1 The Interaction Between a Plant and Its Attacker

1.1 INTRODUCTION

Plants are the only higher organisms on the planet capable of converting energy from the Sun into chemical forms of energy that can be stored or used (Agrios, 2005). Not surprisingly therefore, plants are a source of food for a great many organisms. Indeed, directly or indirectly, plants are a source of nourishment for all humans and animals. Although plants have evolved a bewildering array of defences with which to ward off attack (Walters, 2011), many plants succumb to attack and suffer damage and disease as a result. This, in turn, can affect the growth and reproductive output of the plant, which can exert a significant effect on competitive ability and survival. In terms of crop production, damage and disease can affect the yield and quality of produce, with economic consequences to the farmer or grower. In this book, we examine the mechanisms responsible for the changes in plant growth, development and yield following attack by various organisms. Such knowledge is important because it can be useful in our attempts to protect crops from attack, as well as helping them to cope with the consequences of attack.

Plants that are attacked are likely to show visible signs of the encounter and the resulting after effects. Symptoms can be useful, not only in identifying an affected plant, but also in hinting at the cause of the problem and even the nature of the attacker. We look at symptoms in some detail later in this chapter, but let us turn our attention first to the attackers, because the nature of the attacker and the way it obtains food from the plant can exert a profound influence on the way the plant responds and the symptoms we observe.

1.2 DIFFERENT TYPES OF ATTACKER

The range of organisms that use plants as a source of food includes microorganisms, nematodes, insects, vertebrates and other plants. The major microorganisms attacking plants are fungi, bacteria and viruses, some of which can have devastating effects on plants. Herbivory by insects, invertebrates and vertebrates can also lead to considerable damage and plant death,
while plants are not safe even from other plants, as some have evolved the parasitic habit, with serious economic consequences.

1.2.1 Microorganisms

Microorganisms can obtain food from plants by a number of routes. Some live on dead material, decomposing plant tissues and releasing nutrients that would otherwise remain unavailable to other organisms. These microbes are known as saprotrophs, and they subsist entirely on organic debris. Other microbes have developed the ability to infect plants, living as parasites, taking nourishment from the living plant but giving nothing back in return. If such parasitic microbes, as a result of their association with the host plant, also lead to disruptions in normal functioning of the plant, they are defined as pathogens, and the plant is said to be diseased.

Some pathogens infect a living plant, but then kill all or part of their host rapidly, and survive on the dead plant tissues. These are known as necrotrophs, while those pathogens that infect the plant and then coexist with it for an extended period, causing little damage, are known as biotrophs. Although it might appear that biotrophy and necrotrophy represent absolute categories, they are actually at opposite ends of a continuum (Walters et al., 2008; Newton et al., 2010). At one end of the continuum are pathogens that require living host cells to survive, such as viruses and biotrophic fungi, for example powdery mildews and rusts, while at the other end are the necrotrophic pathogens such as damping-off fungi and soft rot bacteria. As one moves from one end of this continuum to the other, one encounters pathogens with intermediate characteristics. Some of these pathogens possess an initial biotrophic phase in their life cycle, during which they cause little, if any, damage to plant cells and tissues, but then move into a necrotrophic phase, where plant cells and tissues are killed. These pathogens have been termed hemibiotrophs and include the late blight pathogen *Phytophthora infestans* and the pathogenic bacterium *Pseudomonas syringae*. The triggers responsible for the transition between the biotrophic and necrotrophic phases in these pathogens are not known (Newton et al., 2010).

1.2.1.1 Fungi

The vegetative phase of fungi may be quite limited, occurring, for example, as single cells (yeasts) or may be more extensive. For most plant pathogenic fungi, vegetative growth is as filamentous hyphae, which grow by extension at the tips. These hyphae can form a network known as a mycelium, while the interconnected network of hyphae derived from one fungal propagule is known as a colony. The lifespan of the colony and its functional relationship with the growing hyphal tips vary depending on the fungus. Thus, in pathogenic fungi belonging to the genus *Pythium*, as hyphal tips grow and extend, the older parts of the colony die. In these fungi, sporulation occurs at the advancing edge of the colony. Although the hyphal lifespan in fungi such as *Pythium* is short, in other fungi, hyphae live for considerably longer. Good examples are the runner hyphae produced by the take-all fungus *Gaeumannomyces graminis* and rhizomorphs produced by the tree pathogen *Armillaria mellea*. These hyphae grow on plant surfaces or away from the host plant, exposing them to harsh environments. As a result, they possess thick, dark-coloured walls, enabling them to withstand desiccation and the vagaries of the aerial or soil environments. Indeed, the rhizomorphs produced by *A. mellea* are large, elaborate structures, with thick, pigmented walls. Runner hyphae and rhizomorphs allow the fungus to grow from one host plant to another, with nutrients transported from the
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older, established parts of the colony, to the expeditionary hyphae seeking new sources of 
nourishment. In contrast, colonies in biotrophic fungal pathogens such as rusts and powdery 
mildews remain functional for long periods, with nutrients transported from hyphae at the 
outer edges of the colony to the colony centre. In this case, the older, central portion of the 
colony remains functional and is associated with important developmental processes such as 
sporulation.

