al., 2016). Developmental programs for haustorial hairs are shared with those of root hairs since Pjhhd mutants are also defective in root hair formation. The auxin biosynthesis enzyme encoded by PjYUC3 and the auxin signaling marker DR5 are expressed during the development of haustorial hairs, suggesting that auxin may also be involved in haustorial hair formation, as in the root hairs (Ishida et al., 2016).

**Intrusive cell differentiation**

Soon after prehaustoria reach the host tissue surface, the prehaustorium begins penetrating the host (Figure 1A). The most prominent feature during penetration is the formation of intrusion-specific cells, called “intrusive cells” in Orobanchaceae parasitic plants and “searching hyphae” in dodders. These cells have a distinct slender shape and are laterally aligned to each other at the host interface. A recent forward genetic study in P. japonicum identified two mutants defective in intrusive cell formation upon host attachment and failure in host invasion; the responsible genes encode key ethylene signaling genes ETHYLENE INSENSITIVE 2 (EIN2) and ETHYLENE RESPONSE 1 (ETR1), respectively (Figure 1A; Cui et al., 2020). Both mutants are insensitive to ethylene, and the exogenous application of the ethylene signaling inhibitor AgNO$_3$ during host infection completely blocked wild-type P. japonicum invasion. Pjetr1 and Pjeren2 also exhibit prolonged cell division within the prehaustorium apex, giving rise to an elongated prehaustorium. These findings imply that ethylene signaling in parasitic plants plays a key role in host invasion by regulating cell division and differentiation within the haustorial apical region. Regulation of
Cell-wall modification enzymes during penetration

Immediately after entering the cortex layers, intrusive cells grow toward the host’s vascular center by pushing away and compressing host cells (Neumann et al., 1999), a process driven by not only mechanical force but also by modification of host cell walls. Numerous transcriptome analyses have confirmed the upregulation of cell-wall modifying enzymes in haustoria during host infection (Yang et al., 2015; Yoshida et al., 2019). Specifically, pectate lyases are commonly enriched in T. versicolor, S. hermonthica, and O. aegyptiaca (Yang et al., 2015). Also, genes encoding pectin methyl esterases (PMEs) and polygalacturonases that are involved in primary cell-wall modification, and Carbohydrate-Active enzymes (CAZyme) that are involved in cell-wall loosening, lignification, and suberization, are highly upregulated in S. hermonthica during rice infection (Yoshida et al., 2019; Mutuku et al., 2019). High pectinolytic activity and accumulation of pectate lyase were also confirmed in Cuscuta haustoria in their susceptible host interaction (Johnsen et al., 2015). Interestingly, in the interaction between nitrogen-fixing rhizobial bacteria and the legume Lotus japonicus, mutations in a pectate lyase gene in the host plant (LjNPL) arrested rhizobium infection and reduced the number of mature nodules (Xie et al., 2012), indicating a common requirement for pectin degradation in bacteria and parasitic plants in the context of tissue invasion.

Grafting and plant parasitism share many common cellular events including wounding tissue adhesion, and forming a vascular connection (Melnyk, 2017). β-1,4-Glucanase (GH9B3), a secreted type of primary cell-wall modifying enzyme targeting cellulose, was recently shown to function in both interfamily grafting and haustorium maturation (Kurotani et al., 2020; Notaguchi et al., 2020). Nicotiana benthamiana GH9B3 and PjGH9B3 are induced in the grafting junction during compatible grafting and at the interface with the host in haustoria during the invasion stage, respectively. The genetic disruption of the corresponding genes impaired tobacco intergrafting to Arabidopsis and haustorium maturation in P. japonicum. These results suggest that extracellular GH9B3 facilitates tissue adhesion by targeting cellulose in the apoplast; however, many details about how GH9B3 modulates the cell wall to successfully attain grafting and parasitism remain to be investigated.

The question remains open as to how parasites degrade host cell walls, while simultaneously maintaining the integrity of their own cell wall. This is a fascinating topic as bacteria, fungi, and nematodes also digest cell walls in interactions with their hosts; however, among these organisms, only parasitic plants possess cell walls that are structurally similar to those of their hosts. Tissue invasion by parasitic plants, therefore, needs to target cell wall composition or modifications specific to the hosts but not their own, or spatiotemporally produce unique cell walls that are resistant to their own cell-wall degrading enzymes at the interface, or both. Molecular evidence for either of these proposed strategies is scarce as the biochemical activity of cell-wall modifying enzymes and the cell wall modification by parasitic plants have been poorly characterized. There is an interesting link to haustorium initiation: because the HIFs are also derived from cell walls and parasitic plants can avoid self-haustorium formation, parasitic plants may be able to distinguish hosts’ cell walls from their own with yet undiscovered mechanisms.

