

M1 MYCORRHIZA

Key Notes

Types of mycorrhiza

Mycorrhizae occur in most land plants. There are three categories: endomycorrhizae, the commonest form, which penetrate the cortical cell walls in roots; ectomycorrhizae, characteristic of temperate trees, which form a sheath around the absorbing roots; and ectendomycorrhizae, consisting of several specialized types with both structures. A few plant groups have no mycorrhizae. The fungi mostly fruit underground except for some ectomycorrhizae.

Nature of the symbiosis

Normally the interaction has mutual benefit but it varies from the fungus being pathogenic to the plant being parasitic on the fungus. Usually, sugars from the plant are absorbed by the fungus and the fungus absorbs soil nutrients and transfers them to the plant. Numerous fungal species are involved and most are not species-specific. Mycorrhizae have extensive hyphal networks and ectomycorrhizae have hyphae that fuse with neighboring fungi.

Effects of the fungi on plants

Endomycorrhizae are highly efficient at absorbing nutrients from the soil, particularly nitrogen and phosphorus, and ectomycorrhizae are able to digest organic matter. Sugars from the plant are normally absorbed and fixed by the fungi, but in some interactions the plant absorbs sugars from the fungus and the interaction can differ in different species and change in the lifetime of one plant. They can inhibit other fungi, including decay fungi and plant pathogens.

Community interactions

These are not well understood but effects can be profound. Mycorrhizae may be unimportant in early succession but endomycorrhizae and, in some places, ectomycorrhizae, invade and there may be a succession of fungi. In a mature community one species of fungus may enhance the growth of one plant but inhibit another. A diverse plant community relies on a diverse fungus community. Ectomycorrhizal networks may prevent non-mycorrhizal species from invading. Successful conifer forestry needs mycorrhizae in the soil.

Related topics

- | | |
|--|--------------------------------------|
| Roots (C2) | Fungal pathogens and endophytes (M4) |
| Uptake of mineral nutrients by plants (I4) | Parasites and saprophytes (M6) |

Types of mycorrhiza

Mycorrhizae are the associations between the roots of plants and fungi. The great majority of plants have a mycorrhizal association and it is thought to have been vital in the initial colonization of land. Mycorrhizal associations are known in the rhizoids of bryophytes and the gametophytes of spore-bearing vascular plants as well as in the roots of all groups of vascular plants, except perhaps the horsetails. Their effects are profound on many aspects of plant life. Mycorrhizae

fall into three main categories with rather different properties, deriving from a diverse group of fungi. The basic structure of a fungus is the **hypha**. These are strands of cells a single cell thick, although sometimes without dividing cell walls, that grow through a medium. They secrete enzymes and absorb nutrients.

The most common form of mycorrhiza is the **endomycorrhiza**, otherwise known as **arbuscular** or vesicular-arbuscular mycorrhiza. In these the fungal hyphae penetrate through the cell walls of the root cortex, forming a mass of twisted hyphae apparently within the cells, known as arbuscules (Fig. 1). The hyphae do not actually penetrate the cell membrane but this invaginates many times, much increasing its surface area, around the hyphae. In some species, hyphae form oil-filled vesicles, perhaps as food stores, in invaginations in other cells. The fungus does not penetrate beyond the cortex of a root. Endomycorrhizae are found in most herbaceous plants, most tropical trees and some temperate woody plants and are the main mycorrhizae in most habitats. Nearly all endomycorrhizae produce subterranean fruiting bodies.

The second type is the **ectomycorrhiza**, in which the fungi form a dense mat of hyphae known as the **Hartig net** around the outside of the short absorbing roots and may surround cortical cells but do not penetrate the cortical cell walls at all (Fig. 2). This type is found in a small proportion of all flowering plant species but is characteristic of many of the dominant trees of temperate and boreal environments as well as some tropical trees, particularly those growing on nutrient-poor acidic soils. The third type, **ectendomycorrhiza**, is really several highly specialized types that, in structure, have characteristics of both the other types forming a mat around the root and penetrating the cortical cell walls. They are characteristic of certain families, notably the **orchids** (Orchidaceae) and the **heather** family group (Ericaceae and related families). Some species of fungi can form both ectomycorrhizae and endectomycorrhizae depending on the plant species infected. Most form fruiting bodies above the ground, including many familiar ‘toadstools’ of northern woods, but some are subterranean.

A few plant families and genera are rarely associated with mycorrhizae, including the cabbage family (Brassicaceae), the goosefoot family (Chenopodiaceae) and the temperate sedges (*Carex* spp.).

Nature of the symbiosis

The symbiotic relationship between plant and fungus varies from being one in which the fungus gains from the plant but is, in effect, a **pathogen**, through a range of **mutualistic** associations where both benefit to some extent, to one in

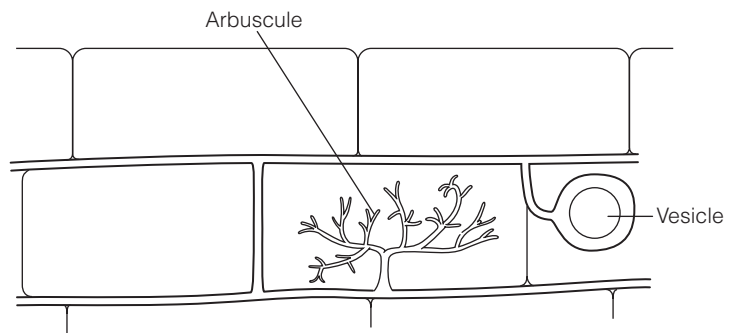


Fig. 1. Root cells infected with an endomycorrhiza showing an arbuscule and a vesicle.

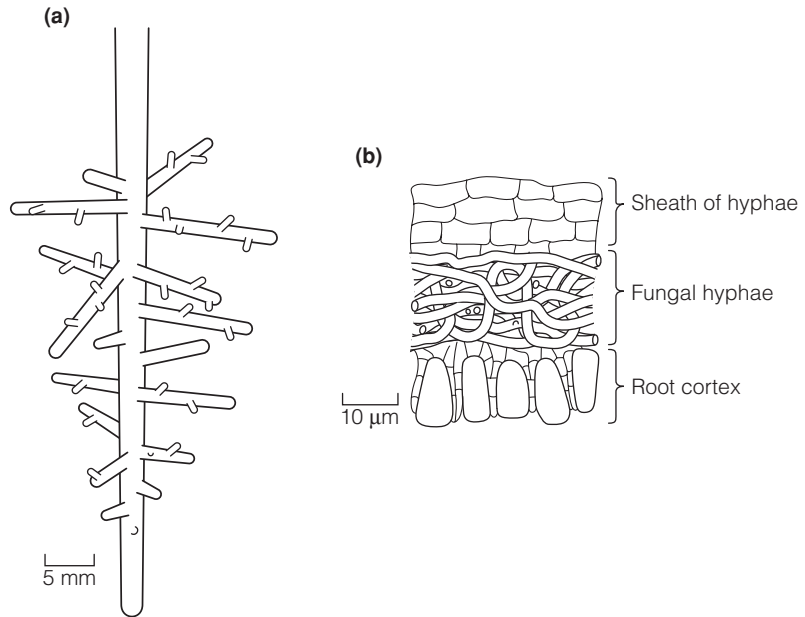


Fig. 2. Roots infected with ectomycorrhizae: (a) absorbing root showing branching and absence of root hairs; (b) dense net of fungal hyphae around root.

which the plant gains at the expense of the fungus. Mycorrhizae resemble pathogenic fungi in many ways and it can be difficult to distinguish the two since sites of **infection** can be the same. When working to mutual benefit, sugars generated by photosynthesis in the plant are transported to the roots and taken up by the fungi, and nutrients, most importantly nitrogen and phosphorus, are absorbed by the fungal hyphae in the soil and conducted to the plant. Many plants with endomycorrhizae can survive without them, particularly on nutrient-rich soils, but those with ecto- and ectendomycorrhizae are normally **obligately** associated at least at some stage in their life cycle.

