Chapter 4
Haustorium Initiation and Early Development

Pradeepa C.G. Bandaranayake and John I. Yoder

4.1 Introduction

The ability to develop invasive haustoria is the key feature of parasitic angiosperms. The haustorium attaches the parasite to the host, penetrates the host while keeping its own tissues intact, develops a vascular continuity between the host and parasite and ultimately provides the conduit through which host and parasite materials flow. The ability to make haustoria distinguishes parasitic from non-parasitic plants; indeed, 'the haustorium embodies the very idea of parasitism' (Kuijt 1969).

This chapter reviews the initiation and pre-attachment development of terminal and lateral haustoria in parasitic Orobanchaceae. Haustoria have been described for many genera of Orobanchaceae, but their initiation and development has been investigated in a relatively small number of species. Most of these studies have investigated the development of terminal haustoria in the weedy species *Striga asiatica* (Saunders 1933; William 1961; Nickrent et al. 1979; Keyes et al. 2007), *S. hermonthica* (Okonkwo 1966; Olivier et al. 1991), *S. gesnerioides* (Okonkwo and Nwoke 1978), *Phelipanche aegyptiaca* (syn. *Orobanche aegyptiaca*) and *O. cumana* (Joel and Losner-Goshen 1994; Zhou et al. 2004) and *Alectra vogelii* (Nwoke and Okonkwo 1978; Visser et al. 1990). Studies in the development of lateral haustoria have primarily focussed on three facultative species: *Agalinis purpurea* (Riopel and Musselman 1979; Baird and Riopel 1984), *Castilleja exserta* (previously known as *Orthocarpus purpurascens*) (Atsatt et al. 1978) and *Triphysaria versicolor* (Jamison and Yoder 2001; Bandaranayake et al. 2010).

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Chemical signalling mechanisms and early haustorium ontogeny are similar in terminal and lateral haustoria; the primary developmental difference between them is that terminal haustoria result in the end point differentiation of the root tip meristems while lateral haustoria do not terminate root growth.

4.2 Early Haustorium Development

Haustorium development in most Orobanchaceae is initiated by chemical and physical stimuli provided by contact with a host root (Saunders 1933; William 1961; Musselman and Dickison 1975; Atsatt et al. 1978; Okonkwo and Nwoke 1978; Attawi and Weber 1980; Baird and Riopel 1984; Riopel and Timko 1995). The notable exceptions are *Orobanche* species that do not require host factors for haustorium development and whose terminal haustoria are not as swollen or morphologically well defined as those of *Striga* (Joel and Losner-Goshen 1994). Lateral and terminal haustorium development can be monitored in vitro by positioning the roots of facultative parasites or the radicle tips of obligate parasites next to those of host plants on agar plates. Alternatively, host root exudates or purified inducing factors can be applied to parasite roots or radicles. While the most responsive cells are near or at the root apical meristem, cortical cells throughout the parasite root are capable of developing lateral haustoria (Riopel and Musselman 1979).

Following exposure to host root exudates, there is an almost immediate cessation in parasite tip growth (Fig. 4.1a) (Baird and Riopel 1984; Riopel and Baird 1987). In *Striga*, the incorporation of H^3-thymidine into newly replicated DNA drops dramatically drops within an hour of exposure to 2,6-dimethoxybenzoquinone (DMBQ), an active haustoria-inducing quinone, and remains low for about 24 h or until the DMBQ is removed (Keyes et al. 2000). Several cell cycle associated genes that are transcriptionally regulated in *Triphysaria* roots during this period are possibly related to this interruption in replication (Torres et al. 2005).