Vascular connection phase

Establishing cells with procambium-like identity in central haustoria

For absorbing water and nutrients, parasitic plants need to connect their vasculatures to those of the hosts. When the intrusive cells reach the host vasculature, some intrusive cells differentiate into tracheary elements. At the same time, some cells near the parasite’s root vasculature also differentiate into tracheary elements, thereby forming a mass of tracheary elements known as plate xylem (Dobinsons and Kuijt, 1973; Mutuku et al., 2020). These tracheary elements are connected in the middle of haustoria and form a xylem
bridge, establishing a xylem connection between the parasite and host (Ishida et al., 2016; Wakatake et al., 2018).

After host invasion but before xylem bridge formation, cells in the central part of the haustorium acquire a procambium cell-like identity (Figure 1D). Procambium cells act as vascular meristems and proliferate and differentiate into xylem, phloem, and cambium during plant vascular development upon receiving appropriate positional and molecular cues (Furuta et al., 2014). ARABIDOPSIS HOMEBOX PROTEIN 15 (HB15) and WUSCHEL-RELATED HOMEBOX 4 (WOX4) are known to regulate the formation and maintenance of procambial/cambial tissues in Arabidopsis (Prigge et al., 2005; Carlsbecker et al., 2010; Hirakawa et al., 2010; Etchells et al., 2013). Phtheirospernum japonicum orthologs of HB15 (PjHB15a and b) and WOX4 (PjWOX4) are expressed in the central region of haustoria before xylem bridge formation (Wakatake et al., 2018), suggesting a procambium-like identity of these cells. The sequential expression of PjHB15 and an ortholog of the xylem-differentiating marker CELLULOSE SYNTHASE CATALYTIC SUBUNIT 7/IRREGULAR XYLEM 3 (PjCESA7/IRX3) resembles the xylem differentiation processes in roots (Wakatake et al., 2018). The expression of these procambial markers is retained in actively dividing cells surrounding the xylem bridge, indicating that these cells maintain meristemic activity for tracheary element differentiation. These activities lead to more xylem bridge formation, while simultaneously proliferating cells to expand haustorium size comparable to the lateral growth of the roots and shoots (Sanchez et al., 2012; Miyashima et al., 2019).

Xylem bridge formation defined by auxin flow
Xylem continuity with host plants is a prominent feature observed in most parasitic plants (Kuijt 1969). In the Orobanchaceae, the formation of xylem bridges is mediated by coordinated expression of auxin transporter and auxin biosynthesis genes. An auxin biosynthesis gene, PjYUC3, is expressed primarily in the prehaustorial epidermis and neighboring cortex cells; expression of this gene is also maintained at the haustorial apex during the early phase of host invasion (Figure 1B; Ishida et al., 2016; Wakatake et al., 2020). After host invasion, the expression of DR5, an auxin-responsive marker, indicates the presence of auxin-response maxima in intrusive cells, the plate xylem-forming region, and the middle of haustoria (Figure 1E). The temporal and spatial expression of DR5 coincides with the expression of PjCESA7/IRX3, a xylem cell differentiation marker, at the site for xylem bridge formation (Wakatake et al., 2020). High levels of cellular auxin signaling are a key determinant for xylem cell identity in Arabidopsis roots (Smetana et al., 2019). Therefore, the function of auxin in the control of cell pattern formation is likely conserved in haustorial vessel differentiation.

The creation of auxin-response maxima in undifferentiated cells at the xylem bridge-forming site is seemingly regulated by auxin transporters, PINs and LAXs. The auxin efflux carriers, PjPIN1 and PjPIN9, and the auxin influx carriers, PjLAX1, PjLAX2, and PjLAX5, are expressed in substantially different regions before and during haustorium formation (Wakatake et al., 2020). Application of inhibitors of auxin-efflux transport blocks xylem bridge formation, and knockdown of PjPIN1 or PjPIN9 by RNAi disrupts tracheary element differentiation at the host interface or plate xylem region, respectively, suggesting different roles for each PIN transporter in xylem bridge formation (Wakatake et al., 2020). Treatment with inhibitors of auxin-influx transport did not block xylem bridge formation but resulted in distorted xylem bridges, indicating that the LAX family of transporters shapes auxin gradients to form simple xylem paths between the host and parasite.

The processes of xylem bridge formation, including the expression of procambium markers and auxin transporters, direct the formation of local auxin maxima followed by xylem cell differentiation. These steps are similar to those for vascular differentiation in Arabidopsis roots (Smetana et al., 2019). In Arabidopsis, AtHB8 encodes an HD-ZIP III whose ectopic expression induces xylem vessel formation. In P. japonicum, expression of PjHB8, the ortholog of AtHB8, is observed in the central region of haustoria (Figure 1D; Wakatake et al., 2018). This finding suggests that procambium-like cells in central haustoria have xylem procambium identity rather than vascular stem cell identity, a proposal supported by the observation that only xylem cells, and not phloem cells, are present in the haustoria of Orobanchaceae hemiparasites.

