Chapter 5
Haustorium Invasion into Host Tissues

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5.1 Introduction

There are several definitions for the word 'invasion', but almost all involve entrance of something troublesome or harmful. Usually, the first definition corresponds to a military action and the second to pathogens and parasites, so it is tempting to find analogies between them. In fact, when a pathogen tries to invade a host, a 'fierce war' develops between them, and success increases the chance of survival for the 'winner'. Nevertheless, the parasite is not acting knowingly and deliberately as an individual attacking another organism. It acts following a natural behaviour resulting from an evolutionary process. Though breeders and agronomists regard the parasite as an enemy and actively construct barriers against it (see Chap. 17), in natural ecosystems the coexistence of the parasite and the host is possible and sometimes even necessary (Rowntree et al. 2011; see Sect. 16.3.3).

Invasion of host tissues is a key step for the parasite because natural barriers to penetration exist even in susceptible hosts. The pathogen must display a wide array of tools to overcome the intrinsic resistance present even in a compatible host. This chapter shows how parasitic Orobanchaceae prepare the 'machinery' for the assault against the host realm, and discusses the parasite tactics.

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5.2 Preparing for Penetration

Following the initiation of a haustorium (see Chap. 4), the first step in the direct attack is the development of the **attachment organ**, which facilitates anchoring to the host root surface. The development at the right place and time is crucial for the invasion. The attachment organ is a device that firmly adheres to the host root. A common feature of attachment organs of many parasites is the development of **haustorial hairs** at the periphery of the attachment site. These hairs are specialized root hairs of various lengths that serve as an additional anchoring device. Long attachment hairs, ca 150–300 μm, are formed by *Agalinis purpurea* prior to contact with the host root. Their surface is covered by a secretion, which shapes upon contact with the host surface and establish a structural bond (Fig. 5.1a). The adhesive substance of *Agalinis* was assumed to be hemicelluloses (Baird and Riopel 1983). Similar haustorial hairs develop around the radicle tip of *Striga* seedlings in contact with the host (Fig. 5.1b) (Hood et al. 1998; Reiss and Bailey 1998). Also in this latter case, a thin film is present between the hair and host root surface at the contact area. The chemical nature of the *Striga* film is also unclear, but it stains with safranin and gives a negative result in histochemical staining for carbohydrates (Musselman and Dickinson 1975). In *Orobanche cumana* and *Phelipanche aegyptiaca*, the external cells of the radicle tip differentiate into a layer of papillae, which are very short cell extensions, and these form the adhesion surface (Fig. 5.1c). The surface of these papillae is coated with a substance that stains for carbohydrates (Joel and Losner-Goshen 1994b; Pérez-de-Luque et al. 2005; Krenner 1955). Attachment hairs of *Triphysaria* spp. secrete a pectinaceous mucilage-like material (Heide-Jørgensen and Kuijt 1995).

However, not all root parasitic plants rely on haustorial hairs for adhering to host roots. For example, only few hairs of *Rhamphicarpa fistulosa* stick to the host root surface, in spite of having many haustorial hairs. In the soil penetration is obviously also supported by soil impaction (Neumann et al. 1998).

While the anchoring device develops, other cells at the apex of the initial haustorium prepare for penetration. In *Striga*, cells that are in contact with the root surface and cells in the next inner layer show a dense cytoplasm with central nucleus and numerous small vacuoles (Hood et al. 1998; Fig. 5.1d; see Sect. 4.2). These **intrusive cells** (Kuijt 1969; or digitate cells, Reiss and Bailey 1998) are usually bigger than the surrounding cells (Musselman and Dickinson 1975). In lateral haustoria of *Triphysaria*, some epidermal cells elongate tangential and perpendicular to the axis of the parasite root, forming the lateral faces of the haustorium (Heide-Jørgensen and Kuijt 1995). In *Rhamphicarpa fistulosa*, the cells that later penetrate the host derive from hypodermal cells (Fig. 5.1e) and have dense cytoplasm, a prominent nucleus with an enlarged nucleolus, numerous mitochondria, small vacuoles, rough endoplasmic reticulum, dictyosomes and lipid droplets (Neumann et al. 1998).

