How pathogens attack plants

Philip Keane

Department of Botany
La Trobe University, Bundoora
VIC 3086
p.keane@latrobe.edu.au

Plants are well protected against microbial invasion by an epidermis of tightly packed cells with rigid, cellulose-strengthened walls covered by a waxy cuticle on the aerial parts. A great diversity of bacteria and fungi come in contact with plants but most never invade. However, some microbes of all types are highly adapted as invasive parasites of particular plant species, often causing disease, and these are reviewed here.

In contrast to the situation in humans where viruses and bacteria are the most important pathogens, the filamentous eukaryotes commonly known as the 'fungi' are the most destructive pathogens of plants where their penetrative hyphae give them a great advantage in invading. Fungi are specialised either as saprotrophs, feeding on dead organic matter mainly in soil, or as plant parasites that are highly adapted for invading and obtaining their nutrients directly from living plants. A few saprotrophs are able to invade immature or senescent plant tissues, killing the tissue with enzymes or toxins[1] and then living on the dead tissue. These fungi have a wide host range and are readily cultured.

Specialised aerial pathogens of plants

Most of the highly adapted parasites invade the leaves of plants with special structures that enable them to infect via stomates (for example, downy mildews and rusts) or directly through the epidermis (for example, powdery mildews) and obtain their nutrients via hyphal branches ('haustoria') formed within the living host cells in a 'biotrophic' relationship. These fungi cannot be cultured axenically and are 'obligate' parasites. They have a high degree of host-specificity and it is likely that such specificity helps to control their populations in highly species-diverse natural plant communities. Rarely, in fungi like the cause of witches' broom disease of cocoa (*Moniliophthora perniciosa*) a biotrophic invasive phase alternates with a saprotrophic reproductive phase of their life cycle[2].

These pathogens form spores that are adapted for either wind or rain-splash dispersal and deposition onto the surfaces from which invasion occurs. The rusts and powdery mildews form exposed masses of dry powdery spores that are readily dislodged by wind. Many ascomycete pathogens produce their wind-dispersed ascospores in flask-shaped structures from which they are forcibly ejected into the air. Wet hydrophilic spore masses extruded onto plant surfaces from embedded structures of some fungi are splash-dispersed. Spores of the rusts germinate on wet leaf surfaces and hyphae locate stomates by directed growth, sometimes in response to the topography of the leaf surface[3]. Each germ tube forms an enlarged appressorium attached to the stomate; from this a hypha penetrates through the pore and proliferates between the mesophyll cells, many of which are penetrated by a thin hypha that expands within the cells to from a larger haustorium which is surrounded by the plasma membrane of the host cell. Eventually, an infection colony forms masses of spores that break through the epidermis, enabling further wind dispersal. While the infected tissues remain alive, they become a sink for photosynthate from the whole leaf and other parts of the plant[4], reducing resources available for plant growth and production. Some 'gall' rusts even stimulate enlargement of the infected tissues. In powdery mildews, hyphae penetrate directly through the cuticle and epidermis to form haustoria within epidermal cells, forming a circular, superficial colony on which powdery spores are formed. The interface between host plasma membrane and the haustorium is the main site of nutrient transfer to the fungi and also the site of interactions that determine whether a pathogen is able to invade the host in a 'compatible' interaction as described above or is excluded by an 'incompatibility' expressed as a sudden death ('hypersensitive necrosis') of the first invaded cells and controlled by the 'gene-for-gene' interaction of resistance genes in the plant and virulence genes in the pathogen[5]. Thus, these specialised pathogens have a degree of specificity at the host species level and also at a host variety level, whereby some 'susceptible' varieties are invaded while in other 'resistant' varieties the potential pathogen is excluded.

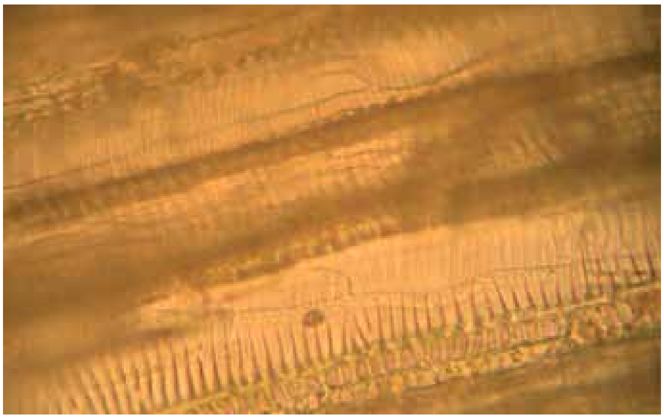

Figure 1. Photomicrograph showing the invasion of xylem vessels of cocoa by the fungal hyphae of *Oncobasidium (Ceratobasidium) theobromae*, the cause of Vascular Streak Dieback of cocoa in Papua New Guinea and Southeast Asia.

Although they don't form haustoria and their intercellular infection hyphae are the main host-parasite interface, smut fungi are another group of highly specialised, ecologically obligate biotrophic parasites, causing diseases in which the seeds of grasses (notably cereals) are replaced by masses of black, sooty fungal spores.

A very few airborne pathogens invade the xylem vessels of plants, causing dieback diseases and killing plants. The basidiomycete *Ceratobasidium* (*Oncobasidium*) *theobromae* is an airborne xylem-invading fungus that causes a serious dieback disease of cocoa in Southeast Asia[6]. Wind-borne basidiospores give rise to infections of xylem in very young expanding leaves and the hyphae grow through the xylem vessels (Figure 1) into the stems and ultimately kill the shoots. The spores of some xylem-invading fungi such as *Ophiostoma ulmi*, the cause of the lethal Dutch elm disease, are transported and inserted into the trees by wood-boring beetles.