Numerous species of fungi are involved and some are specific to particular species or genera of plants, whereas others infect many species; most plants can be infected by many species of fungi. The growth form of the fungi varies greatly, with some producing a mass of hyphae close to the roots, others spreading more widely and thinly. Endomycorrhizae grow out from a root to form an expanding fan and normally do not fuse with other neighboring fungi. Ectomycorrhizae start growing in a similar way but when they meet hyphae from other ectomycorrhizae these can fuse, or **anastomose**, and the mycorrhizae form a network of interconnecting hyphae in the soil.

Effects of the fungi on plants

The main effect of the fungi is absorbing nutrients from the soil. Roots infected with endomycorrhizae retain root hairs and are able to absorb nutrients, but ecto- and ectendomycorrhizal roots generally lose all their root hairs and rely solely on the fungus. Endomycorrhizal fungi have an extensive hyphal network in the soil making absorption more efficient than that by roots alone. Ecto- and ectendomycorrhizae have a similar hyphal network, but are also able to digest

organic matter making organic nitrogen and phosphorus, which is normally unavailable for plants, to be absorbed. This is particularly important in the nutrient-poor acidic soils in which these mycorrhizae are typical since it allows the mycorrhizal plants to absorb almost all the nutrients as they become available. In many soils nitrogen is a limiting plant nutrient and the fungal hyphae absorb nitrogen over a much larger soil area or with greater efficiency over a small area than roots, leading to enhanced growth of the plant. In some soils, particularly those on basic substrates, phosphorus is in short supply and the effect is similar. By contrast, some mycorrhizal associations can reduce a plant's growth where the soil is rich in nutrients.

Sugars from photosynthesis are conducted around the plant and the fungi absorb these as sources of energy. Once they are in the hyphae they are normally stored as complex sugars that cannot be reabsorbed by the host plant. Plants infected with mycorrhizae frequently have higher rates of photosynthesis than uninfected plants and these fungi transport more nitrogen and phosphorus into the plant. The relationship can change through the lifetime of a plant. Some seedlings (e.g. orchids) may absorb carbohydrate as well as nutrients from the fungus but as the plant matures, growth may be reduced by the fungus, so the relationship becomes parasitic first one way then the other. The 'saprophytic' plants (Topic M6) remain parasitic on their fungi throughout their lives. Different plant species respond differently to the interaction, with some fungi enhancing the growth of one species but inhibiting another. The interaction is further complicated (e.g. in legumes) by interaction with the nitrogen-fixing bacteria in root nodules.

Mycorrhizal fungi interact with other fungi in the soil, inhibiting free-living fungi involved in the decay of plant matter, so overall decay can be slower because of the mycorrhizae. They may protect the plant by preventing pathogenic fungi and bacteria from invading. The overall effect of these interactions is that the mycorrhizal plants will be at a competitive advantage over any others.

Community interactions

The effect of mycorrhizae in community ecology is not well understood and their importance has been seriously underestimated. In many habitats they are abundant and the fungi can be responsible for 25% of the respiration in the soil; over 30 m of hyphae have been recorded from 1 cm³. Difficulties in identification and isolating the fungi are serious impediments to study.

In early succession in a rich site and in agricultural soils, many plants have no mycorrhizae and it is in these habitats that the non-mycorrhizal Brassicaceae and Chenopodiaceae are most frequent. Many facultative endomycorrhizal plants colonize these areas and, as the community matures, more mycorrhizae invade. Endomycorrhizae invade first and may initially be rejected by the host plants and be in competition for nutrients, the interaction changing as the community matures. There may be a succession of fungi; some plants such as willows, *Salix* spp. and she-oaks, *Casuarina* spp., can be invaded by either endo- or ectomycorrhizae and, in succession, the endomycorrhizae invade first, followed by ectomycorrhizae. Interactions between mycorrhizal species are not well understood but it seems that during succession the fungus community normally becomes more diverse.

In a mature plant community mycorrhizae can have an enormous influence on plant diversity. From experiments in which artificial grassland communities were created with different numbers of mycorrhizal species, the community with the greatest diversity of fungus species had greater variability within the

ecosystem, with productivity differing in different parts and it supported the most diverse plant communities. Many plant species only survive in a community because of the fungi. Any one fungus species can enhance the growth of one plant species but inhibit another whereas a different fungus can have the reverse effect in the same community.

In communities dominated by ecto- or ectendomycorrhizal fungi, i.e. coniferous forests, heathlands, many temperate woodlands and some tropical and subtropical woodlands on acid soils, all the dominant plants may be connected underground via the network of anastomosing mycorrhiza and the plants may compete for the nutrients within this network. Any plant that is not connected with the mycorrhiza is likely to be unable to obtain nutrients over much of the habitat. Early attempts to plant new forest species, e.g. in Australia and the Caribbean, especially conifers, failed because of the lack of mycorrhiza which had to be imported from their native habitats before the plantations were successful.

M2 NITROGEN FIXATION

Key Notes

Nitrogen fixation	Nitrogen gas cannot be used directly by plants but is fixed to nitrogen-containing compounds by free-living or symbiotic bacteria and cyanobacteria. Nitrogen-fixing legumes form one of the world’s largest families, dominating many plant communities.	
The infection process	The legume root hair secretes a chemo-attractant which causes the bacteria to accumulate. They cause root-hair curvature and enter the root cortex by an infection thread. Cell division is stimulated to form a nodule with vascular connections to the plant.	
Molecular biology of nitrogen fixation	The complex interaction of host and bacterium requires the coordinated action of <i>NOD</i> genes in the host that encode nodulation and leghemoglobin, and <i>nod</i> , <i>nif</i> and <i>fix</i> genes in the bacterium that encode infection, host specificity and components of nitrogen-fixation.	
Biochemistry of nitrogen fixation	Nitrogen fixation requires 16 moles of ATP per mole of nitrogen and almost anaerobic conditions created by the oxygen binding protein leghemoglobin. The bacteria in the cytoplasm are surrounded by the peribacteroid membrane. Nitrogen-fixation is catalyzed by dinitrogenase in three stages: (i) reduction of the Fe-protein; (ii) reduction of the MoFe protein by the Fe protein (requires ATP); (iii) reduction of nitrogen by the MoFe protein. Nitrogen is exported in high-nitrogen containing compounds such as amino acids or ureides.	
Related topics	Movement of nutrient ions across membranes (I3)	Uptake of mineral nutrients by plants (I4)

Nitrogen fixation Nitrogen (N₂) is abundant in the aerial and soil environment, but unlike oxygen cannot be used directly (Topic I4). Nitrogen-fixation occurs in some free-living microorganisms (for instance some cyanobacteria, bacteria and archaeobacteria), but the most complex systems are seen in symbiotic association with some species of plants (Table 1). Nitrogen-fixing symbioses with the nitrogen-fixing bacteria *Rhizobium* and *Bradyrhizobium* are important in agricultural crops (peas, beans and other legumes, and clover in pasture land). In the Far East, the floating water fern *Azolla* that forms a nitrogen-fixing symbiosis with *Anabaena*, a cyanobacterium, is used to fertilize rice-paddy cultivation. Alder (*Alnus*) trees, sweet gale (*Myrica gale*) and mountain lilacs (*Ceanothus*) form nitrogen-fixing symbioses with actinomycetes (a different group of bacteria).