Once all these changes take place and the parasite is firmly attached to the host root surface, the haustorium disrupts host tissues and penetrates the root towards the vascular tissues.
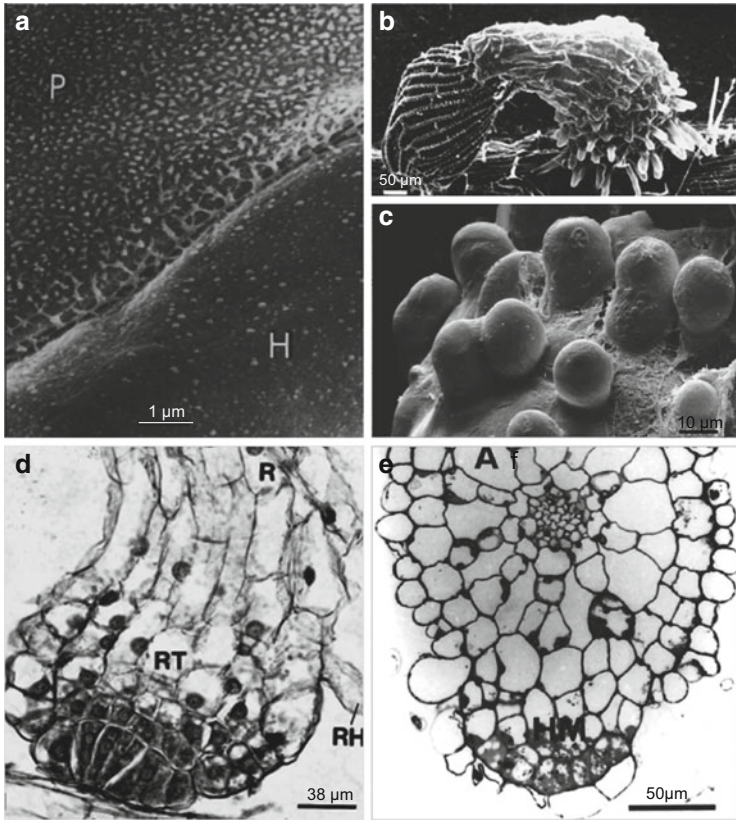
Fig. 5.1 Parasite attachment to host root. (**a**) Interface between an attachment hair of *Agalinis purpurea* (P) and host root surface (H) showing droplets of secreted substance that coalesce and bridge the gap at the contact region. (**b**) Haustorial hairs of *Striga asiatica* seedling attached to sorghum root surface. (**c**) Papillae of the root tip of *Orobanche cumana*. (**d**) Radicle cells of *Striga gesnerioides* in contact with the surface of a host root; they have dense cytoplasm; the nuclei moved into the centre of the cells; *R* parasite radicle; *RH* attachment hair; *RT* radicle tip. (**e**) *Rhamphicarpa fistulosa* root bearing a pre-haustorium; the haustorial meristem (HM) is restricted to cells of hypodermal origin; *A* root aerenchyma (**a** from Baird and Riopel 1983, **b** from Hood et al. 1998, **c** from Joel and Losner-Goshen 1994b, **d** from Reiss and Bailey 1998, **e** from Neumann et al. 1998, with permission)

5.3 Penetration

Thinking about putative similarities between parasitic plants and phytopathogenic fungi is not difficult. Such a comparison is helpful and was reviewed by Mayer (2006). Following on with the siege analogy, fungal hyphae could be compared with a small group of individual soldiers trying to find a gap in the defences. On the contrary, whereas fungal hyphae can penetrate through tiny natural openings, such as stomata or lenticels, or through lesions, a parasitic plant haustorium must open a bigger 'gate' in host tissues to reach the vascular system of the host.