Phloem development in haustoria
Phloem is a nutrient-conductive tissue in plant vascular systems. Some holoparasitic species, including Orobanche crenata (Dörr and Kollmann, 1995), Orobanche cumana (Krupp et al., 2019), and Cuscuta (Forste et al., 2020), directly connect their phloem sieve elements with those of host plants in the haustorium. These phloem–phloem connections have not been observed in hemiparasites regardless of whether they are obligate or facultative parasites (Dörr and Kollmann, 1977; Dörr et al., 1979; Dörr, 1990, Masumoto et al., 2020). Consistently, host-driven mobile green fluorescent protein (GFP) is transported to parasitic plants through haustoria in holoparasitic Phelipanche ramosa and P. aegytiaca (Ackroyd and Graves, 1997; Peron et al., 2016), but not in the hemiparasitic P. japonicum (Spallek et al., 2017). Furthermore, the phloem differentiation marker, Arabidopsis ALTERED PHLOEM DEVELOPMENT (APL; Bonke et al., 2003) was not expressed within haustoria except in the basal region of P. japonicum (Masumoto et al., 2020), suggesting that haustoria lack characteristic phloem cells. These observations suggest that phloem development in haustoria may be associated with the loss of photosynthetic ability. Interestingly, although host-derived GFP is transported to haustoria in holoparasitic P. aegytiaca, phloem sieve elements with typical characteristics of callose accumulation and enucleation are not observed in haustoria (Ekawa and Aoki, 2017); however, NAC45, NEN1, and NEN4, putative orthologs of key regulatory genes for enucleation in
Arabidopsis (Furuta et al., 2014), are expressed in haustoria (Ekawa and Aoki, 2017). These observations suggest that the GFP-transporting cells in P. aegyptiaca haustoria may have partially acquired features of phloem sieve elements despite lacking the typical morphological characteristics of well-studied Arabidopsis phloem sieve elements.

Material transfer

The fundamental function of haustoria is to absorb water and nutrients from their hosts. Nutrient flow from host to parasite suggests that haustoria act as sink organs, whereas the host plants become sources; however, how and whether haustoria create sink strength remain obscure. Orobanche spp. accumulate large amounts of mannitol and may use this sugar-alcohol to generate an osmotic gradient for material flow from the host toward the parasite (Aly et al., 2009). Potential regulatory mechanisms for xylem flow from the host to the parasites were recently revealed at the molecular level in S. hermonthica (Fujioka et al., 2019). The study demonstrated that S. hermonthica bears mutations in a gene encoding a protein phosphatase 2C (PP2C), a key regulator of abscisic acid (ABA) signaling, and is incapable of closing stomata due to its insensitivity to ABA. This insensitivity leads to a higher transpiration rate in Striga than in its host, generating a water potential gradient toward the parasite (Ackroyd and Graves, 1997).

Hyaline bodies, specialized parenchyma cells in the center of haustoria with especially dense cytoplasm, extracellular deposits, and high metabolic activity (Visser et al., 1984; Riopel and Timko, 1995; Pielach et al., 2014), may function as storage organs that can generate sink pressure. Consistent with this hypothesis, the formation of hyaline bodies corresponds well with host compatibility (Gurney et al., 2003; Pielach et al., 2014); however, some parasites including T. versicolor and P. japonicum do not develop hyaline bodies but can increase their fitness upon host infection (Heide-Jorgensen and Kuijt, 1995; Spallek et al., 2017; Honaa et al., 2019; Irving et al., 2019; Masumoto et al., 2020). These observations suggest that strategies for nutrient processing or transport may vary depending on the species.

Recent findings in Cuscuta have remarkably extended the scope of macromolecules that are transported between parasitic plants and their hosts, including mRNAs, miRNAs, artificial siRNAs, and proteins (Alakonya et al., 2012; Kim and Westwood, 2015; Shahid et al., 2018; Liu et al., 2019). Some macromolecules are functional upon delivery, for example, Cuscuta australis whose genome lacks the FLOWERING LOCUS T (FT) gene obtains the FT from the host to regulate its own flowering (Shen et al., 2020). In root parasites, P. japonicum produces cytokinin plant hormones and transfers them to the host to induce host cell proliferation and vascular cell differentiation. These activities result in the thickening of host roots, a phenomenon called hypertrophy, that is thought to be beneficial for the parasite’s postattachment growth (Spallek et al., 2017). Together, these observations indicate that haustoria actuate selective transport; however, the regulatory mechanisms for such directional transport remain an open question. Analyses of the expression and localization of transporter proteins may give us a clue to resolve these questions. Recent transcriptome analysis indicates that sets of sugar transporters are expressed during haustorium formation in Orobanchaceae parasitic plants (Misra et al., 2019). Although the localization and transport direction of these transporters are unknown, they may participate in effective nutrient transport.