The legume–rhizobium symbiosis has been studied in most detail and will be considered here. Legumes (members of the family Fabaceae) are the most widespread and important plants with nitrogen-fixing root nodules and form one of the world’s most abundant plant families, including many trees, such as *Acacia*

Table 1. Organisms involved in nitrogen fixation

Host plant	Nitrogen-fixing organism
Alfalfa (<i>Medicago</i>)	<i>Bradyrhizobium meliloti</i>
Clover (<i>Trifolium</i>)	<i>Rhizobium leguminosarum</i>
Lentil (<i>Lens</i>)	
Pea (<i>Pisum</i>)	
Bean (<i>Viciai</i>)	
Bird’s foot trefoil (<i>Lotus</i>)	<i>Rhizobium loti</i>
Soybean (<i>Glycine</i>)	<i>Bradyrhizobium japonicum</i>
Alder (<i>Alnus</i>)	Actinomycetes
Sweet gale (Bog myrtle; <i>Myrica gale</i>)	Actinomycetes
Water fern (<i>Azolla</i>)	<i>Anabaena</i>

species. The ability of many legumes to fix atmospheric nitrogen has been one of the major factors in their success. Many plant communities, particularly those on soils that are poor in nitrogen, are dominated by legumes, and they can enhance the nitrogen status of the soil for other plants.

The infection process

The legume root hair secretes a chemo-attractant which cause the bacteria to accumulate (Fig. 1). The bacteria secrete lipochito-oligosaccharides (**NOD factors**, see below) that cause more root hairs to be formed and alter root metabolism. They cause root-hair curvature and the bacteria then attach to the hair by sugar-binding proteins called **lectins**. An **infection thread** is then formed, by which the bacteria pass through the root hair to the root cortex, where they proliferate. Cell division is stimulated to form a nodule within which nitrogen fixation occurs. The nodule has good vascular connections through which carbohydrates are supplied to the nodule and nitrogen-containing compounds are exported to the plant.

Molecular biology of nitrogen fixation

The complex interaction of host and bacterium requires the coordinated action of a number of key genes in both organisms. Table 2 lists these genes and their functions. The **NOD gene family** in the host encodes aspects of nodule formation and infection and the production of **leghemoglobin**, which binds oxygen,

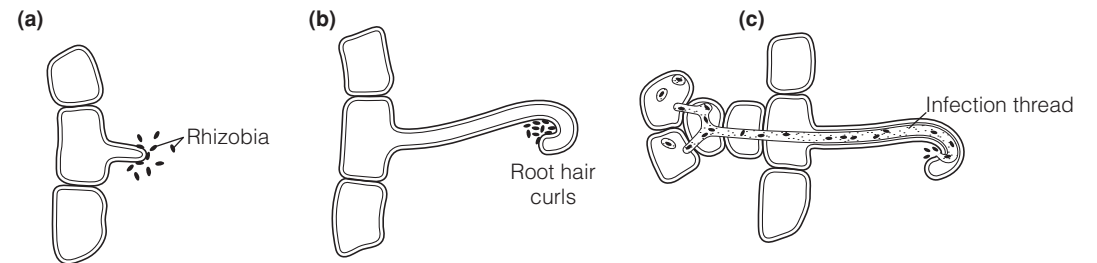


Fig. 1. The infection process. Bacteria are attracted to a root hair (a), bind to it and cause root hair curling (b) and form an infection thread through which they penetrate the cortical cells (c).

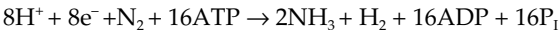
Table 2. Genes involved in nitrogen fixation

Host genes and function	Bacterial genes and function
<i>NOD</i> genes: encode components of the nitrogen-fixing process; activated in order: genes for the infection thread, then nodule growth, and finally leghemoglobin and enzymes involved in metabolizing fixed nitrogen	<i>nod</i> genes: induced by root exudates encodes enzymes producing chito-oligosaccharides involved in bacterial attachment. <i>Nod</i> genes (<i>A</i> , <i>B</i> , <i>C</i> and <i>D</i>) are located in the Sym (symbiosis) plasmid; <i>nodD</i> activates <i>nodA–C</i> and induces <i>nodE–H</i> which give host specificity to the bacterium <i>nif</i> genes: encode dinitrogenase components; also found in free-living nitrogen-fixers <i>fix</i> genes: encode ferredoxin and other components of the bacteroid

lowering the concentration of O₂ in the nodule. The ***nod* family** in the bacterium encodes enzymes that synthesize **NOD factors** (see above). One *nod* gene, *nodD* is activated by root exudates and produces a product that regulates the other *nod* genes. Later in infection, the *nif* and *fix* genes are active in the rhizobium. These produce the enzymes and electron transport pathway required for nitrogen-fixation.

Biochemistry of nitrogen fixation

Nitrogen fixation is a very energy demanding process, requiring at least 16 moles of adenosine triphosphate (ATP) for each mole of reduced nitrogen. It also requires almost **anaerobic conditions** as the key enzyme complex, **dinitrogenase**, is rapidly inactivated by oxygen. In the nitrogen-fixing nodule, the energy required is supplied by the plant, and low oxygen conditions by the oxygen binding protein **leghemoglobin**. The bacteria are contained in the cytoplasm of cells in the nodule as **bacteroids** surrounded by a double membrane, the **peribacteroid membrane**. The bacterium supplies the plant with reduced nitrogen compounds such as ammonium and amino acids. The plant benefits by increased growth and the bacterium from a food supply and enhanced environment in which to grow and replicate. The overall equation of nitrogen fixation is:



The process is catalyzed by the enzyme **dinitrogenase**, a protein complex made of two components: a large component, the **MoFe protein** and a smaller component, the **Fe protein**. Dinitrogenase functions in stages:

- (i) reduction of the Fe-protein (usually by the electron donor ferredoxin);
- (ii) reduction of the MoFe protein by the Fe protein (this step requires ATP);
- (iii) The MoFe protein then reduces nitrogen ($\text{N}_2 + 8\text{H}^+ \rightarrow 2\text{NH}_3 + \text{H}_2$).

After fixation, nitrogen is exported to the plant in the xylem flow, not in the form of ammonium, but as high-nitrogen containing compounds such as amino acids or ureides, depending on the species.

M3 INTERACTIONS BETWEEN PLANTS AND ANIMALS

Key Notes

The herbivores

Insects and mammals are important plant herbivores. Many insects are specific to one plant group. Some form galls. Mammals are not as specific, but certain plants are preferred or avoided, particularly by the smaller animals.

Insects and plants

Plant defenses against insects are mainly secondary compounds along with physical defenses such as a thick cuticle. Secondary compounds may be directly toxic, unpalatable or digestion inhibitors. When an insect evolves to be able to utilize one toxic plant group, it may spread and stimulate further evolution. Many plant families are associated with particular insect herbivores. There are more secondary compounds in tropical plants than temperate.

Vertebrates and plants

Vertebrates influence the entire plant community. Grasses have meristems at nodes and withstand grazing; many grasslands and savannahs are maintained by grazing mammals. Woodlands can be prevented from regenerating and some communities have cyclic patterns. Plants have physical defenses such as spines and stinging hairs as well as secondary compounds. A few plants provide nest sites for aggressive ants which deter animals.