5.3.1 Enzymatic Activity

Early reports about the penetration process, based on low-resolution light micros-
copy, claimed that *O. cumana* dissolved cell walls and cell contents of host cortical
parenchyma (Krenner 1955) by means of a secretion from the intrusive cells and
that the parasite is able to feed on the dissolved substances. Nowadays, despite great
gaps in knowledge, we know that parasitic Orobanchaceae do not dissolve the cells
found in their way, even though some parasites (e.g. *Agalinis aphylla*) may break
through host cells (Musselman and Dickinson 1975). Histological observations
clearly showed that only a combination of mechanical and enzymatic mechanisms,
exerted by the parasite to separate host cells, allows penetration (Joel and Losner-
Goshen 1994a; Neumann 1999). The intrusive cells of *Orobanche* spp. penetrate by
pushing their way between host cells with the help of enzymatic processes (Dörr
and Kollmann 1974; Kuijt 1977). The dissolution of the middle lamella between
host cells and the concomitant mechanical pressure by the penetrating cells pushes
portions of host cell walls aside so that the shape of the host cells changes and the
space between them is occupied by the intrusive cells (Joel and Losner-Goshen
1994a).

The endodermis, with its cutinized or suberized Casparian strips, is another
obstacle which the haustorium needs to cross on its way to host conductive tissues.
Indeed, a combined anatomical and immunocytochemical study revealed that
penetration of the *Phelipanche aegyptiaca* haustorium takes place between host
endodermal cells by the dissolution of the cutin of the Casparian strips (Joel et al.
1998). Similarly, penetration through host endodermis by *Striga hermonthica*
caused no damage to endodermal cells nor any crushing effect. In this latter case
the haustorium was described to advance between the primary and secondary wall
of the endodermis (Neumann 1999). A subtle difference therefore seems to exist
between the parasites in their mode of penetration, but this issue needs further
research.

Which enzymes are involved in the penetration process? Renaudin (1977)
detected cellulolytic and proteolytic activity at the site of penetration of *Lathraea
clandestina* by using tissue impressions on photographic and cellophane films. A
few works presented in vitro evidence about pectolytic, cellulolytic and proteolytic
enzymes being secreted by seedlings of *Phelipanche aegyptiaca* before penetration
(Shomer-Ilan 1992, 1993, 1999). Singh and Singh (1993) also studied the presence
of cell wall-degrading enzymes such as cellulase, polygalacturonase, xylanase and
protease in tissues of the tubercle of *P. aegyptiaca* and inferred that they could also
be involved in establishing haustorial connection with the host. However, neither of
these works presented conclusive results as to the actual enzymes that are active in
situ within host roots.

The first proof of direct involvement of enzymatic activity during the invasion
process came from the work by Losner-Goshen et al. (1998). The authors showed
the presence of pectin methylesterase at the penetration site using cytochemical and
immunocytochemical methods with specific antibodies. In addition, the presence
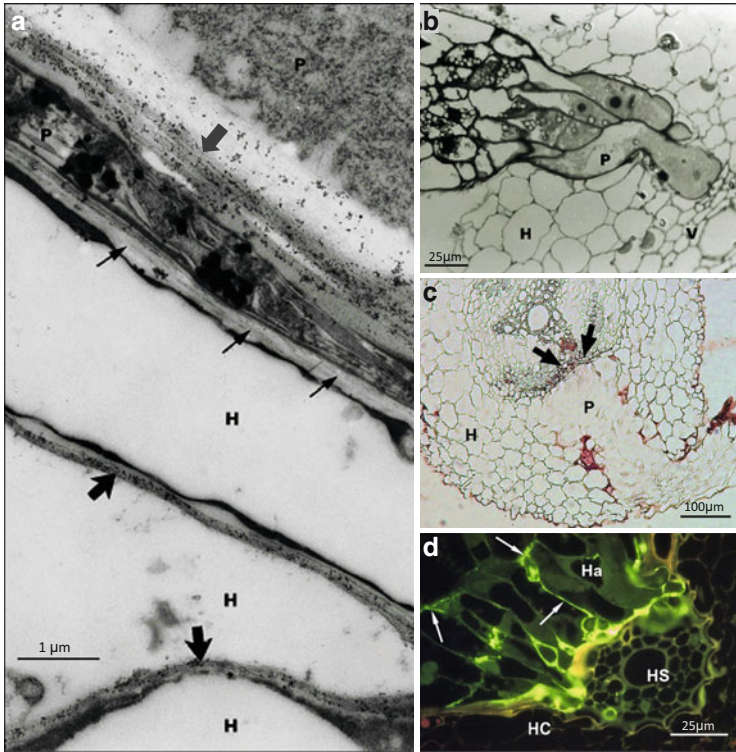
Fig. 5.2 The penetration mechanism. (**a**) Disappearance of pectins in outer cortex cell walls of sunflower root, adjacent to *Orobanche cumana* haustorium, seen after double gold labelling with JIM 5 and JIM 7 antibodies against low- and high-esterified pectins; internal host and parasite cell walls distant from the interface are labelled (*large arrows*), whereas host cell walls that touched the neighbouring parasite haustorium are not (*small arrows*); *P* parasite cell; *H* host cell. (**b**) Intruding cells of *O. cumana* reaching the vascular cylinder (V) of sunflower root. (**c**) Unsuccessful penetration attempt by *O. crenata* (P) in *Vicia sativa* root; the parasite was halted at the root endodermis, which was deformed by the exerted pressure (*arrows*). (**d**) The interface between the haustorium of *Buchnera hispida* and pearl millet root; JIM 5 antibodies labelled the parasite cell walls (*arrows*) whereas host cell walls remained unlabelled; *Ha* Haustorium; *HC* host cortex; *Hs* host stele (**a** and **b** from Losner-Goshen et al. 1998, **c** from Pérez-de-Luque et al. 2005, **d** from Neumann et al. 1999, with permission)