Within 4–8 h of host exposure, the radicle tip or the region just behind the root tip becomes swollen (Fig. 4.1a) as a result of the rounding and isodiametric expansion of cortical cells associated with vacuole enlargement and coalescence. Cell enlargement begins with cells in the inner cortical layers and then spreads to the outer layers (Fig. 4.1b, c; see also Sect. 3.16). The involvement of auxin in modifying cell shape was implicated by dissecting *Triphysaria* root tips before and after exposure to host factors and by transforming *Triphysaria* roots with an auxin-responsive reporter (Tomilov et al. 2005; see also Sect. 3.10). Several genes encoding cell wall-modifying enzymes, including expansins, are transcriptionally regulated during this period (O'Malley and Lynn 2000; Wrobel and Yoder 2001; Torres et al. 2005). These findings show that early stages in haustorium development employ existing plant mechanisms for altering cell shape, size and number.

Epidermal cells at the top of the developing haustorium begin to divide about 10 h after induction, forming a group of densely cytoplasmic cells at the haustorium

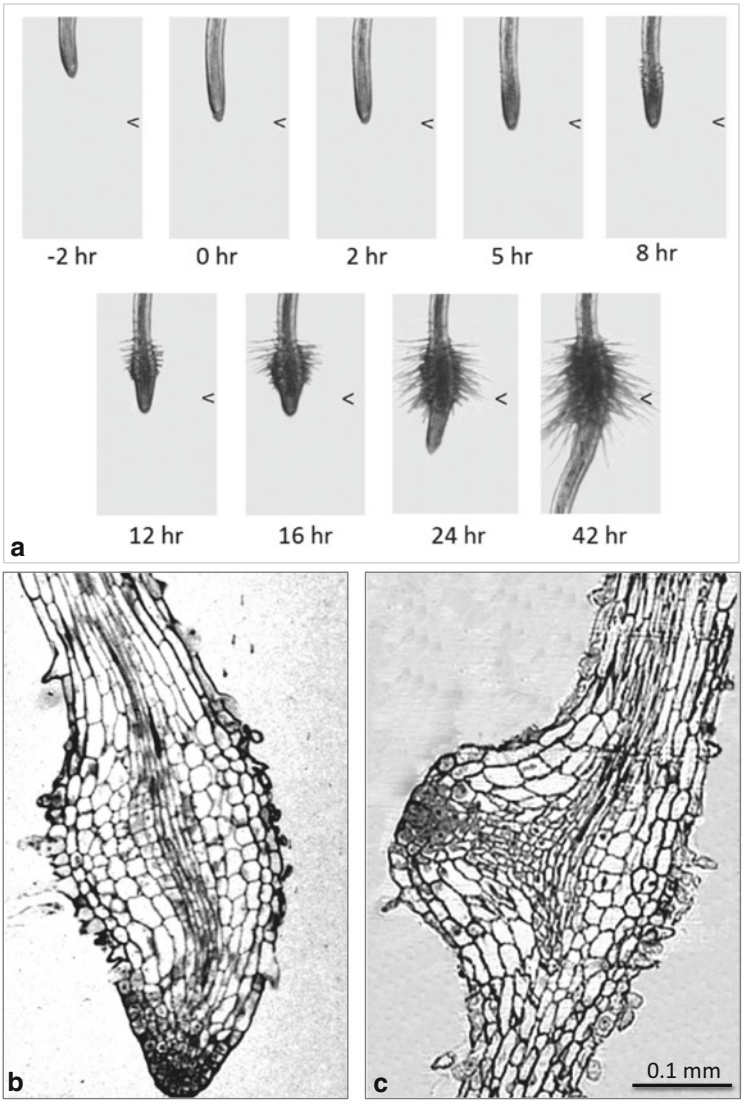

Fig. 4.1 Lateral haustorium development in *Triphysaria*. (**a**) A *Triphysaria* root growing on the surface of an agar plate, as photographed before and after exposure to DMBQ; notice the difference in root tip growth before and after application at time zero. Haustorial hairs can be observed about 5 h later and cortical swelling—by 12 h; at about 24 h the root reverts back to typical growth pattern (from Matvienko et al. 2001a, http://www.plantphysiol.org, Copyright American Society of Plant Biologists). (**b**) Longisection of *Triphysaria* root, following 48 h exposure to *Arabidopsis* root exudates; notice the rounding and isodiametric swelling of the cortical cells in the developing haustorium (from Estabrook and Yoder 1998, http://www.plantphysiol.org, Copyright American Society of Plant Biologists). (**c**) Similar to **b**, but *Triphysaria* roots were exposed to *Arabidopsis* roots for 72 h and then sectioned; this time point was after host attachment but before penetration. Animation of haustorium ontogeny can be seen at http://www.youtube.com/watch?v=9Hv1-aYNxNE