Concluding remarks and future perspectives

Recent advances in the molecular and cellular biology of parasitic plants have begun to reveal the genetic programs for haustorium organogenesis (Ichihashi et al., 2020). A haustorium in the Orobanchaceae develops through reprogramming of root tissues, and the cellular functions and identities change depending on the developmental stage and the relationship with the host. Host signals, such as HIFs, ethylene, and as yet unknown factors for intrusive cell differentiation and vascular differentiation, provoke changes in haustorial cell identity. Concomitantly, parasitic plants avoid self-recognition during haustorium initiation and self-digestion during penetration. The plant hormone auxin functions across all stages of haustorium development. Auxin accumulation at the organ initiation site and xylem pattern formation are also manifested in other plant tissues, suggesting that basic programs for haustorium organogenesis are co-opted from the developmental programs of other plant tissues. Gene expression similarity between lateral root development and haustorium formation has been proposed (Yoshida et al., 2019); however, there are still many gaps remaining to completely understand the regulatory mechanisms controlling haustorium organogenesis (see Outstanding questions). Notably, how interspecies communication regulates organ development remains unknown. Although identifying quinone receptors could provide clues for elucidating the entire signaling pathway for haustorium organogenesis, how the known and unknown HIFs execute a developmental program for haustorium initiation, including the activation of YUCCA3-mediated auxin signaling, remain unknown. Furthermore, the signals for intrusive cell differentiation and how intrusive cells penetrate host tissues without damaging their own cell walls are also unknown. Importantly, the substance used as a host signal for haustorial xylem induction and the subsequent signaling events, such as perception and the downstream targets, are still undetermined. Identifying the signaling compounds and the transduction pathway components will provide a more complete picture of haustorium formation. Advances in these areas will contribute to understanding how interspecies communication affects organ development during plant evolution.

Funding

This work was partly supported by KAKENHI [Grant number 17K15139 to K.M.F., 19K16169 to SC, 18H02464, 18H04838, and
OUTSTANDING QUESTIONS

• What are the identities of host signals that trigger cell fate changes at each step of haustorium development, e.g., key HIF(s), differentiation of intrusive cells, and induction of xylem bridges?
• Are all HIFs perceived by CARD1-like receptors?
• What are the signaling cascades that link HIF perception to the induction of YUCCA3 and other downstream genes to effect haustorium initiation?
• How do parasitic plants avoid self-recognition during haustorium initiation?
• How do parasitic cell-wall modifying enzymes act specifically on host cell walls?
• How are organic materials transported from the host to parasitic plants, and how is the direction of transport defined?

References

Ackroyd RD, 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
Alakonya A, Kumar R, Koenig D, Kimura S, Townsley B, Runo S, Ackroyd RD, Graves JD (2010) Cell signalling by microRNA165/6 directs gene dose-dependent root cell fate. Nature 465: 316–321
Chang M, Lynn DG (1986) The haustorium and the chemistry of host recognition in parasitic angiosperms. J Chem Ecol 12: 561–579
Chante CR, Park SY, Tuosto R, Jia X, Yoder A, Van Mullekom J, Westwood J (2020) Multiple immunity-related genes control susceptibility of Arabidopsis thaliana to the parasitic weed Phelipanche aegyptiaca. PeerJ 8: e9268
Costea M, Tardif FJ (2006) The biology of Canadian weeds. 133. Cuscuta campestris Yuncker, C. granovii Willd. ex Schult., C. umbrosa Beyr. ex Hook., C. epithymum (L.) L. and C. epilimum Weih. Can J Plant Sci 86: 293–316
Cui S, Kubota T, Nishiyama T, IJ K., Shigenobu S, Shibata TF, Toyoda A, Hasebe M, Shirasu K, Yoshida S (2020) Ethylene signaling mediates host invasion by parasitic plants. Sci Adv 6: eabc2385
Cui S, Suzuki T, Tominaga-Wada R, Yoshida S (2018a) Regulation and functional diversification of root hairs. Semin Cell Dev Biol 83: 115–122
Cui S, Wada S, Tobimatsu Y, Takeda Y, Saucet SB, Takano T, Umezawa T, Shirasu K, Yoshida S (2018b) Host lignin composition affects haustorium induction in the parasitic plants Phtheirospermum japonicum and Striga hermonthica. New Phytol 218: 710–723
Cui S, Wakatake T, Hashimoto K, Saucet SB, Toyooka K, Yoshida S, Shirasu K (2016) Haustorial hairs are specialized root hairs that support parasitism in the facultative parasitic plant Phtheirospermum japonicum. Plant Physiol 170: 1492–1503
Dobkins DR, Kuijt J (1973) Studies on the haustorium of Castilleja (Scrophulariaceae). II. The endophyte. Can J Botany 51: 923–931
Dörr I (1990) Sieve elements in haustoria of parasitic angiosperms. In HD Behnke and RD Sjolund, eds, Sieve Elements. Springer, New York, pp 239–256
Dörr I, Kollmann R (1977) Strukturelle grundlagen des parasitismus bei Orobanche. II. Die differenzierung der assimilat-leitungsbahn im haustorialgewebe. Protoplasma 83: 185–199
Dörr I, Kollmann R (1995) Symplasmic sieve element continuity between Orobanche and its host. Botanica Acta 108: 47–55
Dörr I, Visser JH, Kollmann R (1979) On the parasitism of Electra vogeli Benth. (Scrophulariaceae) III. The occurrence of phloem between host and parasite. Z Pflanzenphysiol 84: 213–222
Ekawa M, Aoki K (2017) Phloem-conducting cells in haustoria of the root-parasitic plant Phelipanche aegyptiaca retain nuclei and are not mature sieve elements. Plants 6: 60
Etchells JP, Provost CM, Mishra L, Turner SR (2013) WOX4 and WOX14 act downstream of the PKY receptor kinase to regulate plant vascular proliferation independently of any role in vascular organisation. Development 140: 2224–2234
Fernandez-Aparicio M, Masi M, Maddau L, Cimmino A, Evidente M, Rubiales D, Evidente A (2016) Induction of haustorium development by sphaeropodines in radicles of the parasitic weeds Striga and Orobanche. A structure-activity relationship study. J Agric Food Chem 64: 5188–5196
Furuta et al.