of pectin methylesterase was associated with the appearance of de-methylated pectins (galacturonic sequences with less than 50 % esterification) in the cell walls adjacent to intrusive cells, which is in accordance with the enzyme activity (Fig. 5.2a). This enzyme was previously identified and purified from calli and germinating seeds of *Orobanche* (Ben-Hod et al. 1993; Bar Nun et al. 1996). Other enzymes have been identified in *Orobanche* calli, such as polygalacturonase, but its involvement in host penetration still has not been proven (Ben-Hod et al. 1997). Nevertheless, Losner-Goshen et al. (1998) found degraded cell walls,

supporting the possible involvement of polygalacturonase. Putative cutinase activity was also found at the endodermis penetration point by means of immunocytochemistry by Joel et al. (1998).

Cell wall-degrading enzymes were also found in *Striga*. Penetration of sorghum roots by *S. hermonthica* involved alterations of the host cell walls at the infection point (Olivier et al. 1991), and softening and dissolution of the middle lamella was observed with *S. gesnerioides* attacking cowpea (Reiss and Bailey 1998). In other hemiparasitic Orobanchaceae, there is no direct evidence indicating the accumulation or secretion of enzymes in the penetration process, but the presence of a densely staining cytoplasm in intrusive cells of the parasites has been pointed as a putative indication of the synthesis of cell wall hydrolytic enzymes (Baird and Riopel 1984). Enzymatic breakdown is implicated as well as part of the penetration process in *Triphysaria* (Heide-Jørgensen and Kuijt 1995) and *R. fistulosa* (Neumann et al. 1998).

5.3.2 Mechanical Pressure

In addition to the enzymatic process, a mechanical pressure is used during intrusion in host tissues. *Orobanche* intrusive cells force their way by successive and gradual splitting the cell walls between host cells without lysing them (Privat 1960). This is combined with elongation of the cells inside host tissues until they reach the vascular cylinder (Fig. 5.2b) (Losner-Goshen et al. 1998). Penetration of the host cortex by *Striga asiatica* implies anticlinal and periclinal divisions in the distal most cells and acropetal vacuolation of the haustorium cells (Hood et al. 1998). The distal most cells lengthen and form a palisade arrangement when they reach the endodermis and penetrate it 6–8 days after contact (see Sect. 5.4).

The existence of a mechanical force in addition to the enzymatic activity is evidenced by the presence of compacted and compressed host cells at the interface between host and parasite (Heide-Jørgensen and Kuijt 1995; Neumann et al. 1998, 1999; Reiss and Bailey 1998). When the intrusive cells find a physical resistance to penetration, for example, at the endodermis, the parasite tissues deform, and the host endodermis and pericycle are bent by the exerted pressure (Fig. 5.2c) (Pérez-de-Luque et al. 2005).