apex (Figs. 4.1c and 5.1d, e). Epidermal cells surrounding the haustorium apex elongate into long haustorial hairs that adhere to host tissues and thereby function in host attachment (Baird and Riopel 1985) (Figs. 3.3a, b, 4.3c, d, and 5.1b). Haustorial hairs do not develop in *Orobanche* but rather the external cells of the haustorium develop short secretory papillae that provide the adhesion surface (Fig. 5.1c; Joel and Losner-Goshen 1994; see Sect. 5.2). About 12 h after contact with a host, cells in the inner cortex and pericycle begin to divide and form a penetration peg that invades through the host tissues. Without host attachment the radial swelling, cell divisions and haustorial hair proliferation continue for about 24 h. If the haustorium is laterally positioned, the root meristem will resume its normal apical growth and haustoria will appear as 'beads on a string' (see Sect. 3.15). In contrast, there is no resumption of normal root growth distal to terminal haustoria unless functional host connections are established. Within a few days of host contact, a successful haustorium will have invaded the host and established a functional connection between the host and parasite vascular systems.

4.3 Haustorium Initiation Factors

The ability to monitor haustorium development in vitro provided an assay for identifying host factors that induce haustoria; these have been termed xenognosins or haustorium-inducing factors (Steffens et al. 1982; Riopel and Timko 1995). The first xenognosins identified were the flavonoids xenognosin A and xenognosin B that were isolated by fractionating a commercially available exudate from the legume *Astragalus* and assaying the fractions for haustorium-inducing activity in *Agalinis* (Lynn et al. 1981; Steffens et al. 1982). Subsequently, the flavonoid peonidin (Fig. 4.2a) was identified as a haustorium inducer for *Triphysaria* (Albrecht et al. 1999).

The only haustorium-inducing compound isolated from host roots is 2,6-dimethoxybenzoquinone (DMBQ) (Fig. 4.2b; Chang and Lynn 1986). Benzoquinones are widely present in plants and synthesized through the shikimate pathway, by oxidative decarboxylation of phenolic acids and by the enzymatic degradation of polyphenols by peroxidases and laccases (Caldwell and Steelink 1969; Krisnangkura and Gold 1979; Conn 1986). DMBQ was isolated from sorghum roots only after they were physically abraded or co-incubated with *Striga* cultures, processes that lead to the release of DMBQ through peroxidase-mediated oxidation of sorghum cellular components (Fig 4.2b) (Chang and Lynn 1986; Lynn and Chang 1990). Hydrogen peroxide generated in *Striga* radicles provides the rate-limiting substrate for host peroxidases that catalyse the conversion of their own cell wall components into haustoria-inducing benzoquinones (Keyes et al. 2000). In this model, *Striga* radicles enzymatically extract xenognosins from the surface of host roots, thereby ensuring close proximity of the parasite and host before committing to haustorium development (Keyes et al. 2007). David Lynn and colleagues propose that this may be a generalized mechanism by which even non-parasitic roots can establish subterranean spatial relationships (Palmer et al. 2009).