Herbivores and plant populations

Many plant populations may be controlled in numbers by herbivores, mainly insects, and this is the basis of biological control. If a plant is introduced to an area without its herbivores it may spread to places in which it would not occur in its native region. Monocultures are susceptible to herbivores and in natural communities they stimulate plant diversity. Short-lived plants may live longer if their reproductive capacity is reduced in one season.

Related topics

Plant communities (K2)
Populations (K4)

Regeneration and establishment (L3)
Fungal pathogens and endophytes (M4)

The herbivores

Plants provide a wide range of food for animals, and ultimately, all animals rely on plants as the primary producers. A few interactions between animals and their food plants are of mutual benefit, such as the pollination of flowers and dispersal of fruits and seeds (Topics L1 and L2), but most plant-herbivore relationships involve the animal eating and damaging a part of the plant. This usually involves leaves and growing shoots but can involve almost any part of the plant. The most important herbivores of living plants are insects and mammals along with other vertebrates, and molluscs in places. Some invertebrates, including insects such as

bugs and grasshoppers eat a range of plants but many insects, particularly the larvae of moths and butterflies, some beetles and others, are specific to one family, genus or even species. They may be abundant on some plants and can defoliate or kill them. Some insects form galls on plants, stimulating the plant to grow unusual structures (Topic M4) which enclose the insect larva, e.g. 'oak apples' on the European oak, *Quercus robur*.

Vertebrate herbivores mostly eat a wide range of plants, but in general the smaller the vertebrate the more selective it is. Certain plants are frequently preferred such as many legumes (Fabaceae) which are rich in protein associated with their nitrogen-fixing capacity (Topic M2), or avoided owing to their toxicity, unpalatability (e.g. high silica content) or their physical defenses such as spines. Microorganisms in the gut are vital in the digestion of plant material since vertebrates cannot digest many of the structural molecules that form plants, such as cellulose and lignin, without bacteria.

Insects and plants

Plant defenses against insect herbivores include physical barriers such as a thick cuticle but the most important deterrents are secondary compounds (Table 1; Topic G5). These must be localized in the plant separately from sites of metabolism, e.g. in the cell wall or vacuole if they are not to be toxic to the cell synthesizing them. They work in many different ways. Some are directly poisonous such as the monoterpene **pyrethroids**, or indirectly such as the **phytoecdysones** that mimic insect moulting hormones (ecdysones). Others inhibit digestion, such as tannins or enzyme inhibitors, and others make the plant unpalatable or irritating to the herbivore. In many plants, young leaves are the most nutritious since they are softer than mature leaves, have a greater water content and have fewer secondary compounds. Many insects eat young leaves mostly or exclusively, and insects feeding on mature leaves nearly always grow more slowly.

Insects can evolve the ability to digest the toxic secondary compound in any one plant group, or can eat the leaves avoiding the toxin. Some insects can sequester the toxic substance unchanged in their bodies and use it for their own defense. If an insect group manages to utilize a toxic plant group, the insects are likely to flourish in the absence of competition and the volatile compounds given off by the plant may act as a signal for the insect to find it as a food plant. These interactions normally involve a specialized insect group, such as a family of butterflies, on one plant family. The evolution of insect herbivory in this way resembles an arms race. Plants evolve a novel toxic secondary compound and spread in the absence of much herbivory, then a group of insects evolve the ability to deal with that compound and so spread on the plants. This has happened many times, e.g. the toxic milkweed family is fed on by monarch butterflies; the passion-flowers are food plants for *Heliconius* butterflies. Many species may be involved. It is a situation in which diversity in one group stimulates diversity in the other and this may be one of the major stimuli for the production of biodiversity generally.

Certain plant families are susceptible to numerous insects, such as the cabbage family, whereas others generally have very few, such as the largely tropical Rubiaceae (which includes coffee). Tropical plants generally have a greater quantity and range of secondary compounds than temperate plants and there is a strong negative correlation between quantity of toxic compounds and latitude. This may be true even within one species, such as the white clover in which some plants are cyanogenic (i.e. producing cyanide, mainly deterring molluscs); in southern Europe almost all plants are cyanogenic, but in northern

Table 1. Examples of secondary compounds produced by plants

Class of compound	Examples	Effects	Example species
Terpenes	Monoterpenes (pyrethroids)	Insecticidal	Pine (resins); <i>Chrysanthemum</i>
	Sesquiterpenes gossypol	Insecticidal	Cotton
	Diterpenes phorbol esters	Skin irritant to mammals	Euphorbias
	Triterpenes phytoecdysones	Insecticidal (induce moulting)	Common polypody fern (<i>Polypodium vulgare</i>)
	Polyterpenes latex	Discourage herbivory	Rubber tree (<i>Hevea brasiliensis</i>)
Phenolics	Coumarins furanocoumarins	DNA repair damage; wide range of animals	Umbellifers (parsnip)
	Lignin	Not digested by most herbivores	Woody plants
Tannins	Various, condensed and hydrolyzable	Bind proteins and prevent digestion	Many species
Alkaloids	Various, including nicotine, morphine, strychnine, cocaine	Various, neuroactive or inhibitors of enzymes etc	Various
Cyanogenic glycosides	Various	Release hydrogen cyanide	Cassava (eliminated by adequate processing)
Non-protein amino acids	Various (e.g. canavanine)	Block protein synthesis or uptake; incorporated to give non-functional protein	Various; Jack bean (<i>Canavalia ensiformis</i>)
Enzyme inhibitors	Proteinase inhibitors	Prevent protein digestion	e.g. some legumes, tomato

Europe very few are. This implies that there is a cost to producing secondary compounds (Topic J5).

In temperate latitudes it has been shown that those trees that are most abundant or have been in an area for the longest time have more species of insect herbivore than more recent arrivals or rarer trees.

Vertebrates and plants

Vertebrates can have major effects on the structure of a plant community. Grazing mammals maintain most of the grasslands of the world. Grasses themselves are well adapted to withstand grazing pressure since their meristems are at the nodes rather than the tips of stems (Topic K2). Without the constant presence of grazing mammals, many grasslands would be invaded by shrubs or trees. In many partially wooded areas, such as savannahs, the density of trees is kept low by grazing mammals and in some places there can be cyclic

changes in the community with mammals creating open spaces which may then suffer drought. The drought may kill many of the mammals, allowing trees to regenerate. The most significant mammals in these places are the large herbivores, such as elephants, which occurred in almost all regions until their numbers were depleted by humans within the last 100 000 years or so. In all grasslands the particular herbivores present and their relative abundances have a profound effect on the composition of the plant community.

In woodlands, grazing and browsing mammals can prevent regeneration and keep the understorey open. Continuing dense populations of herbivorous mammals can open up a woodland by stopping regeneration. Some mammals, such as pigs, root in the soil and disturb the vegetation allowing gaps to appear for short-lived plants to colonize. Tree-dwelling herbivores, such as sloths and some primates, rarely appear to influence the plant community significantly.

Adaptations by plants to withstand grazing often involve physical defenses. Spines or thorns deter herbivorous vertebrates and are particularly frequent in places where growth is slow such as arid areas. Stinging hairs are a feature of certain families such as the nettle family (Urticaceae). Many plants have thick waxy cuticles, resin ducts or large deposits of silica in their leaves making them unpalatable. Toxic secondary compounds (*Table 1*) deter many vertebrates in the same way as invertebrates. Many tree leaf herbivores vary their diet to avoid too much of any one compound. Most starch-rich roots and tubers have toxic compounds in them, and for human use these must be reduced by plant breeding or, in cassava, by cooking in a particular way.