5.3.3 Internal Anchorage

A problem arises when considering a mechanical force exerted by the pathogen on the host tissues: the Newton's third law about action–reaction—if the intrusive cells are pressing against the host cells, why is the haustorium not driven out of the root? The parasitic plant must anchor in some way to the host root tissues in order to avoid being expelled by its own pressure. Several studies have shown that the

interface between host and parasite plays this important role. Neumann et al. (1999) showed by means of immunocytochemistry that pectins are implicated in sticking the parasites *Buchnera hispida*, *R. fistulosa* and *S. hermonthica* to the host within its tissues (Fig. 5.2d). Similarly, an osmiophilic material was found filling the interface between *P. aegyptiaca* and the outer cortex regions of host root (Losner-Goshen et al. 1998), and a safranin-staining substance was observed at the infection points of legumes with *O. crenata* (Pérez-de-Luque et al. 2005, 2006). Such substances also stained with ruthenium red, pointing towards pectins as a component of these secretions (Pérez-de-Luque et al. 2006), which are probably similar to those secreted during the initial attachment of the parasite to host root surface; these substances similarly act as a cement that allows internal anchoring of the parasite to the host tissues (Joel et al. 1996), facilitating further physical efforts to penetrate between the host cells.

5.3.4   Reaching Host Conductive System

Once the parasite reaches the central cylinder of the host, the invasive process is almost complete, and connections with the vascular tissues must be developed. Concomitantly with endodermal penetration, differentiation of vascular elements occurs in the *S. asiatica* haustorium (Hood et al. 1998). After breaching the endodermis, *Striga* cells penetrate into host vessel elements, sometimes with more than one intrusion from a single parasite cell and developing absorbing structures termed oscula (see Sect. 3.9.2).

Further differentiation causes these haustorial cells and the oscula to lose the protoplast and become part of the water-absorbing system of the parasite in the form of xylem elements. In other parasitic plants, such as *Orobanche*, intrusive cells differentiate into transfer cells and later into xylem vessels with open connections with the host vessels (Privat 1960; Dörr and Kollmann 1976; see Sect. 3.9.1). These open xylem connections are possible when a simultaneous differentiation of adjacent host and parasite cells is induced (Dörr 1997). Open xylem connections are also present in other parasitic species (Kuijt 1977; Heide-Jørgensen and Kuijt 1995; Neumann et al. 1998; see Sect. 3.9.1). In addition, continuity between host and parasite sieve elements has been shown in *O. crenata* parasitizing *Vicia narbonensis* (Dörr and Kollmann 1995), so it is possible that connections with host phloem elements also develop in some other parasitic plants (see Sect. 3.9.3).

5.4   Duration of Penetration

The duration of all the penetration processes has not been studied in detail in terminal and lateral haustoria of the different Orobanchaceae. In some cases, the time lapse of penetration was assumed to be a week. Hood et al. (1998) developed a

detailed study of the terminal haustoria of *Striga asiatica*. They found that invasion of sorghum root cortex was completed 2–3 days after parasite attachment to the host, the host endodermis was penetrated 3–4 days after first contact with the host, and the vascular connections started to be established within 6 days. This gives an interlude of a week from contact to vascular connection of *S. asiatica* in vitro. Recent experiments with *Orobanche crenata* in pea (*Pisum sativum*) have shown that the time lapse can vary (Cifuentes and Pérez-de-Luque 2011; unpublished results). No penetration of host tissues was detected until 4 days after contact of germinated parasite seeds with the host, during which the apical meristem of the *Orobanche* radicle differentiated into a haustorium. In this case the intrusive cells reached the endodermis and the central cylinder 11 days after inoculation, establishing vascular connections in 12 days. However, Losner-Goshen et al. (1998) mentioned that penetration of *P. aegyptiaca* and *O. cumana* haustoria into tomato roots is a very rapid process. All these point out differences in the duration of the penetration process, depending on several factors related to both the parasite and the host species and probably also on the experimental setup. Special attention should be paid to this question, because it can alter and distort studies requiring accurate sampling, such as the analysis of enzyme secretion and gene expression (Losner-Goshen et al. 1998).

5.5 Avoiding Defences: Tricks of War

How is it possible that the alarm is not raised in the host during the compatible invasive process? How can the parasitic plant manage to cross the natural barriers and avoid the activation of defensive mechanisms? This is one of the key issues still unknown in parasitic plant research.