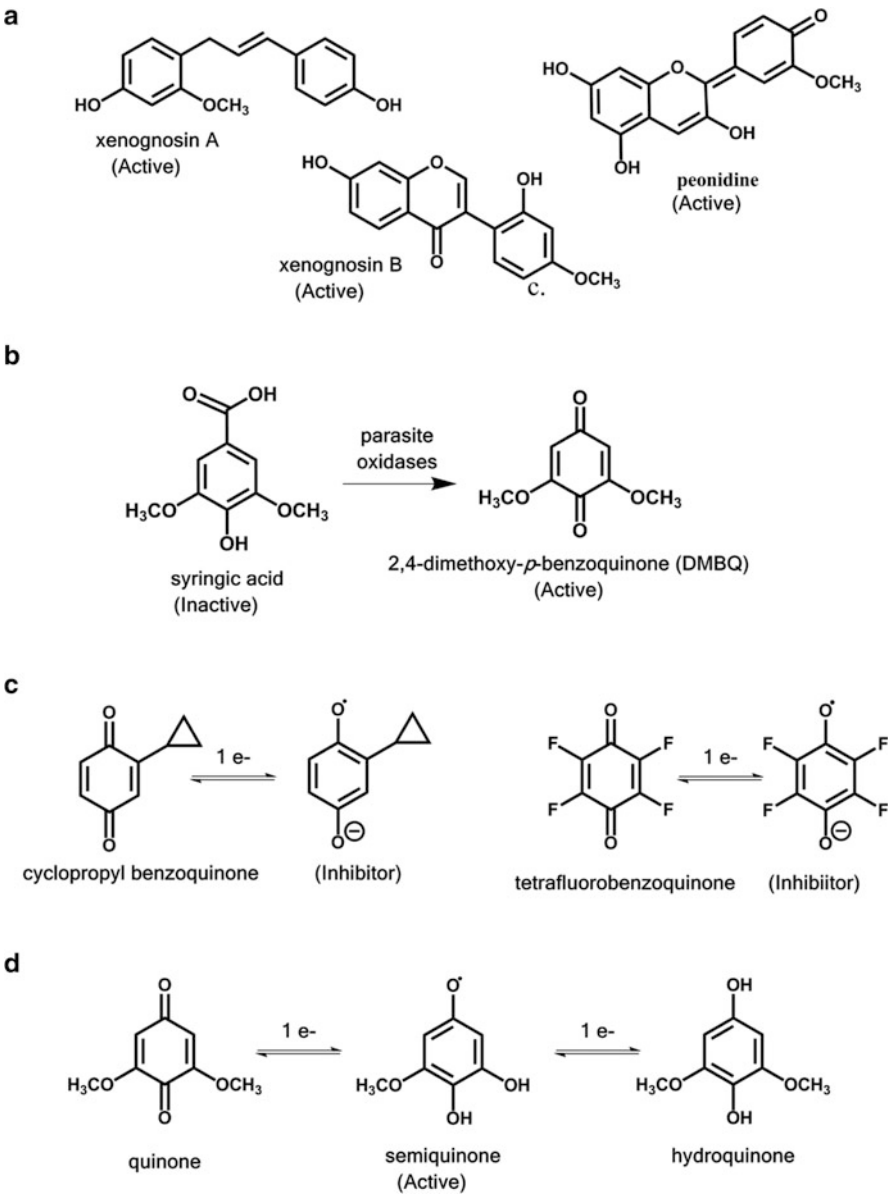

Fig. 4.2 Molecules and reactions associated with haustorium induction. (**a**) Three haustoria-inducing flavonoids, xenognosin A, xenognosin B and peonidin (Lynn et al. 1981; Steffens et al. 1982; Albrecht et al. 1999). (**b**) The enzymatic oxidation of syringic acid to the haustorium inducer DMBQ (Lynn and Chang 1990). (**c**) Single-electron reductions of cyclopropyl benzoquinone and tetrafluorohydroquinone generate inhibitors of haustorium development (Zeng et al. 1996; Keyes et al. 2000). (**d**) The single-electron reduction of DMBQ to the active semiquinone (Keyes et al. 2000); this step is catalysed by the enzyme TvQR1 in *Triphysaria* (Bandaranayake et al. 2010); further reduction of the semiquinone results in the relatively stable, inactive hydroquinone

The phenols, flavonoids and quinones that initiate haustorium development in vitro (Fig. 4.2) are structurally distinct from the strigolactones that are largely responsible for parasite seed germination (see Sect. 10.2). Not all xenognosins are equally active and different concentrations or times of exposure are needed for optimal haustorium development. For example, haustorium initiation in response to syringic acid requires several more hours of exposure than DMBQ because the phenolic acid needs to be enzymatically oxidized in order to be active (Fig. 4.2b) (Lynn and Chang 1990).