20H05909 to S.Y.], JST PRESTO [Grant number JPMJPR194D], and the International Atomic Energy Agency Research [Contract number 20645 to S.Y.]. K.M.F. was supported by JSPS Restart Postdoctoral Fellowship program (RPD).

Conflict of interest statement. Authors declare that they have no conflicts of interests.
absic acid insensitivity and high transpiration in parasitic Striga. Nat Plants 5: 258–262

Furuta KM, Yadav SR, Lehesranta S, Belevich I, Miyashima S, Heo JO, Vaten A, Lindgren O, De Rybel B, Van Isterdael G, et al. (2014) Plant development. Arabidopsis NAC45/86 direct sieve element morphogenesis culminating in enucleation. Science 345: 933–937

Goyet V, Billard E, Pouvreau J-B, Lechat M-M, Pelletier S, Bahu M, Montaou F, Spichal L, Delavault P, Montiel G, et al. (2017) Haustorium initiation in the obligate parasitic plant Phelipanche ramosa involves a host-exuded cytokinin signal. J Exp Bot 68: 5539–5552

Goyet V, Wada S, Cui S, Wakatabe T, Shirasu K, Montiel G, Simier P, Yoshida S (2019) Haustorium inducing factors for parasitic Orobancheaceae. Front Plant Sci 10: 1056

Gurney AL, Grimanelli D, Kanampiu F, Hoisington D, Scholes JD, Press MC (2003) Novel sources of resistance to Striga hermonthica in Tripsacum dactyloides, a wild relative of maize. New Phytol 160: 557–568

Heide-Jorgensen HS, Kuijt J (1995) The haustorium of the root parasite Triphysaria (Scrophulariaceae), with special reference to xylem bridge ultrastructure. Am J Bot 82: 782–797

Hirakawa Y, Kondo F, Fukuda H (2010) TDIF peptide signaling regulates vascular stem cell proliferation via the WOX4 homeobox gene in Arabidopsis. Plant Cell 22: 2618–2629

Honaas LA, Jones S, Farrell N, Kamerow W, Zhang H, Vescio K, Kamaya Y, Nakatsubo F, Higuchi T, Iwahara S, Ishida JK, Yoshida S, Shirasu K (1981) Degradation of d,l-syringaresinol, a beta-1,4-glucanase. Science 210: 784–97

Hozumi A, Bera S, Fujiwara D, Obayashi T, Yokoyama R, Ichihashi Y, Hakoyama T, Iwase A, Shirasu K, Ishida JK, Yoshida S, Takebayashi Y, Kasahara H, Arakawa JO, Vaten A, Lindgren O, De Rybel B, Van Isterdael G, Muller N, Help-Rinta-Rahko H, Otero S, Smet W, et al. (2016) Local arabinogalactan proteins regulate haustorium development in the parasitic plant Phtheirospermum japonicum. Plant Cell Physiol 58: 1868–1877

Ichihashi Y, Hokoyama T, Iwase A, Shirasu K, Sugimoto K, Hayashi M (2020) Common mechanisms of developmental rearrangement in plants—lessons from regeneration, symbiosis, and parasitism. Front Plant Sci 11: 1–10