1.2.1.2 Bacteria

Although bacteria are important as pathogens of animals, including man, relatively few are 
known to be plant pathogens. Bacteria are prokaryotic. In other words, they possess no nuclear 
membrane or mitotic apparatus, and additionally, mitochondria and a visible endoplasmic 
reticulum are lacking. Most bacteria are unicellular, although some occur in groups or chains 
of cells. Bacterial cells are small (5–10 μm), and some are rod shaped (bacilli) or spherical 
(cocci), while others have unusual shapes. All plant pathogenic bacteria are rod shaped, and 
many possess flagella, making them motile and capable of moving along nutrient gradients.

Within the plant, bacterial cells can spread throughout an organ, as is the case with soft 
rot bacteria in potato tubers, or can spread widely in the plant, as with vascular wilt bacteria, 
which can be spread throughout the plant in the xylem.

1.2.1.3 Viruses

Most plant viruses consist of a single strand of RNA surrounded by a protein sheath (the 
capsid), although a few consist of double-stranded RNA or of DNA. In fact, five classes of plant 
virus have been described on the basis of whether the nucleic acid is RNA or DNA, whether it 
is single or double stranded and whether the strand is of the same (+) or opposite (−) polarity to 
messenger RNA (Table 1.1). Most plant viruses described to date belong to Class IV, consisting 
of single-stranded RNA. Inside the plant cell, once this single strand of RNA is freed from its 
protein coat, it can act as messenger RNA in the synthesis of new virus particles. Examples 
of plant viruses belonging to Class IV include tobacco mosaic virus (TMV) and cucumber 
mosaic virus (CMV). Viral parasitism is unique, because viruses act as ‘molecular pirates’, 
hijacking the synthetic machinery of the plant to make more virus particles (Lucas, 1998).

Class VII in Table 1.1 contains viroids. These differ from viruses in the size of their RNA 
genome and the fact that they lack a protein coat. A viroid consists of a single stranded but 
covalently closed RNA molecule, ranging in size from 246 to 401 nucleotides. They do not 
encode any pathogen-specific peptides, and they replicate autonomously. Viroids can be clas-
sified into two major families, the Pospiviroidae (e.g. the potato spindle tuber viroid RNA) and 
the Avsunviroidae (e.g. avocado sunblotch viroid) (Tabler & Tsagris, 2004).

1.2.1.4 Phytoplasmas

Phytoplasmas are wall-less bacteria that inhabit the phloem and are known to cause disease 
in more than a thousand plant species. They are transmitted by phloem-feeding insects, 
mainly leafhoppers, planthoppers and psyllids. In 2004, phytoplasmas, known previously 
as mycoplasma-like organisms, were assigned to the novel provisional genus Candidatus 
Phytoplasma (Firrao et al., 2005). They represent a monophyletic group within the class
Table 1.1  The Baltimore system for virus classification, based on the type of nucleic acid present (RNA or DNA), whether it is double (ds) or single stranded (ss) and whether the strand is of the same (+) or opposite (−) polarity to messenger RNA.

<table>
<thead>
<tr>
<th>Genome</th>
<th>Examples of plant viruses</th>
</tr>
</thead>
<tbody>
<tr>
<td>Class I ds(±)DNA</td>
<td>Cauliflower mosaic virus (CaMV)</td>
</tr>
<tr>
<td>Class II ss(±)DNA</td>
<td>Gemini viruses, e.g. African cassava mosaic virus (ACMV)</td>
</tr>
<tr>
<td>Class III ds(±)RNA</td>
<td>Wound tumour virus (WTV)</td>
</tr>
<tr>
<td>Class IV ss(±)RNA</td>
<td>Tobacco mosaic virus (TMV)</td>
</tr>
<tr>
<td>Class V ss(−)RNA</td>
<td>Rhabdoviruses, e.g. lettuce necrotic yellows virus (LNYV)</td>
</tr>
<tr>
<td>Class VI ss(±)RNA transcribed</td>
<td>No plant-infecting examples known</td>
</tr>
<tr>
<td>Class VII ssRNA does not</td>
<td>Viroids, e.g. potato spindle tuber viroid</td>
</tr>
<tr>
<td>contain structural genes and has no protein coat</td>
<td></td>
</tr>
</tbody>
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Mollicutes (trivial name, mycoplasmas) and are thought to have evolved from gram-positive bacteria (Maniloff, 2002). In contrast to most mycoplasmas, phytoplasmas cannot be grown in culture and, as a consequence, are poorly characterised on a physiological and biochemical basis. Diseases caused by phytoplasmas include chrysanthemum yellows, clover phyllody, soybean phyllody, elm witches’ broom and pear decline.

1.2.1.5 The host–pathogen interface

The site of contact between the host cell and the pathogen is known as the host–pathogen interface, and five types of interface can be distinguished (Table 1.2). Pathogens that grow intercellularly have no intimate contact with living host cells but rather grow between cell walls and in the spaces between cells. This apoplastic space contains various soluble nutrients, such as sugars and amino acids, which can be taken up by pathogens. Some intercellular pathogens are necrotrophic, secreting hydrolytic enzymes or toxins, which kill host cells in advance of invasion, making any interface between host and pathogen short-lived. A rather different and in many cases, longer-lasting interface, is observed with intracellular pathogens. In the interaction between the club root pathogen *Plasmodiophora brassicae* and a brassica host, the interface consists of the membrane of the pathogen cell or plasmodium, surrounded by another membrane that is assumed to be of host origin. Another pathogen attacking roots of brassicas, *Olpidium brassicae*, has an even more intimate interface with the host cell. In this case, the fungal cell is in direct contact with the cytoplasm of the host, as it is not surrounded by a host-derived membrane. The ultimate in terms of an intracellular interface must surely lie with viruses and viroids, because during virus replication, the host–pathogen interface is between a nucleic acid molecule and the nucleic acid synthetic machinery of the host cell.