Many of the molecules associated with haustorium development are widely and commonly distributed among plants, and it is likely that host exudates contain multiple xenognosins. Therefore it might be expected that exudates from many plants should be active in inducing haustoria in parasites and this is by and large the case. Facultative parasites tend to have a broad, generalist host range (Werth and Riopel 1979; Gibson and Watkinson 1989). *Triphysaria*, for example, associates in the wild with at least 27 families of plant hosts and in pot cultures will parasitize maize, rice, legumes and *Arabidopsis* and hence will make haustoria in response to exudates from monocots and dicots (Atsatt and Strong 1970; Goldwasser et al. 2002). Obligate parasites tend to be more host specific; *Striga* species are either monocot- or dicot-specific and *Orobanche* species recognize specific dicots as hosts (see Chap. 18 and Sect. 14.4.2). However, host specificity in parasitic plants is generally not associated with haustorium initiation but rather with the ability of haustoria to functionally establish after invading the host (Nickrent et al. 1979; Hood et al. 1998; Li and Timko 2009). One known exception is the extensive variability among wild sorghum accessions in haustorium-inducing activity (Rich et al. 2004; see Sect. 21.2.1). Some sorghum lines with low levels of xenognosin activity also did not stimulate *Striga* seed germination, suggesting either that the biosynthesis of xenognosin and germination stimulants are co-regulated in sorghum or that they are inhibited by the same host factors.

The most striking examples of plants that do not induce haustoria in Orobanchaceae roots are those from closely related parasites. Self-parasitism or auto parasitism is frequently observed in mistletoes, *Cassytha* and *Cuscuta* (Sect. 1.5; Heide-Jørgensen 2008), but more rarely in Orobanchaceae (Riopel 1983, but see Sects. 3.4.2 and 3.5). In *Triphysaria* self-recognition is observed at the species level, and haustoria develop less frequently in associations between two *Triphysaria versicolor* plants than between *T. versicolor* and *Triphysaria eriantha* and much less frequently that between *T. versicolor* and *Arabidopsis* (Yoder 1997). The ability of parasites to distinguish self from non-self must have evolved soon after the origin of invasive haustoria because a plant would receive little benefit by parasitizing its own roots or those of a sibling. While the rationale for self-recognition seems obvious, the responsible mechanisms are unknown. Generalist parasites parasitize a broad range of host plants and so xenognosin signals are likely conserved among different plants. However these same signalling molecules are somehow missing, ignored, inhibited or not activated when two parasite roots come in contact. Identifying the molecular basis of this vegetative self-recognition system may suggest novel approaches for engineering resistance against parasitic weeds.

4.4 Haustorium Signal Transduction

Significant insights into the mechanism of xenognosin recognition came from the correlations between the redox potential of quinones and their haustorial inducing activity (Smith et al. 1996). The redox potential of quinones that induced *Striga* haustoria falls within a narrow redox window while inactive molecules fall outside that window. This suggests the propensity of a molecule to be oxidized or reduced is an important characteristic of xenognosins. The involvement of radical molecules in haustorium signalling was substantiated by two chemical spin traps, cyclopropyl-*p*-benzoquinone and tetrafluoro-benzoquinone, both of which inhibit haustorium formation when reduced to their semiquinone states (Fig. 4.2c) (Zeng et al. 1996; Smith et al. 1996). These experiments led to a redox model for xenognosin signalling in which semiquinone intermediates formed during transitions between quinone and phenolic states activate a redox-sensitive signal transduction pathway (Fig. 4.2d) (Keyes et al. 2001).