A few plants, such as the bullhorn acacia of central America, provide nest sites and oil bodies for aggressive ants which attack any herbivore, vertebrate or invertebrate, and may eat off any invading plant such as a climber as well. In many ways, these ants perform the same function as a secondary compound.

Herbivores and plant populations

Some plant populations may be controlled in their numbers by herbivores. This is the basis of biological control of plant pests. Examples include the reduction of the prickly pear cactus population introduced into Australia when the cactus moth was introduced, and a similar reduction of the introduced European St Johnswort (Klamath weed) in Canada by a *Chrysolina* beetle. These examples of introduction of a plant across continents without their herbivorous animals show how important such herbivores are; until these 'experiments' it was not clear that the herbivores were controlling the plant populations in their native lands. In addition, the St Johnswort apparently changed in its ecology and colonized open places in Canada that it does not occupy in its native Europe. It was reduced to semi-shade by the insect, which preferred open places. Many plants may be controlled in their numbers by herbivorous insects.

Herbivory, particularly of seedlings, along with fungal infection may prevent a plant regenerating or growing near an adult since the adult provides a source for the herbivores. In agriculture, monocultures are always more susceptible to pests than planting many species together and pests can build up in any one place making rotational cropping more effective. In a natural plant community the result will be an increase in plant diversity in the community as a whole, and this may be one of the reasons why tropical rainforests are so diverse.

Some plants, particularly ephemerals and other short-lived plants, may live longer as a result of herbivory. If the flowers or other parts of a shoot are removed and the plant fails to reproduce in any one year or produces below a certain proportion of its potential seeds, it may live a further year or longer.

M4 FUNGAL PATHOGENS AND ENDOPHYTES

Key Notes

Fungal diseases

Fungi are important saprophytes that recycle dead plant material. They also cause a wide range of plant disease. Fungal spores germinate on a leaf surface or wound site and form a mycelium through the plant. Their life cycles may involve more than one host plant (e.g. wheat rust, which is heteroecious) or a single host plant (e.g. smut fungi, which are autoecious).

Plant defenses against fungal diseases

Defenses may be mechanical, preventing spore adherence or penetration, or chemical, e.g. saponins that disrupt fungal membranes. Other defenses are induced when a pathogen attacks, genes being activated by an elicitor binding to a plasma membrane receptor. In a hypersensitive response, cells fill with phenolic compounds and form a necrotic lesion. A lignin or callose barrier may form. In many species, antimicrobial phytoalexins are produced. Systemic acquired resistance occurs when resistance is enhanced as a result of an infection. Fungi may stimulate changes in metabolism or phytohormone levels in the plant leading to changes in growth form.

Fungal endophytes

Fungi are often found growing freely within plants which have no, or minimal symptoms. They can be particularly dangerous to humans as they can be very toxic. Best known is ergot, a fungus growing in rye that generates a toxic precursor to LSD. Some may become parasites as the plant ages.

Related topics

Amino acid, lipid, polysaccharide and secondary product metabolism (J5)	Stress avoidance and adaptation (G5) Mycorrhiza (M1)
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Fungal diseases

Different fungal species possess a wide range of methods capable of degrading a vast range of materials, including lignin and cellulose. Many fungi are **saprophytes** and live by degrading material from plants that have already died, and these are essential in soil formation. Others are **pathogens** that cause a wide range of plant diseases resulting in significant losses in agriculture. *Table 1* gives some examples of fungal diseases and the organisms that cause them.

Infection occurs when a **spore** germinates on a leaf surface or wound site. The fungus penetrates, often through stomata, and forms fine threads of cells (**hyphae**) which ramify to form a mat (**mycelium**) throughout the plant. Infection in cells frequently resembles the arbuscules of endomycorrhizae (Topic M1).

Fungi have complex life cycles, which may involve one or more host plant (**heteroecious** life cycle). **Wheat rust**, *Puccinia graminis* for instance, a **Basidiomycete**, invades two host plants. Commonly, the first host is the barberry (*Berberis* sp.) from which **aeciospores** (containing two nuclei, one +

Table 1. Examples of fungal diseases and the causal fungi

Species and plant disease	Phylum of fungus
Various species (soft rots)	Zygomycota
Corn (brown spot)	Chytridiomycota
Various (powdery mildew)	Ascomycota
Elm (Dutch Elm Disease)	
Cereals (smuts, rusts)	Basidiomycota

strain, the other – strain) are produced which infect the wheat. The wheat then produces **uredospores**, which spread the infection in the wheat field. The fungus overwinters as diploid **teliospores**, produced when the two (+ and –) nuclei fuse (**karyogamy**). Meiosis occurs in spring to release **basidiospores** (+ or – strain) which then infect the barberry host (Fig. 1). **Smut fungi** have a simpler life cycle involving only one host (**autoecious**) and produce masses of **teliospores** (the resting stage of the fungus). They are known to infect at least 4000 species of flowering plants, many of economic importance.

Plant defenses
against fungal
diseases

Some defenses are **mechanical barriers**, for instance the **waxy cuticle**, which prevents spores from adhering to the leaf or the fungus from penetrating the leaf. Pathogenic fungi can often only infect a wound site or by entering the leaf through stomata. Other defenses are **endogenous chemicals**, for instance the **saponins** are **triterpenes** (Topic J5) produced by plants which disrupt the membranes of fungi. Other defenses against fungi are not induced until a pathogen attacks. This involves expression of **defense genes** which are activated by a signaling cascade (Topic F3) within the plant. This is triggered by the

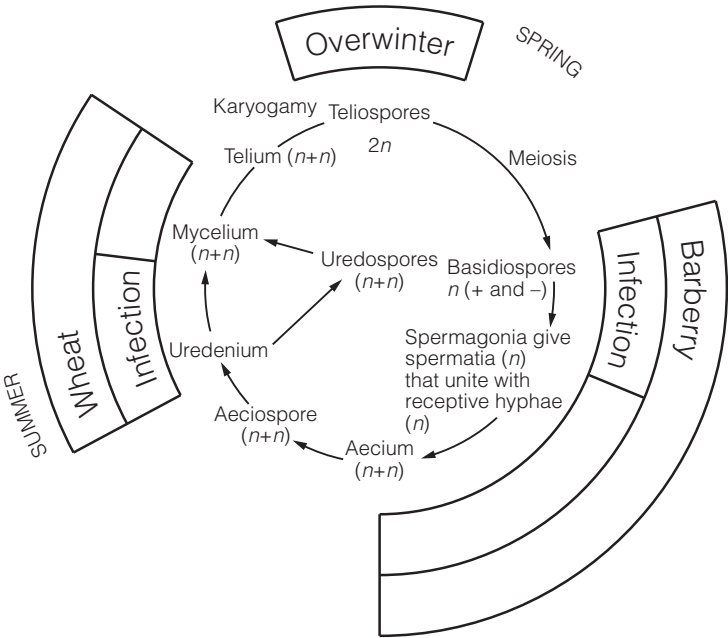


Fig. 1. Life cycle of a rust fungus, black stem rust of wheat.

binding of a product of the pathogen (an **elicitor**) to a **receptor** in the plant plasma membrane (Fig. 2). In some instances, a **hypersensitive response** occurs, where cells around the fungus fill with **phenolic** compounds and die to form a **necrotic lesion**. This isolates the point of infection and may stop further spread of the fungus. The infection site may also be surrounded by deposits of **lignin** or **callose** (Topic J5) synthesized by surrounding cells which form a physical barrier to the spread of the infection. Another group of antimicrobial compounds, the **phytoalexins** are produced in many species as a response to infection. Phytoalexin is a generic name for a range of compounds that differ between species. After infection, expression of genes for the enzymes of their biosynthetic pathway is initiated and high levels of phytoalexins accumulate. An infection which has been successfully overcome may lead to the plant being more resistant to further infection. This **systemic acquired resistance** involves the spread of signaling molecules (possibly **salicylic acid**) within the plant (Fig. 2).