Ishida JK, Wakatabe T, Yoshida S, Takebayashi Y, Kasahara H, Wafela E, dePamphilis CW, Nambo S, Shirasu K (2016) Local auxin biosynthesis mediated by a YUCCA flavon monooxygenase regulates haustorium development in the parasitic plant Phtheirospermum japonicum. Plant Cell 28: 1795–1814

Ishida JK, Yoshida S, Shirasu K (2017) Quinone oxidoreductase 2 is involved in haustorium development of the parasitic plant Phtheirospermum japonicum. Plant Signal Behav 12: e1319029

Irving LJ, Kim D, Schwier N, Vaughan JKE, Ong G, Hama T (2019) Host nutrient supply affects the interaction between the hemiparasite Phtheirospermum japonicum and its host Medicago sativa. Envir Exp Bot 162: 125–132

Joel DM (2013) The haustorium and the life cycles of parasitic Orobancheaceae. In: DM Joel, J Gressel, LJ Musselman, eds, Parasitic Orobancheaceae. Springer, New York, pp 21–24

Joel DM, Losner-Goshen D (1994) The attachment organ of the parasitic plant species in the Orobanchaceae. Plant Physiol 101: 1795–1814

Johnsen HR, Striberny B, Olsen S, Vidal-melgosa S, Fangel JU, Willats WGT, Rose JKC, Krause K (2015) Cell wall composition profiling of parasitic giant dodder (Cuscuta reflexa) and its hosts: a priori differences and induced changes. New Phytol 207: 805–881

Kamaya Y, Nakatubo F, Higuchi T, Iwahara S (1981) Degradation of d-l-syringaresinol, a beta-l-beta' linked lignin model compound, by Fusarium solani M-13-1. Arch Microbiol 129: 305–309

Keyes WJ, O’Malley RC, Kim D, Lynn DG (2000) Signaling organogenesis in parasitic angiosperms: xenogonin generation, perception, and response. J Plant Growth Regul 19: 217–231

Kim G, Westwood JH (2015) Macromolecule exchange in Cuscuta-host plant interactions. Curr Opin Plant Biol 26: 20–25

Krupp A, Heller A, Spring O (2019) Development of phloem connection between the parasitic plant Orobanche cumana and its host sunflower. Protoplasma 256: 1385–1397

Kuijt J (1969) The Biology of Parasitic Flowering Plants. University of California Press, Berkeley, CA

Kuijt J (1977) Haustoria of phanerocarpous parasites. Annu Rev Phytopath 15: 91–118

Kurotani K-I, Wakatabe T, Ichihashi Y, Okayasu K, Sawai Y, Ogawa S, Cui S, Suzuki T, Shirasu K, Notaguchi M (2020) Host-parasite tissue adhesion by a secreted type of beta-1,4-glucanase in the parasitic plant Phtheirospermum japonicum. Commun Biol 3: 407

Lakavitsa A, Wakatabe T, Ishihama N, Mulvey H, Takizawa K, Suzuki T, Shirasu K (2020) Quinone perception in plants via leucine-rich-repeat receptor-like kinases. Nature 587: 92–97

Li X, Feng T, Randle C, Schneeweiß GM (2019) Phylogenetic relationships in Orobancheaceae inferred from low-copy nuclear genes: consolidation of major clades and identification of a novel position of the non-photosynthetic Orobanche clade sister to all other parasitic Orobancheaceae. Front Plant Sci 10: 902

Liu N, Shen G, Xu Y, Liu H, Zhang J, Li S, Li J, Zhang C, Qi J, Wang L, Wu J (2019) Extensive inter-plant protein transfer between Cuscuta parasites and their host plants. Mol Plant 13: 573–585

Lynn DG, Chang M (1990) Phenolic signals in cohabitation - Implications for plant development. Annu Rev Plant Physiol Plant Mol Biol 41: 497–526

Markmann K, Parniske M (2009) Evolution of root endosymbiosis with bacteria: how novel are nodules? Trends Plant Sci 14: 77–86

Masumoto N, Suzuki Y, Cui S, Wakazaki M, Sato M, Shibata A, Furuta KM, Ichihashi Y, Shirasu K, Tooyoka K, et al. (2021) Three-dimensional reconstructions of haustoria in two parasitic plant species in the Orobancheaceae. Plant Physiol 185: 1429–1442

Matvienko M, Torres MJ, Yoder JJ (2001) Transcriptional responses in the hemiparasitic plant Triphysaria versicolor to host plant signals. Plant Physiol 127: 272–282

Melnik CW (2017) Plant grafting: insights into tissue regeneration. Regeneration (Oxf) 4: 3–14