Redox cycling is catalysed by quinone oxidoreductases (E.C.1.6.5) that reduce quinones by either one- or two-electron transfer mechanisms (Testa 1995). Single-electron reductions generate highly reactive radical semiquinones that in the presence of oxygen form reactive oxygen species (ROS) that can be cytotoxic. Two-electron reductions do not generate reactive intermediates, and the enzymes that catalyse these reactions are considered detoxification enzymes that defend cells against electrophilic quinones (Ross et al. 2004).

Genes encoding each type of quinone oxidoreductase were isolated on the basis of their being transcriptionally regulated in *Triphysaria* roots by xenognosins (Matvienko et al. 2001b). Based on sequence comparisons and biochemical assays of protein activity, the gene *TvQR1* encodes a zeta-crystallin-like, NADPH-dependent quinone oxidoreductase (ZcQR) (EC 1.6.5.5) that catalyses single-electron quinone reductions (Bandaranayake et al. 2010) (Rao et al. 1992; Mano et al. 2000). *TvQR2* encodes a flavin binding quinone oxidoreductase (EC 1.6.5.2) that reduces quinones via the simultaneous transfer of two electrons that circumvents semiquinone intermediates (Sparla et al. 1996; Wrobel et al. 2002). While both *TvQR1* and *TvQR2* are transcriptionally up-regulated in parasite roots in response to xenognosins, only *TvQR1* is up-regulated by contact with a host root (Matvienko et al. 2001b; Bandaranayake et al. 2010). *TvQR1* regulation is also strongly correlated with haustorium development in *Triphysaria* species that form haustoria at different rates (Jamison and Yoder 2001). *Triphysaria* roots were transformed with inhibitory RNAi constructions targeting *TvQR1* or *TvQR2* for gene silencing, and roots silenced for *TvQR1* formed less haustoria than control transformants while those silenced for *TvQR2* formed haustoria at control levels (Bandaranayake et al. 2010). This work identified TvQR1 as one of the first parasite genes on the haustorium signalling pathway. Because TvQR1 generates the semiquinones that induce haustoria while TvQR2 encodes a detoxifying enzyme that eliminates them, the relative activities of these enzymes in parasite roots likely play a significant role in the parasite's commitment to haustorium development (Fig. 4.3).