Some fungi stimulate changes in the metabolism of the plant. The plant's respiration rate increases and sometimes it shifts more to the pentose phosphate pathway rather than the tricarboxylic acid pathway (Topic J4). This allows for the production of more nucleic acid (which use pentoses) and NADPH, important for the fungus. The fungus may prevent much or all of the export of carbohydrate from leaves to storage organs. The fungus may also stimulate changes in phytohormone levels (Topic F2) which lead to unusual growths, one of the most common being 'witches brooms', a dense group of short stems in many trees such as birches (*Betula* spp.).

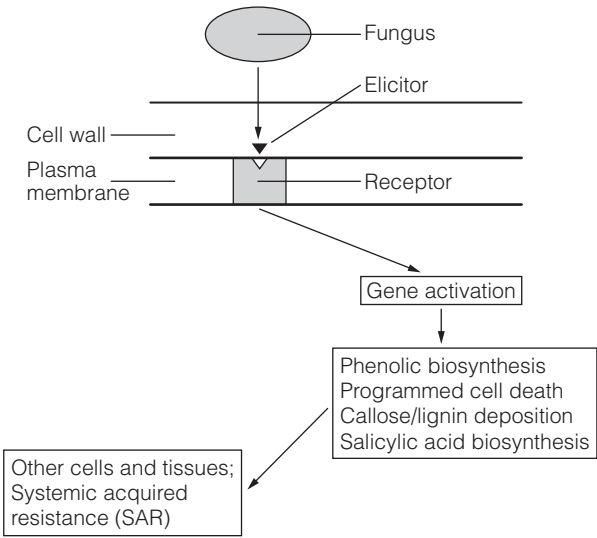


Fig. 2. Simplified model of the induction of a range of defense genes by a fungal elicitor.

Fungal endophytes

Plants are often found with fungal hyphae growing freely within their tissues. They often produce either no, or minimal symptoms of their presence and may provide advantages to the host in deterring herbivores and other pathogens. These **fungal endophytes** can be particularly dangerous to humans. One of the

best known, **ergot** (*Claviceps purpurea*), grows in **rye** and generates **lysergic acid amide**, the precursor of lysergic acid diethylamine (**LSD**). LSD is hallucinogenic and fatal in relatively small doses and throughout history, communities have been devastated by outbreaks undetected in the rye harvest. Other endophytes include *Sphacelia typhina*, an ascomycete which grows in the prairie grass *Festuca arundinacea* and causes cattle disease and death. Detection and elimination of endophytes in agriculture and food processing is an important area.

There is no absolute distinction between fungal endophytes and parasites and some fungi may remain as endophytes for many years before starting to damage a plant significantly. Many only reproduce sexually once the plant or the infected part is killed.

M5 BACTERIA, MYCOPLASMA, VIRUSES AND HETEROKONTS

Key Notes

Bacteria

Bacterial diseases include blights, wilts and soft rots. Most plant-infecting bacteria are Gram negative and rod-shaped, except streptomycetes which are filamentous. Some bacteria are beneficial; Rhizobia fix nitrogen and Agrobacteria have been used as the basis for plant genetic engineering.

Mycoplasma

Mycoplasma are bacteria-like organisms, lacking a cell wall, that infect sieve tubes. Commercially damaging phytoplasmas exist for many species.

Viruses

Viruses consist of a protein capsid encasing DNA or RNA and replicate using the host cells. Most plant viruses contain RNA, though a few contain DNA. They are transmitted by a vector. Infection may be limited to one site, or they may travel systemically through plasmodesmata or phloem. Control methods include: meristem tip culture; controlling vectors; and genetic modification to introduce viral capsid genes into plants.

Heterokonts

Heterokonts include oomycetes, which include some important plant pathogens. They produce biflagellate zoospores and resistant oospores that can survive many years in soil before germination. The best known is *Phytophthora infestans* which causes potato blight.

Related topics

Nitrogen fixation (M2)

Fungal pathogens and endophytes (M4)

Bacteria

Bacterial diseases can affect almost any plant and can result in great crop losses. Almost all plant-infecting bacteria are **Gram negative** and **rod-shaped**, although members of the genus *Streptomyces* will infect plants and are **filamentous**. Some bacteria are beneficial; *Rhizobium* fixes nitrogen in symbiotic association in root nodules (Topic M2). *Agrobacterium*, which cause plant galls by inserting bacterial genes into the plant genome, have been used as the basis for plant genetic engineering (Topic O3). The range of diseases caused by other bacteria include: **blights** in which necroses, areas of dead tissue, form and spread rapidly through stems, leaves and flowers; **wilts** in which xylem tissue is destroyed and the plant wilts and dies; and **soft rots** where fleshy tissue is decayed, particularly in storage tissues. *Table 1* gives examples of bacterial diseases.

Mycoplasma

Mycoplasma are bacteria-like organisms lacking a cell wall. Mycoplasma-like organisms that infect plants are known as **phytoplasmas** and many are commercially important diseases. Carrots, peaches, pears, ornamental flowers

Table 1. Examples of bacterial diseases

Genera of bacteria	Symptoms
Rods	
<i>Agrobacterium</i>	Galls (swellings); hairy roots
<i>Erwinia</i>	Blights (necrosis), wilts (wilting) soft rots (decay)
<i>Pseudomonas</i>	Wilts, galls, blights, cankers (swellings)
<i>Xanthomonas</i>	Cankers, blights, rots
<i>Clavibacter</i> and <i>Rhodobacter</i>	Rots, cankers, wilts
Filamentous	
<i>Streptomyces</i>	Scabs

and coconuts can all be seriously affected. Phytoplasmas normally infect **sieve tubes**. They are conveyed from plant to plant by **vector** organisms, such as aphids, that feed on sieve-tube contents.

Viruses

Viruses are non-cellular structures containing DNA or RNA that use the host’s synthetic capability to replicate. Many of the viral diseases known (of which there are more than 2000) are virtually symptom-less other than marked reductions in yield. Examples include tomato mosaic virus. The virus consists of a coat (**capsid**) made of protein, encasing DNA or RNA that contains the information for infection and replication of the virus. Most plant viruses contain **RNA** as their genetic information, though three (the badnaviruses, caulimoviruses and geminiviruses) contain **DNA**. Viruses are frequently transmitted from plant to plant by a **vector organism**, e.g. an insect, but seldom infect the vector. Viruses may have a limited site of infection, or may travel **systemically** through plasmodesmata from cell to cell, or through the phloem. Movement through plasmodesmata involves the synthesis of **movement proteins**, encoded by the virus, which modify the plasmodesmata. Control methods include: **meristem tip culture** (using plant tissue culture; Topic O2) in which plants are propagated from virus-free tissue; developing **resistant strains**; controlling vectors. Recently, genetic modification (Topic O3) has been used to introduce viral capsid genes into some plants, thereby preventing the virus from replicating. Diagnosis of viral disease is often difficult, with few visual symptoms. Viruses can build in plants while old individuals can be weakened by them.