Many biotrophic and hemibiotrophic fungal pathogens have a long-lasting intracellular relationship where host cells remain viable for a prolonged period. In many cases, the host–pathogen interface involves the formation of specialised structures known as haustoria, which represent the hallmark of obligate biotrophs such as powdery mildews, rusts and
Table 1.2  Modes of pathogen growth within host tissues and host–pathogen interfaces.

<table>
<thead>
<tr>
<th>Type</th>
<th>Pathogen</th>
<th>Host</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subcuticular</td>
<td>Rhynchosporium</td>
<td>Barley</td>
</tr>
<tr>
<td></td>
<td>Venturia</td>
<td>Apple</td>
</tr>
<tr>
<td>Intercellular</td>
<td>Cladosporium fulvum</td>
<td>Tomato</td>
</tr>
<tr>
<td></td>
<td>Sclerotinia</td>
<td>Bean</td>
</tr>
<tr>
<td></td>
<td>Monilinia</td>
<td>Pear</td>
</tr>
<tr>
<td></td>
<td>Most bacteria</td>
<td>Various</td>
</tr>
<tr>
<td>Vascular</td>
<td>Fusarium</td>
<td>Various</td>
</tr>
<tr>
<td></td>
<td>Verticillium</td>
<td>Various</td>
</tr>
<tr>
<td></td>
<td>Ophiostoma</td>
<td>Elm</td>
</tr>
<tr>
<td></td>
<td>Some bacteria, phytotplasmas</td>
<td></td>
</tr>
<tr>
<td>Haustorial</td>
<td>Powdery mildews</td>
<td>Various</td>
</tr>
<tr>
<td>Epiphytic with haustoria</td>
<td>Hyaloperonospora parasitica</td>
<td></td>
</tr>
<tr>
<td>Intercellular with haustoria</td>
<td>Bremia</td>
<td>Lettuce</td>
</tr>
<tr>
<td>Intracellular vesicle, with intercellular hyphae and haustoria</td>
<td>Phytophthora</td>
<td>Potato</td>
</tr>
<tr>
<td>Intracellular</td>
<td>Colletotrichum</td>
<td>Bean</td>
</tr>
<tr>
<td></td>
<td>Pyrenophora</td>
<td>Wheat</td>
</tr>
<tr>
<td></td>
<td>Plasmidiospha</td>
<td>Crucifera</td>
</tr>
<tr>
<td></td>
<td>Polymyxa</td>
<td>Cereals, beet</td>
</tr>
<tr>
<td></td>
<td>Viruses</td>
<td>Various</td>
</tr>
</tbody>
</table>


oomycetes. They develop as side branches from intercellular, intracellular and epicuticular hyphae and terminate inside the host cell (Fig. 1.1; Voegele & Mendgen, 2003; O’Connell & Panstruga, 2006). Some hemibiotrophs, such as species of Colletotrichum and Magnaporthe, and obligate biotrophs such as the monokaryotic rust Uromyces vignae, produce filamentous intracellular hyphae, which, rather than terminating in the first penetrated host cell, penetrate from cell to cell, thereby colonising a small number of host cells (e.g. Wharton et al., 2001). Once these haustoria and intracellular hyphae (IH) have breached the host cell wall, they develop inside the cell but never penetrate the host plasma membrane. With haustoria, this gives rise to an interface comprising the plasma membrane and cell wall of the biotrophic pathogen, a plant-derived interfacial membrane (known as the extrahaustorial membrane, EHM), and an interfacial matrix layer (the extrahaustorial matrix, EHMA) (Fig. 1.2). In most haustoria, a discrete, electron-dense ring is visible in the fungal cell wall in the neck region (Fig. 1.2). This neck band is not observed in haustoria formed by oomycete pathogens. Haustoria are diverse in morphology, ranging from small, club-shaped extensions, to larger, branched structures (Fig. 1.2).
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Fig. 1.1 Light micrographs illustrating the infection structures of some intracellular biotrophs. (a) Haustoria (H) developing from intercellular hyphae (*) of the obligately biotrophic oomycete *Hyaloperonospora parasitica* inside epidermal cells of *Brassica oleracea* (b) Haustoria (H) of the obligately biotrophic powdery mildew fungus *Blumeria graminis* f.sp. avenae developing inside epidermal cells of *Avena fatua*. Arrows indicate the EHM. (c) Intracellular hyphae (IH) of the hemibiotrophic crucifer anthracnose fungus *Colletotrichum higginsianum* have developed from a melanized appressorium (A) and penetrated into an epidermal cell of *Arabidopsis thaliana*. Bars, 10 μm. Image (a) was provided by Raffaella Carzaniga, Rothamsted Research, Hertfordshire, UK. Image (b) was provided by George Barron from the MycoAlbum CD-ROM, University of Guelph, Guelph, Ontario, Canada. Image (c) was provided by Richard O’Connell. O’Connell and Panstruga (2006). Reproduced with permission from John Wiley & Sons.
The much branched structure of haustoria provides a large surface area and, taken together with their location, frequently close to chloroplasts, suggests a role in nutrient uptake. Thus, ATPase, an enzyme involved in active solute transport, was detected in the host membrane and in the fungal plasma membrane inside the haustorium but not in the EHM. This suggested that host and fungal protoplasts import solutes actively, whereas the membrane enclosing the haustorium, with reduced control of solute transport, leaks nutrients into the extrahaustorial matrix, from where they could be taken up by the fungus. In this model, the neck band of impermeable material would prevent solutes diffusing along the haustorial wall in the neck region. Thus, the haustorial wall and the extrahaustorial matrix represent a sealed compartment, where any nutrients crossing the EHM could only enter the pathogen by active transport across the plasma membrane of the haustorium. Later work using molecular tools showed that a gene encoding a hexose transporter (HXT1) is highly expressed in haustoria of the rust *Uromyces fabae*. The gene is localised exclusively in the haustorial plasma membrane (HPM), where it is likely to mediate the uptake of the hexoses glucose and fructose from the extrahaustorial matrix (Fig. 1.3; Voegele *et al*., 2001). It would appear that the hexoses derive from the cleavage of sucrose by invertases, because an invertase (*Uf-INVI*) was found to be highly expressed in *U. fabae* haustoria, and moreover, the enzyme protein was secreted into
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Fig. 1.3  Localization of HXT1p in the periphery of fully developed haustoria and along the HPM.  
(a) Superimposed Nomarski differential interference contrast and fluorescence images depicting two 
haustoria. Labeling of HXT1p with S651p resulted only in fluorescence signals in the periphery of the distal 
parts of the haustorium (f, fluorescence); proximal parts and haustorial neck are not labeled. h, haustorium; 
hn, haustorial neck. (Bar, 5 mm.) (b) Electron micrograph depicting considerable gold labeling along the 
HPM only (small arrows), but no labeling over the h, the EHMA, the EHM, or the plant cytoplasm (c). (Bar, 
0.1 mm.). Voegele et al. (2001). Reproduced with permission from PNAS.