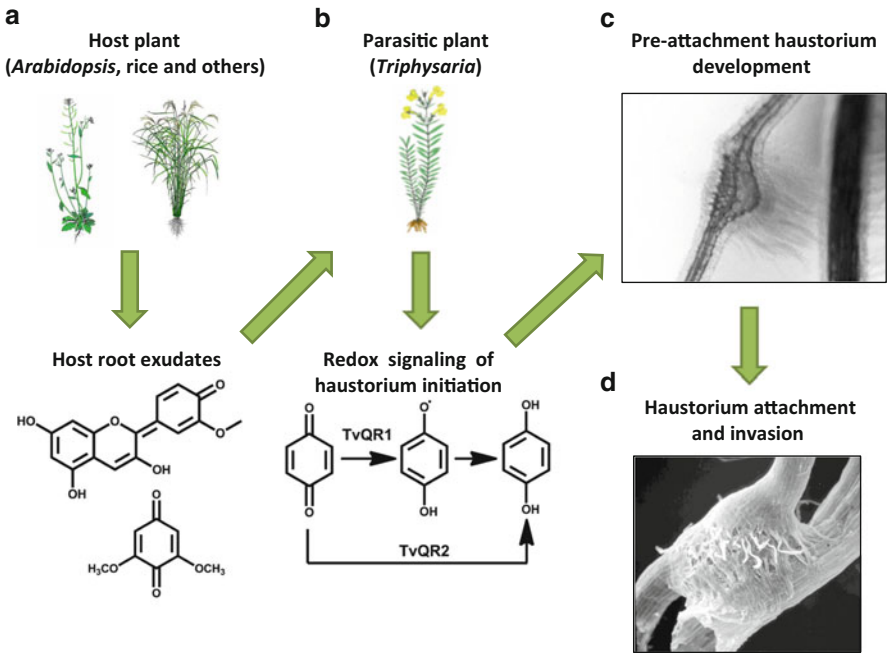

Fig. 4.3 Summary of lateral haustorium development. (**a**) Exudates released by plant roots contain molecules that induce haustorium development in parasite roots. The flavonoid peonidin and DMBQ are shown as potential haustorial inducers, though their significance as natural inducers in undisturbed root exudates is not known. (**b**) The enzyme TvQR1 catalyses the single-electron reduction of xenognosins producing the radical semiquinones that initiate haustorium signal transduction (Bandaranayake et al. 2010). (**c**) The cortical swelling and development of haustorial hairs in *Triphysaria* is a chemotropic response to xenognosins released from the lupine host root on the *right*. (**d**) Haustorial hairs attach the parasite root to the host root on the *right* (**c** and **d** from Yoder 1999, with permission from Elsevier)

Redox signal transduction pathways are common in both plant and animal systems (Ahmad et al. 2008; Foyer and Noctor 2009). Higher plants can sense, transduce and translate redox signals into appropriate cellular responses, influencing the expression of a number of genes and signal transduction pathways. For example, *NPR1*, a master regulator of defence gene expression in plants, contains cysteine residues that are targets of oxidoreduction reactions that cause conformational changes to the protein (Mou et al. 2003). Under normal conditions intermolecular disulfide bonds form structures that are sequestered to the cytoplasm. These disulfide bonds are broken under reduced conditions, and a monomerized NPR1 protein is translocated to the nucleus where it regulates a set of disease resistance genes. A similar system may act to transduce xenognosin signals from the semiquinones to the nucleus.

The generation of ROS may also be directly involved in eliciting the morphological changes associated with haustorium development. ROS have been detected

using electron paramagnetic resonance in rapidly growing cells of maize roots, cucumber and *Arabidopsis* seedlings and are involved in cell wall loosening reactions associated with root growth (Liszkay et al. 2004). ROS molecules also control root hair elongation by activating plasma membrane calcium ion channels that generate a calcium gradient needed for tip growth (Foreman et al. 2003; Carol and Dolan 2006). ROS accumulation catalysed by TvQR1 may be directly responsible for the cortical cell expansion and haustorial hair elongation that are characteristic of early haustorium development.

The transcription factor-associated protein TvPirin is also necessary for effective haustorium development. *TvPirin* transcription is rapidly up-regulated in *Triphysaria* roots exposed to host root factors, and haustorium development is reduced when *TvPirin* transcripts are silenced by inhibitory RNAi (Matvienko et al. 2001a; Bandaranayake et al. 2012). The steady-state levels of several xenognosin-regulated transcripts were reduced in *Triphysaria* roots silenced for *TvPirin*, but their regulation by xenognosin exposure was not affected (Bandaranayake et al. 2012). This is consistent with *TvPirin* encoding a generalized transcription factor associated with the expression of several genes, some of which may be involved in haustorium development and others not.

While critical, chemical xenognosins are not the only stimuli that induce haustoria. Haustoria can form on inanimate surfaces such as rocks or Petri dishes, suggesting that tactile stimuli facilitate haustorium development (Kuijt 1969; Atsatt et al. 1978; Riopel and Timko 1995). Physical stimuli appear to play a larger role in the development of lateral haustoria than terminal because *Striga* seedlings develop terminal haustoria in liquid culture (Riopel and Baird 1987), but *Striga* and *Triphysaria* roots need contact with a solid support for effective lateral haustorium development (Wolf and Timko 1991; Matvienko et al. 2001a).