Heterokonts

Heterokonts are eukaryotic organisms with one long and one short flagellum. They include diatoms and algae and the phylum *Oomycota*, the **oomycetes**, which include some important plant pathogens. The *Oomycota* produce **biflagellate zoospores**, the means of asexual reproduction of the organism, and can also reproduce sexually to produce **oospores**, which are resistant and can survive many years in soil before germination. Oomycetes form hyphae within infected tissue and are very destructive. Examples are *Phytophthora infestans*, the **potato blight**, which reached Europe in the 1840s and spread with devastating consequences of famine and emigration; *P. cynamoni*, which kills avocado trees; *Plasmopara viticola* which causes **downy mildew** of grape vines and *Pythium* species which cause **damping-off** of seedlings.

The great majority of plants use only sunlight and inorganic molecules for all their energy and nutritional needs, but there are some exceptions. There are around 3000 species of plants that are at least partially parasitic on other plants, i.e. a little over 1% of all flowering plants. Only about 20% of these are entirely dependent on their hosts, the remainder having some green parts so potentially making some of their own sugars (known as **hemiparasites**). A few of these can live without a host plant, although they rarely do. At least eight plant families have parasitic members, some of which also have non-parasitic species, so the habit has probably evolved several times within the flowering plants. Among land plants only angiosperms have become parasitic (one unusual conifer of

New Caledonia may be partially parasitic on other conifers). About 60% of plant parasites are attached to the roots of their hosts, the remainder to stems. A few are specific to a single host species but most can parasitize a range of species, often within one family. They are distributed throughout the world, favoring disturbed places, though root parasites are particularly common in grasslands of the Mediterranean and subtropical climates.

There is a range of life cycles among parasites. Most are herbaceous ranging from ephemeral plants to long-lived perennials, but there are several woody plants such as the **mistletoes** (Topic K2) among stem parasites, and, among root parasites, **sandalwoods**, some of which are medium-sized trees. Their reproduction is similar to non-parasitic flowering plants, and the largest known single flower, up to 1 m in diameter, is a parasite of the south-east Asian forests, *Rafflesia*. Most **root parasites** have small seeds and some, such as the broomrapes, have dust-like seeds produced in great quantity, dispersed by the wind. Almost all **stem parasites** have fleshy fruits dispersed mainly by birds. Those parasites that are specialized to one or a few host species tend to be longer lived and produce more, smaller seeds than the generalists, many of which are short-lived.

Growth of parasites

In root parasites, the seeds germinate in response to **chemical signaling** from the roots of a host plant. A sesquiterpene chemical, **strigol**, has been identified as an important stimulant but this substance comes from non-host plants too and may be secreted by microorganisms associated with the root rather than the root itself. Other substances, as yet unidentified, must be important. The best studied parasite is *Striga hermonthica*, a pest of several species of cereal. It seems that the parasite has several strains, each strain occurring on one host species and responding only to exudates from that host.

Once a seed has germinated, a short radicle may grow and this must come into contact with root hairs from the host or it will die. It can then stick onto the root hairs and penetrate the root by mechanical pressure and through the action of hydrolytic enzymes. It may meet some resistance at the endodermis but once it gets through that it reaches the vascular tissue and penetrates the xylem vessels through pits or by dissolving the cell walls, making direct vascular connection with its host. Once it has penetrated, it obtains all its nutrients and energy from the host. The attachment structure is known as the **haustorium** (Fig. 1). In most parasite species, immediately above the site of connection the haustorium becomes swollen and full of vascular tissue and parenchyma cells. In hemiparasites, once the shoot grows out of the ground it becomes green and can photosynthesize; it reproduces by seed.

Some parasites do not produce well defined haustoria and members of the Rafflesiaceae grow numerous thin strands resembling fungal hyphae through its host cortex and cambial cells. Stem parasites develop in a similar way to root parasites, forming haustoria making a connection between the vascular systems of the stems.

Economic importance of parasites

Parasites take up water and nutrients from the host and this weakens the host plants. Sometimes a parasite causes visible damage resulting in wilting, reduction in plant size, lower yield and lower quality of the crop and can cause up to **30% crop loss**. They are important agricultural **pests** in Africa, parts of Asia and the Mediterranean, and their spread to other areas via contaminated seed is causing concern for food production.

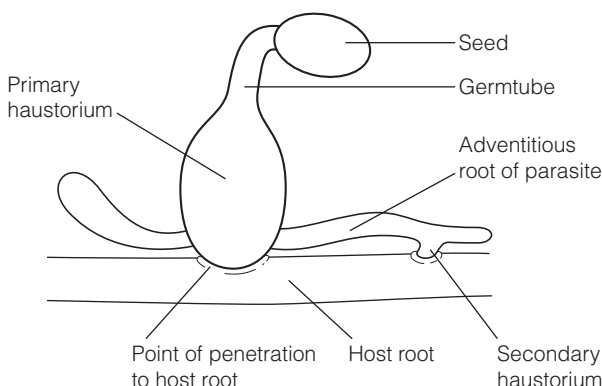


Fig. 1. A germinating seed of a root parasite such as *Striga* sp. with a primary and secondary haustorium where it penetrates a host root.

The most serious pests are species of **witchweed**, *Striga*, particularly *S. hermonthica*, which seriously reduce yields of maize, rice, sorghum, millet and sugar cane in the African Sahel and Asia. They are root hemiparasites in the Scrophulariaceae, a family containing many hemiparasites. The related *Alectra* species, mainly found in West Africa, parasitize groundnut, cowpea and sunflowers. The **broomrapes**, *Orobanchae* spp., in the Orobanchaceae, closely related to Scrophulariaceae, can be serious pests of beans, lentils, tobacco, tomatoes and sunflowers, *Orobanchae crenata* causing serious crop losses in the Mediterranean. A quite different group, the **doddgers**, *Cuscuta* species, related to the bindweeds, Convolvulaceae, are stem parasites of dicots with low host specificity and can attack many different crops.

In natural plant communities, parasitic plants may reduce diversity in some places but their ecological importance is minor.

Saprophytes

A **saprophyte** is an organism that decays dead vegetation. No plant of any kind is capable of that, but many **fungi** are saprophytic, including ecto- and ectendomycorrhizal fungi (Topic M1). Flowering plants that are dependent on these mycorrhizal fungi for all their nutrients and energy are referred to as 'saprophytes', although any plant that has such a mycorrhizal association must be regarded as, in part, saprophytic. All orchids and some other plants are saprophytic when they first germinate, being dependent on their mycorrhizae. Most later grow green stems and leaves and are partially autotrophic, but many terrestrial orchids live on woodland floors where photosynthesis is severely limited and many of these must remain mainly saprophytic.

Fully saprophytic plants are found among two of the highly specialized ectendomycorrhizal groups, the orchids, such as the coralroot and birdsnest orchids, and the birdsnests (Fig. 2) or Indian pipes among the heather family group (usually in a separate family Monotropaceae). They are entirely dependent, in effect parasitic, on their mycorrhizae and have small restricted root systems, some rounded like a bird's nest or branching like a coral giving the plants their common names, and having scale-like leaves and no green parts at all. Most live in deep shade on woodland floors. The plant's mycorrhizae may be connected with trees, and nutrients have been traced passing from tree to

saprophytic plant via the mycorrhizae. In their form and color the fully saprophytic plants closely resemble root parasites.

The gametophytes of some clubmosses, horsetails and ferns (Topics Q3 and Q4) are entirely subterranean and live saprophytically with their associated mycorrhizae, although the sporophytes are autotrophic.