the extrahaustorial matrix. Additional glucose and fructose might also be generated at the 
host–pathogen interface by a host cell-wall-associated invertase (CWINV2) (Voegele et al., 
2006). Also highly expressed in U. fabae haustoria, as well as in intercellular hyphae, are three 
genes encoding amino acid transporters, suggesting that amino acids can be taken up not only 
by haustoria, but also by intercellular hyphae (Struck et al., 2002). Interestingly, the hexose 
transporter protein HXT1p and the amino acid transporter protein AAT2p were localised in the 
apices of intracellular hyphae formed during the monokaryotic phase of U. fabae. This finding 
suggests that intracellular hyphae function as feeding structures in this fungus. Perhaps, this 
should be surprising, as detailed studies on colonies of the rust Puccinia hordei on barley esti-

mated that haustoria accounted for less than 20% of colony surface area, while most contact 
between the host and the rust was between intercellular hyphae and host cell walls (Kneale & 
Farrar, 1985). The picture that has emerged, especially from studies on U. fabae, suggests that 
rust fungi might use two strategies for nutrient uptake from the host: uptake of amino acids 
via haustoria and intercellular hyphae and carbohydrate uptake by haustoria (Fig. 1.4; Voegele 
& Mendgen, 2003). It is not yet known whether intracellular hyphae in hemibiotrophic fungi 
play any role in nutrient uptake. See Box 1.1 for more on sugar uptake by fungal pathogens.

Irrespective of the physical nature of the host–pathogen interface, it is now clear that the 
early stages of the host–pathogen interaction are associated with a pathogen-induced repro-
gramming of host metabolism. This is crucial to the establishment of a nutritional relationship
with the host, and to pathogen development, and is dealt with in Chapter 9. In an attempt to uncover mechanisms associated with the ability of a powdery mildew to satisfy its demand for host nutrients while limiting host defences, Chandran et al. (2010) used laser microdissection of Arabidopsis cells at the powdery mildew infection site. They found evidence for induced host endoreduplication, a process that increases gene copy number and could enhance the metabolic capacity of host cells at the infection site. In support of this role, they found elevated expression of genes required to increase metabolic capacity (such as genes involved in transcription, translation and energy generation), as well as genes encoding, for example, nutrient transporters. This strategy of using localised endoreduplication to meet enhanced metabolic demands has also been found in plant–nematode interactions (see Section 1.2.2).

### 1.2.1.6 Colonisation of host tissues by pathogens

After infection, colonisation of the host plant can be restricted to the particular tissue or organ (localised) or can be extensive, with the pathogen spreading widely within the plant (systemic).

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**Fig. 1.4** Model for amino acid and hexose uptake and redistribution in rust fungi. Depicted is a schematic representation of a fungal spore, an intercellular hypha and an haustorium, an infected plant cell and the interphase, the extrahaustorial matrix. The neckband is indicated by two black rectangles. (a) invertase INV1p; (b) hexose transporter HXT1p; (c) amino acid transporters AAT1p and AAT2p; (d) major alcohol dehydrogenase MAD1p; Glc: D-glucose; Frc: D-fructose; Man: D-mannitol; Suc, sucrose; AA: amino acids. Solid arrows specify confirmed enzymatic conversions or transport processes; dotted arrows indicate postulated solute fluxes. Voegele and Mendgen (2003). Reproduced with permission of John Wiley & Sons.
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Some pathogens colonise specific plant tissues, such as vascular wilt pathogens, which grow in the host xylem, while less specialised necrotrophic pathogens can spread indiscriminately through plant organs. The way a pathogen colonises its host can influence the type of symptoms observed and the physiological effects on the plant. However, the extent to which the pathogen colonises the host and the eventual severity of disease are not always correlated. Thus, a pathogen localised to a particular tissue, such as the xylem, can disrupt water transport, with knock-on consequences for other physiological processes, thereby exerting profound effects on the plant. In contrast, some virus infections become systemic, although the host exhibits no symptoms.