4.5 Evolutionary Origins

The competence to develop haustoria has originated at least 11 times during angiosperm evolution (Westwood et al. 2010; see Chaps. 1 and 14). There are two general hypotheses for the evolutionary origin of genes encoding parasitic plant functions: (1) parasitic genes were introduced into an autotrophic progenitor by horizontal gene transfer, or (2) parasite genes originated through neofunctionalization of plant genes encoding non-parasitic functions (see also Chap. 15).

Based on the morphological similarity of haustoria to nodules and crown galls, Atsatt proposed that haustoria evolved from endophytic microorganisms colonizing the plant roots (Atsatt 1973). A similar hypothesis was suggested by Kuijt (1969) who proposed that haustoria arose from mycorrhizal fungi that bridged the roots of different plants. Horizontal gene transfer between microbes and plants is well established, the most notable being the transfer of T DNA from bacteria to plants as a consequence of *Agrobacterium* infection (Nester et al. 2005). The phylogenetic placement of the *Rafflesia* mitochondrial gene *nad1B-C* into a clade associated with

its host *Tetrastigma* suggests a horizontal gene transfer event over an evolutionary timescale (Davis and Wurdack 2004). Similarly, multiple *Plantago* species contain an *atp1* pseudogene that is phylogenetically related to the *atp1* homolog in *Cuscuta*, a parasite that infects *Plantago* (Mower et al. 2004). More recently, EST analysis provides evidence for the movement of a sorghum nuclear gene into the genome of *S. hermonthica* (Yoshida et al. 2010). Therefore the horizontal transfer of genes between plants and other organisms is well documented.

The alternative hypothesis is that parasite-specific functions are encoded by genes present in autotrophic plants where they perform functions unrelated to parasitism. Novel functions can arise in genes that have amplified following the duplication of genes or genomes or by ectopic expression of genes that have modified promoters (Hegarty and Hiscock 2008; Flagel and Wendel 2009). For example, many of the genes associated with floral development have homologues in non-flowering plants, indicating that these fulfil different functions in flowering and non-flowering plants (Floyd and Bowman 2007). Another example is DM13, a calmodulin-dependent protein kinase required for nodulation in legumes exposed to *Rhizobia* (Geurts et al. 2005). Because *DM13* homologues are also detected in rice and tobacco, DM13 clearly fulfils different functions in leguminous and non-leguminous plants (Mitra et al. 2004).

While there are precedents for both models, current evidence best supports the endogenous model for the origin of haustorial genes. EST databases of parasite transcripts expressed in roots during haustorium development do not contain sequences of obvious microbial origin (Torres et al. 2005). Additionally, genes that have been identified as functioning in haustorium development also function in autotrophic plants. For example, there are homologous genes to both *TvQR1* and *TvPirin* in non-parasitic plants, and the catalytic activities of the ZcQR1 enzymes are similar in *Triphysaria* and *Arabidopsis*. However, the expression profiles of these genes are different in parasitic and non-parasitic plants. It is possible that promoter mutations in the homologues of these genes in progenitors of parasitic plants altered the expression of these genes so that they were induced in parasite roots after contact with a host, thereby providing on demand of some of the components of a redox-sensitive signalling pathway. This model suggests that the evolutionary origin of plant parasitism is associated with changes in the regulation of plant genes that typically fulfil non parasitic functions (for further discussion of parasite genome evolution, see Chap. 15).

4.6 Conclusions

Phenols and quinones are common in the rhizosphere where they are known to function as signal molecules acting between plant roots and other organisms, including roots of other plants. The biological activity of these molecules is often associated with their redox state, and in some cases bioactivity is a function of the oxidoreduction cycle itself (O'Brien 1991; Appel 1993). Plants and other organisms

have evolved detoxification systems that limit the cytotoxicity of radical molecules generated during redox cycling, and these mechanisms function in parasitic plants as well. However, parasitic plants have further evolved to use the redox-active molecules as signals to initiate haustorium development. In this way parasitic plants recruit biologically active and generally toxic molecules to signal the transition to a heterotrophic lifestyle.

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