Misra VA, Wafula EW, Wang Y, dePamphilis CW, Timko MP (2019) Genome-wide identification of MST, SUT and SWEET family sugar transporters in root parasitic angiosperms and analysis of their expression during host parasitism. BMC Plant Biol 19: 196

Miyashima S, Roszak P, Sevilem I, Toyokura K, Blob B, Heo JO, Mellor N, Help-Rinta-Rahko H, Otero S, Smet W, et al. (2019) Mobile PEAR transcription factors integrate positional cues to prime cambial growth. Nature 565: 490–494

Mutuku JM, Cui S, Horii C, Takeda Y, Tobimatsu Y, Nakabayashi R, Mori T, Saito K, Demura T, Umezawa T, et al. (2019) The structural integrity of lignin is crucial for resistance against Striga hermonthica parasitism in rice. Plant Physiol 179: 1796–1809

Mutuku JM, Cui S, Yoshida S, Shirasu K (2020) Orobancheaceae parasite-host interactions. New Phytol 230: 46–59

Neumann U, Vian B, Weber HC, Salle G (1999) Interface between haustorium of parasitic members of the Scrophulariaceae and their hosts: a histochemical and immunocytochemical approach. Protoplasma 207: 84–97

Notaguchi M, Kurotani KI, Sato Y, Tabata R, Kawakatsu K, Tsukada Y, Okayasu K, Sawai Y, Okada R, Ashima H, Ichihashi Y, et al. (2020) Cell-cell adhesion in plant grafting is facilitated by beta-1,4-glucanases. Science 369: 698–702

Ogawa S, Wakatabe T, Spallek T, Ishida JK, Sano R, Kurata T, Demura T, Yoshida S, Ichihashi Y, Schaller A, et al. (2020) Subtilase activity in the intrusive cells mediates haustorium maturation in parasitic plants. Plant Physiol 185: 1381–1394

Olkonkwo SNC (1967) Studies on Striga senegalensis Benth. I. Mode of host-parasite union and haustorial structure. Phytochemistry 16: 453–463
Olivier A, Benhamou N, Leroux GD (1991) Cell surface interactions between sorghum roots and the parasitic weed Striga hermonthica: cytochemical aspects of cellulose distribution in resistant and susceptible host tissues. Can J Bot 69: 1679–1690

Peirce GJ (1893) On the structure of the haustoria of some phanerogamic parasites. Ann Bot os7: 291–324

Peron T, Candat A, Montiel G, Veronesi C, Macherel D, Delavault P, Simier P (2016) New insights into phloem unloading and expression of sucrose transporters in vegetative sinks of the parasitic plant Phelipanche ramosa L. (Pomel). Front Plant Sci 7: 2048

Pielach A, Leroux O, Domozycz DS, Knox JP, Popper Z A (2014) Arbiningalactan protein-rich cell walls, paramural deposits and ergastic globules define the hyaline bodies of rhinanthoid Orobanchaceae haustoria. Ann Bot 114: 1359–1373

Prigge MJ, Otsuga D, Alonso JM, Ecker JR, Drews GN, Clark SE (2012) From thin to thick: major transitions during stem development. Trends Plant Sci 17: 1679–1690

Ranjan A, Ichihashi Y, Farhi M, Zumstein K, Townsley B, David-Schwartz R, Sinha NR (2014) De novo assembly and characterization of the transcriptome of the parasitic weed Cuscuta pentagona identifies genes associated with plant parasitism. Plant Physiol 166: 1186–1199

Rioupol JL, Timko MP (1995) Haustorial initiation and differentiation. In MC Press, JD Graves, eds, Parasitic Plants. Chapman & Hall, New York, pp 39–79

Rodenburg J, Demont M, Zwart SJ, Bastiaans L (2016) Parasitic weed incidence and related economic losses in rice in Africa. Agric Ecosyst Environ 235: 306–317

Sanchez P, Nehlin L, Greb T (2012) From thin to thick: major transitions during stem development. Trends Plant Sci 17: 113–121

Shahid S, Kim G, Johnson NR, Wafula E, Wang F, Coruh C, Bernal-Galeano V, Phifer T, dePamphilis CW, Westwood JH, et al. (2018) MicroRNAs from the parasitic plant Cuscuta campestris target host messenger RNAs. Nature 553: 82–85

Shen G, Liu N, Zhang J, Xu Y, Baldwin IT, Wu J (2020) Cuscuta australis (dodder) parasite eavesdrops on the host plants’ FT signals to flower. Plant Cell 117: 23125–23130

Smetana O, Makila R, Lyu M, Amiryousefi A, Sanchez Rodriguez F, Wu MF, Sole-Gil A, Leal Gavarron M, Siligato R, Miyashima S, et al. (2019) High levels of auxin signalling define the stem-cell organizer of the vascularembry. Nature 565: 485–489