Box 1.1 Stealing sweets: sugar uptake from the host by plant pathogenic fungi

In higher plants, the main long-distance and storage form of assimilated carbon is sucrose. Indeed, sucrose concentrations in the low millimolar range have been measured in the apoplast of several plants (Nadwodnik & Lohaus, 2008). However, transport proteins identified to date from plant pathogenic and symbiotic fungi are specific for monosaccharides (e.g. Voegele et al., 2001; Polidori et al., 2007). It has been suggested that host sucrose is hydrolysed extracellularly by plant and/or fungal cell wall invertases, yielding glucose and fructose for fungal uptake (Scholes et al., 1994; Tang et al., 1996). But herein lies a problem. It would appear that plants have evolved mechanisms to sense changes in apoplastic glucose concentrations and to respond by activating defence responses (e.g. Ehness et al., 1997; Kocal et al., 2008). In addition, accumulation of hexoses could lead to reductions in photosynthetic rates (Roitsch et al., 2003; Rolland et al., 2006), thereby reducing carbon availability to the pathogen. The evolution of feeding strategies based on sucrose uptake, avoiding the need to hydrolyse it to glucose and fructose, could therefore be highly beneficial to pathogenic fungi. Interestingly, such a strategy has been suggested for the biotrophic fungal pathogen, Ustilagomaydis. Thus, Wahl et al. (2010) identified and characterised a novel sucrose transporter (Srt1) from U. maydis, with an affinity for sucrose that was not only very high, but also greater than the sucrose affinity of equivalent plant transporters. The possession of Srt1 would enable U. maydis to compete efficiently and successfully for sucrose with host cells (Fig. 1A). Moreover, it would also out-compete the invertase (INV)-dependent plant monosaccharide transporter proteins (STP), because despite being high affinity transporters, the plant extracellular invertases, which supply them with hexoses, have a low affinity for sucrose. Wahl et al. (2010) also found that the srt1 gene was expressed exclusively during infection, and importantly, its deletion greatly reduced fungal virulence.

Soon after uptake by the fungus, the host sugars are converted into fungal sugars, including the polyol, mannitol. Indeed, mannitol concentrations have been shown to increase in leaves infected with biotrophs, hemibiotrophs and necrotrophs (Voegle et al., 2005; Dulermo et al., 2009; Parker et al., 2009). Since mannitol is membrane impermeable, conversion of host sugars to mannitol might maintain a gradient for continued uptake and sequestration of host sugars (Lewis & Smith, 1967).
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1.2.2 Nematodes

Several hundred species of nematodes are known to feed on living plants, causing a variety of plant diseases worldwide. Plant parasitic nematodes are small: most are less than 1 mm long, although some are up to 4 mm long, with a width of 15–35 μm. They are worm-like in appearance but possess smooth, unsegmented bodies, with no appendages. In some nematode species, the female nematodes become swollen at maturity, with pear-shaped or spheroid bodies. Although most parts of the plant can be attacked by at least one species of nematode, from an economic perspective, the most important nematodes are those that feed on roots. Most plant parasitic nematodes possess a hollow stylet or spear (Fig. 1.5), although some have a solid modified spear. The stylet is used to penetrate plant cells, enabling the nematode to withdraw nutrients. Ectoparasitic nematodes, such as *Xiphenema* and *Longidorus* species, do not enter the plant root but feed by inserting the stylet into epidermal or cortical cells. In contrast, endoparasitic nematodes feed and reproduce within the plant. Sedentary endoparasites, such as root-knot and cyst nematodes, induce an amazing transformation of host cells into metabolically active transfer cells. After hatching in the soil, second-stage juveniles (J2s) move towards and penetrate plant roots. Once in the root, a root-knot nematode, such as *Meloidogyne incognita*, will move through the root intercellularly until the zone of cell division is reached.
Fig. 1.5  Stylet of *Pratylenchus*, a plant-feeding lesion nematode. Soil and Water Conservation Society (SWCS) (2000). Reproduced with permission from Soil and Water Conservation Society.

In this case, the nematode injects secretions into a small number of cells, resulting in their redifferentiation into metabolically active ‘giant’ cells. Division of the surrounding cortical and pericycle cells results in localised swelling of the root and formation of the characteristic ‘root-knot’ (Fig. 1.6; Fuller et al., 2008). In contrast to root-knot nematodes, cyst nematodes move through the root intracellularly, before reaching the zone of elongation, where a cell at the periphery of the vascular system is selected to become the syncytium or feeding site. In the feeding sites of both root-knot and cyst nematodes, nuclei are enlarged and endoreduplication is associated with cell enlargement (Wildermuth, 2010; also see Section 1.2.1.5). It is thought that endoreduplication is a mechanism to support the enhanced metabolic demands associated with these plant–nematode interactions. Although the feeding sites of root-knot and cyst nematodes possess different structures, both act as nutrient sinks and transfer cells, providing the nematode with the nourishment necessary for development to a mature, egg-laying female (Fuller et al., 2008).