Despite the very thick cuticle on eucalypt leaves, many ascomycetes have become highly adapted as parasites on them[7]. Two *Mycosphaerella* (*Teratosphaeria*) species have become serious pathogens of eucalypts in plantations, but show different degrees of parasitic adaptation: *M. nubilosa* can invade only via stomates and is confined to the open spongy mesophyll of juvenile leaves of young trees, while *M. cryptica* can penetrate directly through the cuticle and epidermis and invade between the tightly packed mesophyll of adult leaves[8]. Some pathogens such as *Pachysacca* invade between the epidermis and the mesophyll tissue and form haustoria in the mesophyll cells[9].

Many viruses and bacteria are highly host-specific and specialised plant pathogens but have little capacity to invade the aerial parts of plants by themselves. Many are carried and inserted into plants by sap-sucking insects and a few infect via wounds. The fireblight pathogen of apples and pears infects through wounds and natural opening such as nectarthodes and stomates. Following penetration, bacteria often directly kill plant tissue, resulting in soft rots or blights in which the bacteria derive their nutrition as saprotrophs from the dead tissue.

Most viruses are inserted into plants by phloem-sap sucking insects such as aphids. Once inside plant cells, viruses reproduce themselves using the biosynthetic apparatus of the living cells and spread systemically in the plant, usually resulting in distorted and reduced growth. Infecting all except the youngest meristem tissues, viruses are readily transmitted by vegetative propagation of crops.

Some phloem-invading bacteria (*Candidatus* spp.) are transmitted and inserted into plants by phloem-feeding psyllid and leafhopper insects, causing very destructive diseases such as 'citrus greening' in Southeast Asia. Phytoplasmas are also transmitted and inserted into plants by phloem-sap sucking leafhoppers, causing diseases like the little leaf disease of sweet potato in Papua New Guinea and tomato big bud. A recently discovered species of xylem-infecting bacterium, *Xylella fastidiosa* which causes Pierce's disease of grapevines in the USA, is transmitted and inserted into plants by xylem-feeding insects.

Root-infecting pathogens

Most root-infecting microbes are less specialised parasites, usually living partly as saprotrophs or surviving as resting structures in soil. Some soil-borne fungi such as *Fusarium* species infect through wounds in the roots, invading and clogging up the xylem vessels and causing wilting[10]. The destructive soil-borne bacterial pathogen, *Ralstonia* (*Pseudomonas*) *solanacearum*, penetrates through wounds (for example, caused by the emergence of lateral roots), invades and clogs the xylem and causes wilting disease of many crops. A unique soil-borne bacterium, *Agrobacterium tumefaciens*, also infects through wounds. In the infected cortex cells a small section of the bacterial DNA (the T-DNA) becomes incorporated into the genome of the host cell[11] and controls the proliferation of the plant cells to form a gall and produce a special nutrient that can be used only by *Agrobacterium*. This unique parasitic mechanism of *Agrobacterium*, in which the host cells are genetically transformed, has been developed as a means of inserting extraneous genes into plants (in the process of genetic engineering).

The oomycete *Phytophthora cinnamomi*, the cause of devastating eucalypt vegetation dieback in southern Australia, is a relatively unspecialised soil-borne pathogen with a very wide host range on woody plants. It survives as spores which germinate in saturated soil to form motile flagellate zoospores that are attracted to susceptible roots and establish the invasive phase that immediately begins killing the roots leading to the above-ground symptoms of dieback[12]. The protozoan-like pathogen, *Plasmodiophora brassicae*, which causes club-root of cabbage, also survives as a resting spore in soil and forms motile spores that are attracted to roots, leading to infection. In this case, however, the parasite is a biotroph, invading and stimulating the proliferation and enlargement of root cells to form massive galls within which it lives.

Of the very great diversity of nematodes in soil, only a few groups are plant parasites, distinguished by their spear-like mouthparts used to penetrate roots and feed on cell contents. Like the highly specialised fungal pathogens, plant parasitic nematode species tend to be highly host-specific, surviving in soil as dormant eggs that are stimulated to hatch by root exudates of susceptible plant species. Many types feed on the surface of roots, causing stunting, but two of the best known genera, the root knot nematode *Meloidogyne* and the cyst nematode *Heterodera*, are biotrophs, invading the roots and causing the proliferation and enlargement of the group of cortex cells on which they feed.

Summary

The photosynthetic products of plants are the primary source of energy for all microbes. Most microbes live on dead plant matter, but some have developed a capacity to invade and obtain their nutrients from living plants, often causing disease. The crowding together of plants in our highly intensive farming systems has greatly favoured the spread and build-up of microbial pathogens in our crops, to the extent that they are now one of the main constraints on crop production. Research into their invasive capacity is aimed at improving our ability to reduce the damage they cause.

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Biography

After growing up in rural South Australia and completing a degree in agriculture at the Waite Agricultural Research Institute of the University of Adelaide, **Dr Philip Keane** studied the cause of the destructive Vascular Streak Dieback disease of cocoa while living in Papua New Guinea and working at the Lowlands Agricultural Experiment Station, Keravat, and the University of Papua New Guinea under the supervision of K.P. Lamb and N.T. Flentje. He has since taught botany and plant pathology at the University of Papua New Guinea in Port Moresby and at La Trobe University in Melbourne, where he and his students studied diseases of eucalypts. He has maintained a life-long interest in pests and diseases of cocoa and agricultural development in the tropics and has travelled periodically to support research and development in Papua New Guinea and in Java, Lombok and Sulawesi in Indonesia. Since 2001 he has led an Australian Centre for International Agricultural Research project aimed at improving the sustainability of cocoa production in Sulawesi where serious pest and disease problems and declining soil fertility are threatening the future of the cocoa industry that has greatly boosted the welfare of smallholder farming families in the region.