Smith CE, Dudley MW, Lynn DG (1990) Vegetative/parasitic transition: control and plasticity in Striga development. Plant Physiol 93: 208–215

Smith CE, Rutledge T, Zeng Z, O’Malley RC, Lynn DG (1996) A mechanism for inducing plant development: the genesis of a specific inhibitor. Proc Natl Acad Sci USA 93: 6986–6991

Spallek T, Melnyk CW, Wakatake T, Zeng Z, Sakamoto Y, Kiba T, Yoshida S, Matsunaga S, Sakakibara H, Shirasu K (2017) Interspecies hormonal control of host root morphology by parasitic plants. Proc Natl Acad Sci USA 114: 5283–5288

Stribeny B, Krause K (2015) Cell wall glycoproteins at interaction sites between parasitic giant dodder (Cuscuta reflexa) and its host Pelargonium zonale. Plant Signal Behav 10: e1086858

Thorogood CJ, Bauer U, Hiscock SJ (2018) Convergent and divergent evolution in carnivorous pitcher plant traps. New Phytol 217: 1035–1041

Tomilov AA, Tomilova NB, Abdallah I, Yoder JI (2005) Localized hormone fluxes and early haustorium development in the hemiparasitic plant Triphysaria versicolor. Plant Physiol 138: 1469–1480

Umeezawa T, Nakatsubo F, Higuchi T (1982) Lignin degradation by Phanerochaete chrysosporium: metabolism of a phenolic phenylcoumaran substructure model compound. Arch Microbiol 131: 124–128

Visser JH, Deink G, Kollmann R (1984) The “hyaline body” of the root parasite Alectra orobanchoides benth. (Scrophulariaceae)—its anatomy, ultrastructure and histochemistry. Protoplasma 121: 146–156

Wada S, Cui S, Yoshida S (2019) Reactive oxygen species (ROS) generation is indispensable for haustorium formation of the root parasitic plant Striga hermonthica. Front Plant Sci 10: 328

Wakatake T, Ogawa S, Yoshida S, Shirasu K (2020) An auxin transport network underlies xylem bridge formation between the hemiparasitic plant Phtheirospermum japonicum and host Arabidopsis. Development 147: dev187781

Wakatake T, Yoshida S, Shirasu K (2018) Induced cell fate transitions at multiple cell layers configure haustorium development in parasitic plants. Development 145: dev164848

Wang Y, Murdoch M, Lai SWT, Steele DB, Yoder JI (2020) Kin recognition in the parasitic plant Triphysaria versicolor is mediated through root exudates. Front Plant Sci 11: 560682

Wang Y, Steele D, Murdoch M, Lai S, Yoder J (2019) Small-molecule screens reveal novel haustorium inhibitors in the root parasitic plant Triphysaria versicolor. Phytopathology 109: 1878–1887

Westwood JH, Yoder JI, Timko MP, dePamphilis CW (2010) The evolution of parasitism in plants. Trends Plant Sci 15: 227–235

Wu F, Chi Y, Jiang Z, Xu Y, Xie L, Huang F, Wan D, Ni J, Yuan F, Wu X, et al. (2020) Hydrogen peroxide sensor HPCa1 is an LRR receptor kinase in Arabidopsis. Nature 578: 577–581

Xiang L, Li Y, Sui X, Li A (2018) Fast and abundant in vitro spontaneous haustorium formation in root hemiparasitic plant Pedicularis kansuensis Maxim. (Orobanchaceae). Plant Divers 40: 226–231

Xie F, Murray JD, Kim J, Heckmann AB, Edwards A, Oldroyd GED, Downie JA (2012) Legume pectate lyase required for root infection by rhizobia. Proc Natl Acad Sci USA 109: 633–638

Yang ZZ, Wafula EK, Honaaas LA, Zhang HT, Das M, Fernandez-Aparicio M, Huang K, Bandaranayake PGC, Wu B, Der JP, et al. (2015) Comparative transcriptome analyses reveal core parasitism genes and suggest gene duplication and repurposing as sources of structural novelty. Mol Biol Evol 32: 767–790

Yoder JI (1997) A species-specific recognition system directs haustorium development in the parasitic plant Triphysaria (Scrophulariaceae). Planta 202: 407–413

Yoshida S, Cui S, Ichihashi Y, 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, Tansakren J, Kim YM, Honaaas 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

Yoshida S, Shirasu K (2009) Multiple layers of incompatibility to the parasitic witchweed, Striga hermonthica. New Phytol 183: 180–189

Zhang X, Berkowitz O, Teixeira da Silva JA, Zhang M, Ma G, Whelan J, Duan J (2015) RNA-Seq analysis identifies key genes associated with haustorial development in the root hemiparasite Santalum album. Front Plant Sci 6: 661