1.2.3 Insects

Amazingly, it is estimated that more than 400,000 herbivorous insect species live on some 300,000 species of vascular plant (Schoonhoven et al., 2005). Among the different insect groups, herbivores are found in the Coleoptera (beetles, weevils, etc.), Lepidoptera (butterflies and moths), Hemiptera (aphids, leafhoppers, etc.), Orthoptera (grasshoppers and locusts) as well as in the Thysanoptera (thrips). There is a high degree of food specialisation among herbivorous insects, with some found on one or a few closely related plant species (monophagous), while others feed on a number of plant species (oligophagous), and yet
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Fig. 1.6 Arabidopsis root being parasitized by a female Meloidogyne incognita, a root-knot nematode. Specialized feeding cells, termed giant cells, are induced by the nematode and are located at its head; they are connected to the vascular cylinder. Note the swelling of the root cortex around the animal and feeding cells. Fuller et al. (2008). Reproduced with permission of John Wiley & Sons.

others that appear to exercise little choice of plant host (polyphagous). Monophagous insects include many lepidopterous larvae, hemipterans and coleopterans, oligophagous insects include the cabbage white butterfly (Pieris brassicae) and the Colorado potato beetle (Leptinotarsa decemlineata), while the green peach aphid (Myzus persicae) is a good example of a polyphagous insect, feeding on members of up to 50 plant families during the summer (Schoonhoven et al., 2005). However, because this classification is fairly arbitrary, it is probably more useful to distinguish between specialists (monophagous and oligophagous species) and generalists (polyphagous species).

Insects feed either by biting off and chewing plant material or by imbibing liquid from plant cells and tissues, and the two main functional groups of insect mouthparts, mandibulate and haustellate, reflect this. Mandibulate insects, which feed by biting and chewing, such as beetles and caterpillars, possess the more general type of mouthparts: (i) the labrum, a simple fused structure, often called the upper lip, and which moves longitudinally. This often contains taste sensilla, (ii) mandibles, paired structures that move at right angles to the body and which are used for biting, chewing and severing food, (iii) maxillae, paired structures that can move at right angles to the body and possess segmented palps. The maxillae help to manipulate food and guide it towards the mouth, (iv) the labium or lower lip, which is a fused structure that moves longitudinally and possesses a pair of segmented palps (Fig. 1.7). Insects that feed by imbibing liquid from the plant possess haustellate mouthparts, which can be further classified as piercing-sucking, siphoning and sponging. In piercing-sucking insects such as aphids, the mandibles and maxillae are modified to form a needle-like structure called a stylet (Fig. 1.8). This can be used to pierce the cuticle and cell wall and take up food. Some insects with haustellate mouthparts lack stylets. These insects are unable to pierce tissues and must rely on easily accessible food sources such as nectar at the base of a flower. These insects have siphoning
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mouthparts, a good example of which is the long proboscis of butterflies and moths (Fig. 1.9). Sponging mouthparts of insects such as house flies are used to sponge and suck up liquids.

Sucking insects can obtain food from several different sources in the plant. Thus, many insects belonging to the Heteroptera feed on parenchyma or xylem sap, while phloem sap is imbibed by many homopterans and psyllids. However, thrips feed on sap extracted from epidermal or parenchyma cells, using a feeding structure where several mouthparts are fused to form a mouth cone and through which the piercing organs are protruded (Schoonhoven et al., 2005).

It is clear from the previous two paragraphs that there is a great deal of specialisation with regard to the feeding sites insects occupy on their hosts, with mandibulate insects such as beetles, caterpillars and grasshoppers ingesting relatively large amounts of leaf material, while insects with haustellate mouthparts imbibe liquid nourishment from the plant. However, it would be wrong to think that all mandibulate insects munch indiscriminately on leaves. Thus, leaf miners live and feed during their larval stage between the upper and lower epidermis of
Fig. 1.8  Diagrams of the mouthparts of a Hemipteran insect. (1) upper lip or labrum (2) lower lip or labium (3) and (4) mandibles and maxillae, each having the form of bristles or stylets (5) compound eyes (6) small eyes or ocelli (7) base of the antenna. Courtesy of David Darling.

Fig. 1.9  Diagram of the siphoning mouthparts found in butterflies and some moths (Lepidoptera).

a leaf-blade, feeding on parenchymal tissues. As if this was not enough, different species of leaf miner excavate different layers of the leaf parenchyma. For example, of two hymenopterous leaf miners that attack birch leaves, *Fenusa pumila* feeds on the mesophyll, while larvae of *Messa nana* feed on palisade tissues (DeClerck & Shorthouse, 1985). In terms of root herbivory, some root-feeding insects live in the soil and eat small rootlets, others, including larvae
of cabbage root flies and carrot flies, bore directly into roots, while some aphid species pierce roots and take in liquid nourishment.

The way a plant responds to insect attack is determined, in part, by the feeding style of the attacker and by the presence of herbivore-derived elicitors in the insect’s oral secretions (OS) (Rodriguez-Saona et al., 2005; Felton & Tumlinson, 2008). OS from lepidopterous insects include regurgitant from the gut and saliva produced by the labial and mandibular salivary glands. These herbivore-derived elicitors, or herbivore-associated molecular patterns (HAMPs), include fatty acid conjugates such as volicitin, as well as inceptins, and can trigger biosynthesis of jasmonic acid and the release of volatile compounds (Felton & Tumlinson, 2008).