In almost every plant, some cells grow between other cells. In these cases the neighbouring cells do not identify them as alien and do not react against their 'invasion'. This is the 'intrusive growth', which is the plant analogue of dendrite and axon growth in animals (Lev-Yadun 2001). Could the parasitic plant mimic the compatible intrusive growth of pollen tubes and laticifers? The question is not easy to answer, and there is almost no research on the topic. However, Joel and Portnoy (1998) showed that a susceptible host recognizes the parasite as an alien, and it does not grow in co-ordination with the host tissues. The activation of PR proteins (Joel and Portnoy 1998) and expression of 3-hydroxy-3-methylglutaryl-CoA reductase gene (Westwood et al. 1998) are evidences pointing towards the recognition of the attack not only by resistant hosts but also by compatible hosts.

Nevertheless, most of the studies are focused on resistant host genotypes and incompatible interactions (see Chap. 7), so no clear information exists about the process by which the parasite hampers the defensive responses of a compatible host. Mayer (2006) suggested two possibilities, the first one being due to the biochemical and physiological similarities between the parasite and the host, both being higher plants, and the second possibility that the parasitic plant actively prevents activation

of host defence response. Being closely related, the host would find it difficult to recognize the parasitic plant as non-self. But we have already seen that during invasion, the parasite makes a real wound in the host root tissues, disrupting and separating them, and that the host recognizes it as alien. Why is the physical damage not detected? Why does the susceptible host not react to the invasion? The logical answer could be that there is an active parasitic mechanism preventing host reactions. At this point, only speculation is possible. For example, peroxidases, secreted by seedlings of *O. cumana*, were suggested as suppressors of a specific sunflower resistance (Antonova and ter Borg 1996). Mayer (2006) pointed out that phenolic compounds from the parasite could act as deterrents against host defence reactions. The lack of intracellular reactive oxygen species (ROS), either belonging to the host or to the parasite, might be an indication of the inability of the compatible host to react against parasitic attack (Mor et al. 2008). In addition, it is known that established parasitic plants interfere with the normal flux and synthesis of host hormones, e.g. abscisic acid (ABA) (Jiang et al. 2004; see Sect. 6.4), and despite that no mutual co-ordination seems to exists with the host tissues during the invasion process (Joel and Portnoy 1998). The alteration of the plant hormonal balance at the infection site (see Sect. 3.10) could perhaps delay or nullify a defensive response. Recently, Hiraoka et al. (2009) have shown, by means of suppression subtractive hybridization (SSH), that compatible interactions between *P. aegyptiaca* and *Lotus japonicus* imply the up-regulated expression of several genes in the host related with nodulation. So a new question arises: does this parasitic plant mimic the nodulation process similar to the exploitation of the mycorrhizal recognition signals? (Akiyama et al. 2005; see Chap. 10; see also Chap. 7 for host reactions to attack by the parasite).

5.6 Conclusions

During recent years, very little has been published on the cytology of host–parasitic plant interactions, and most of the studies are focused in genomics, proteomics and metabolomics, in species of *Triphysaria*, *Orobanche* or *Striga*, and centred on resistance vs. susceptibility. Knowledge about the behaviour of the parasite tissues inside the host is still lacking, and more comparative studies involving several different hosts and parasites should be conducted. These kinds of studies are not easy because of the similar nature of the two partners in the parasite–host system. In addition, the infestation takes place underground, so special and complex experiments need to be designed.

Further research is still needed on the composition of the adhesive substances allowing anchoring, the enzymes released during penetration, the development of phloem connections, a more precise understanding of the various steps during invasion in both host and parasite as well as the development of secondary haustoria from adventitious roots and their role in pathogenesis.

In addition, research is needed for the key questions of how the parasite avoids activation of host defences and how the parasite communicates with host tissues during the invasion.

Only a few genera of parasitic Orobanchaceae have been studied among the more than the 300 known species so we cannot know if all of them have the same mechanism of invasion, although some general assumptions can be made on the basis of the current knowledge. Correlated studies ranging from more primitive hemiparasitic and facultative species towards more evolved and specialized obligate holoparasitic species should be of great help for understanding particular traits in some cases and for getting a better perspective of this unique and fascinating plant group.

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