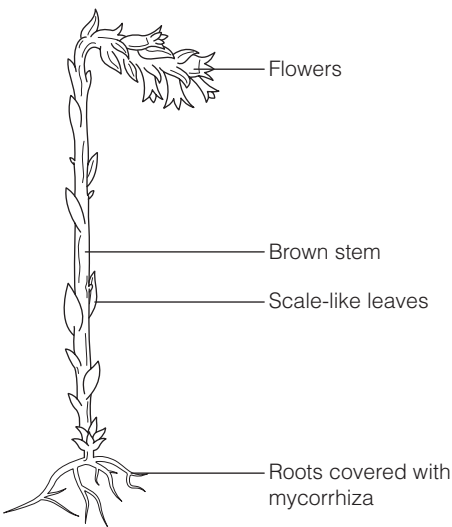


Fig. 2. Yellow bird's nest, *Monotropa hypopitys*.

M7 CARNIVOROUS PLANTS

Key Notes

Carnivorous plants	A few plants supplement their nutrients by trapping and digesting animals. All can photosynthesize as well and have roots capable of absorbing water and nutrients but, typically, they live in acid nutrient-poor environments, often bogs.	
Pitcher plants	There are three unrelated groups of pitcher plants, all of which have furred leaves sealed along a keel in the shape of a pitcher. Sugar-secreting glands occur on a flap and attract insects and other animals and these then cannot get out because of downward-pointing hairs and waxy surfaces. They are digested in collected rain water and a mix of digestive enzymes and absorbed by cells at the base of the pitcher.	
Other carnivores	Sundews and butterworts have sticky secretions on their leaves that catch animals. Some other plants have sticky secretions that trap insects, and carnivorous plants probably evolved from this. The rare Venus fly-trap has an elaborate hinge mechanism triggered by an electrical impulse that responds rapidly; the waterwheel plant is similar but smaller and under water. The aquatic bladderworts have an equally elaborate trap mechanism involving a partial vacuum that sucks small invertebrates into the bladder.	
Related topics	Nastic responses (G3)	Parasites and saprophytes (M6)

Carnivorous plants

Carnivorous plants trap animals using **specialized leaves** or parts of leaves. All carnivorous plants are green and can photosynthesize but rely on catching animals to supplement their nutrient supply. They are characteristically plants of **nutrient-poor** acidic and often boggy soils, although a few species have colonized richer sites. Some are aquatic. These sites are especially poor in available nitrogen and supplementing this and other nutrients by carnivory is a selective advantage. The root systems of all carnivorous plants are poorly developed but can absorb some nutrients and most carnivorous plants can survive for a time without catching any animals.

The true carnivorous plants have sophisticated **traps**, sometimes involving movements by the plant, into which insects and other small invertebrates and even occasionally small vertebrates are enticed. There are about 400 species of carnivorous plants in at least five families and carnivory appears to have arisen independently several times.

Pitcher plants

There are three separate families of pitcher-plants, the **Sarraceniaceae** from north and south America, the **Nepenthaceae** of Asia and the **Cephalotaceae** of Australia. All have a funnel-shaped pitcher (*Fig. 1*) deriving from part or all of a curled leaf fused at the edges with a keel. These families are not closely related

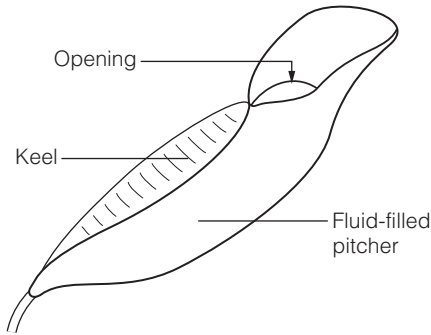


Fig. 1. A pitcher (modified leaf) of the pitcher plant *Sarracenia*.

and the pitchers look alike through similar life style, and are a remarkable example of convergent evolution. Details of the structure differ in the three families but all have a flap of leaf above the pitcher, mainly used as an attractant, sometimes with **sugar-secreting glands**, leading insects to the lip. On the insides of the pitchers are downward pointing hairs and waxy surfaces making escape difficult or impossible. Pitchers catch rain water and the simplest drown their prey and allow bacteria to digest them. The more elaborate pitchers secrete **enzymes** such as proteases, lipase, esterase and other enzymes and acid into the pitcher. Small animals can be digested quickly, often within 2 days, leaving just the chitinous husk of an insect. Bacteria living in the pitchers may digest this too. Cells in some areas at the base of the pitcher have no cuticle and nutrients can be absorbed.

Despite the digestive enzymes in pitchers, a small community of fly larvae, crustacea and spiders live inside pitchers in some parts of their distribution, apparently resistant to the enzymes.

Other carnivores

Two unrelated plant families have leaves that act like fly-paper, catching insects in a **sticky secretion**. The **sundews** and their relatives (*Droseraceae*) have specialized glandular hairs on their leaves (and on stems in some) and the **butterworts** (*Pinguicula* spp.) have leaves that are sticky all over the surface. In some, the leaves roll around the animal once it is caught. They have **digestive glands** in the leaves secreting a similar range of enzymes to the pitcher plants and, with the help of bacteria secreting chitinase, insects are digested quickly. Many plants that are not regarded as carnivorous produce sticky secretions, normally on stems, buds or seeds, and insects and other small animals can become trapped and killed in these. If these animals decay while remaining attached to the plant some of these species may be able to absorb the nutrients from them and this is likely to be how carnivorous plants first evolved.

The most elaborate of carnivorous plants are the famous **Venus fly-trap**, *Dionaea muscipula*, a rather rare plant of bogs in eastern USA and the aquatic waterwheel plant, *Aldrovanda vesiculosa*, both related to the sundews, and **bladderworts**, *Utricularia*, with about 250 species related to the butterworts. The Venus fly-trap has a modified leaf in which two lobes are joined by a hinge region (Fig. 2), in which **motor cells** are capable of rapid turgor changes. When an insect lands on the leaf surface and touches the two to five sensitive hairs, an electrical stimulus is sent through the leaf triggering a rapid release of pressure

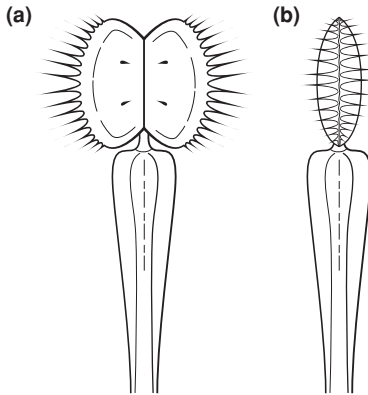


Fig. 2. Leaf of the Venus fly-trap, *Dionaea muscipula*: (a) open; (b) shut.

in the motor cells if the hairs are stimulated several times. How this trigger works is still little known. This shuts the two halves of the leaf sufficiently to trap the insect and the leaf completes its shutting more slowly through normal growth processes, crushing any animal that is caught. The waterwheel plant has a similar but much smaller aquatic trap no more than 2 mm in diameter in which it catches tiny aquatic animals.

The bladderworts have elaborate tiny bladders under water, 0.25–5 mm in diameter. These are spherical to conical or cylindrical and water is extracted from them until the walls are pulled inwards to develop considerable suction pressure. There is a trap door that is kept closed but under tension. This is released by an animal that triggers surrounding hairs and the animal is sucked rapidly in by the pressure, after which the door immediately closes again, all this taking about one hundredth of a second. The suction pressure is restored after an hour or two.