1.2.4 Parasitic plants

Parasitic plants are taxonomically and geographically diverse, comprising about 1% of the angiosperm flora (∼4000 species). Interestingly, parasitic gymnosperms are considerably rarer, with only one species, Parasitaxus ussuriensis, identified to date (Feild & Brodribb, 2005). Broadly speaking, parasitic plants can be split into two groups, facultative parasites and obligate parasites. The former parasites possess the ability to complete their life cycle independently of the host, although their growth and reproductive potential suffer, while obligate parasitic plants cannot complete their life cycle without the host plant (Irving & Cameron, 2009). Parasitic plants can also be classified according to their site of attachment to the host plant (root or shoot) and can be defined further according to whether they contain chlorophyll. Parasitic plants containing chlorophyll are said to be hemiparasitic, while those without chlorophyll are said to be holoparasitic. Thus, *Striga hermonthica* is a root parasite that contains chlorophyll and can photosynthesise, thereby enabling it to obtain some of its resources from the host plant. Moreover, because *S. hermonthica* is dependent on the host for the period before its shoot emerges from the soil, it is an obligate hemiparasite. However, *Orobanche* species do not possess chlorophyll and derive all their resources for growth from the host plant, making them obligate holoparasites. A good example of a facultative hemiparasite is *Rhinanthus minor*, which attaches to the roots of its host and can live independently of the host plant or as a parasite (Irving & Cameron, 2009).

Parasitic plants have evolved specialist mechanisms to allow them to obtain resources from their hosts. They attach to their host using a structure known as a haustorium, which acts as a physical and physiological bridge between the parasitic plant and its host. Depending on the species of parasitic plant, contact between parasite and host can involve (i) xylem vessels of parasite and host lying adjacent to one another, (ii) direct lumenal contact between the xylem of both partners, (iii) symplastic continuity between the phloem of host and parasite or (iv) movement of either xylem or phloem solutes via specialised transfer cells into the vascular system of the parasitic plant (Fig. 1.10; Hibberd & Jeschke, 2001). In the xylem-feeding *R. minor*, the mature haustorium surrounds the host root, forming a penetration peg that forces its way through the cortex and endodermis, before being driven into the stele, gaining access to the host’s vascular system (Fig. 1.11; Cameron & Seel, 2007). In the obligate parasitic plant dodder (*Cuscuta* species), the haustorium penetrates the host, producing hyphae or filaments that grow towards the host vascular system. Plasmodesmata are formed at the tip of these hyphae, creating a point of contact with the host parenchyma cells. Thereafter, parenchyma cells in the
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Fig. 1.10 Potential pathways via which parasitic plants could contact their hosts and access host solutes.

(a) Contact between xylem of host and parasite. The xylem of parasite 1 (ParX 1) contacts the xylem of its host (HX), but there are no direct lumenal connections. The xylem of the parasite 2 (ParX 2), however, forms lumenal links with the host xylem. No connections are made to the host xylem parenchyma (host XP).

(b) Transfer cells with fewer (ParX 3) or greater (ParX 4) degrees of cell membrane invagination of the parasite xylem parenchyma (ParXP) to facilitate solute flux, link parasite and host xylem. (c) The host sieve elements (HSE) of the phloem are lined by haustorial transfer cells (HauTC) of the parasite, which then allow unloading of host phloem solutes into the parasite haustorium. CC, companion cell; PAR, parenchyma.

(d) Interspecific plasmodesmata or even interspecific sieve plates (ISSP) appear at the interface of HSE and parasite phloem sieve elements (PSE). Hibberd and Jeschke (2001). Reproduced with permission of Oxford University Press.
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**Fig. 1.11** Schematic diagram showing the ontogeny of haustoria formed by *Rhinanthus minor* on the potential hosts *Cynosurus cristatus* (a–c); *Leucanthemum vulgare* (e–g); and *Plantago lanceolata* (i–k). Transverse sections of the mature host–parasite interface with the same potential hosts are also shown (d,h,l). PR, parasite root; PP, penetration peg; IH, immature haustorium; MH, mature haustorium; DSX, developing parasite secondary xylem; HB, hyaline body; SX, fully differentiated parasite secondary xylem; LR, lignified region; FC, fragmenting host cells; T/O, thickened/occluded host vasculature; TV, thickened host vasculature; OV, occluded host vasculature. Schematic diagrams and cross-sections of haustoria are shown on different scales; bars represent 110 μm in both cases. Cameron and Seel (2007). Reproduced with permission of John Wiley & Sons.
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Fig. 1.12  Parasite–host interaction of tomato (Solanum lycopersicum) and dodder (Cuscuta pentagona). (a) Dodder parasitizing a 7-week-old tomato plant, 4 week after attachment. Bar, 5 mm. (b) Haustorium formation on tomato petiole (arrow). Bar, 500 μm. (c) Scanning electron microscope (SEM) image of young haustoria (arrow) in dodder–tomato interaction. (d) SEM image of mature haustoria (arrow) detaching from tomato leaf demonstrating the interactions between the two organisms. (e) A cross-section of two adjacent haustoria establishing an internal connection (arrow) with the tomato host leaving a penetration fissure behind. Bar, 500 μm. David-Schwartz et al. (2008). Reproduced with permission of John Wiley & Sons.

Parasite haustorium differentiate into xylem and phloem elements, which then associate with the host vascular system. This results in the formation of phloem–phloem and xylem–xylem connections between the parasite and its host (Fig. 1.12; David-Schwartz et al., 2008). Such vascular connections were shown to be continuous and functional by following the transfer of various molecules from the host to the parasitic plant. For example, labelled amino acids and sugars were found to move from the host into Cuscuta, while green fluorescent protein was demonstrated to cross the host–dodder vascular junction (Tsivion, 1978; Haupt et al., 2001; Birschwilks et al., 2006).
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In *Cuscuta reflexa* and *Orobanche crenata*, both of which lack roots, all minerals must come from the host, and in both cases, most are derived via the phloem rather than the xylem. Because *Orobanche* lacks chlorophyll and therefore cannot photosynthesise, all of its carbon must also come from the host plant. Interestingly, although *Cuscuta* retains functional photosynthetic apparatus in a ring of cells around the stele, nearly all of its carbon also comes from the host (Jeschke *et al.*, 1994; Hibberd & Jeschke, 2001). Xylem feeders tend to be hemiparasites, using the xylem of the host plant to bolster their own resources. However, although they were thought to be largely self-sufficient for carbon, it is clear that hemiparasites such as *R. minor*, which can photosynthesise, also obtain carbon from their hosts. Indeed, the Australian hemiparasite *Olax phyllanthi* was found to abstract roughly 27% of recent photosynthate from its host (Tennakoon *et al.*, 1997). Facultative hemiparasites also obtain substantial quantities of nitrogen from their hosts, with *O. phyllanthi* taking 56% of newly fixed nitrogen from its leguminous host, *Acacia littorea* (Tennakoon *et al.*, 1997). As mentioned previously, the obligate hemiparasite *S. hermonthica* is entirely reliant on its host for the 4–6-week period when the young plant remains underground. Once *S. hermonthica* emerges from the soil and can photosynthesise, it becomes less reliant on the host for carbon. However, since its photosynthetic rates are very low, it still obtains up to 33% of its carbon from the host (Press *et al.*, 1987).

1.3 SYMPTOMS EXHIBITED BY PLANTS FOLLOWING ATTACK

As we have seen in the previous sections, different organisms have different approaches to attacking or entering a plant and obtaining the nourishment necessary for continued growth and development. The method of interaction with the plant is likely to affect its functioning, resulting in the appearance of symptoms. A symptom is a visible or measurable sign that the plant is not functioning normally. Sometimes, a symptom can be diagnostic for a specific disease, for example, but more often, a given symptom on a host might be due to one or more of a variety of causes.

The major symptoms exhibited by plants attacked by pathogens, pests, nematodes and parasitic plants are listed in Table 1.3. Associated with these symptoms are the functions likely to be affected, although, as pointed out by Lucas (1998), this means of classification is arbitrary and non-specific. He uses the example of permanent wilting, which could be the result of a blockage in the host xylem, destruction of root tissues or increased transpiration. Just how important a particular symptom is depends on a number of factors, including the stage of plant growth or development and the duration and severity of the symptom. This can be illustrated by two examples, chlorosis and necrosis. Chlorosis, or yellowing of leaves, is associated with impairment of photosynthesis (see Chapter 3). Although chlorosis in young cereal plants will reduce rates of photosynthesis, this is unlikely to exert much effect on grain yield, as most assimilates required for grain filling come from the flag leaf and ear tissues. Necrosis, or cell and tissue death, in the stem of a seedling, could completely disrupt transport of assimilates from leaves to roots and water and nutrients from roots to shoot, resulting in plant death. However, necrosis in the stem of a mature, woody perennial might result in the loss of a branch or twig, rather than the whole plant.
Table 1.3  Symptoms caused by pathogens, herbivores and parasitic plants in relation to function in higher plants.

<table>
<thead>
<tr>
<th>Vegetative organs</th>
<th>Reproductive organs</th>
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<td>Roots</td>
<td>Fertilization</td>
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<td>Support</td>
<td>Seeds</td>
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<td>Uptake</td>
<td>Development</td>
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<td>Transport</td>
<td>Flower, fruit</td>
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<td>Anchorage</td>
<td>Survival</td>
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<td>Necrosis</td>
<td>Seedlings</td>
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<td>Hypertrophy</td>
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<td>Hyperplasia</td>
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<td>Excessive</td>
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<td>branching</td>
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<td>Lodging</td>
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Pathogen/ Pest/parasitic plant examples

- Root rots
- Club root
- Rhizomania
- Root knot nematodes
- Heart rots
- Foot rots
- Cankers
- Crown gall
- Witch's broom
- Bakanae disease
- Cereals eyespot
- Mosaic
- Leaf spots
- Blight
- Leaf roll/curl
- Vascular wilts
- Leaf cast
- Coffee rust
- Cynipid wasp larvae
- Striga infection
- Choke
- Ergot
- Anther smut
- Seed decay
- Damping-off
- Storage rots


1.4 CONCLUSIONS

As we have seen in this chapter, plants are attacked by a great many organisms, which use a variety of approaches to obtain the nourishment locked away within their tissues. The physical damage caused can be minor or can be quite considerable. In addition, even if little physical damage is caused, physiological function can be impaired. The combined effects of physical damage and disruption of plant function can be serious, reducing plant growth and reproduction and, in some cases, leading to death of the whole plant. This can have far-reaching consequences for plants in both natural and managed systems, resulting in changes in plant populations and loss of crop yield and quality. These aspects are covered in the next chapter.

RECOMMENDED READING

22 Physiological Responses of Plants to Attack


REFERENCES

The Interaction Between a Plant and Its Attacker


