Introduction to Plant Pathology

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To my dear wife, Lilian,
with love and appreciation for her patience
and support over the last several months.

Contents

Preface

Pathogenic agents which infect plants are many, both in kind and number, and they are in direct competition with us for our food and our cash crops. They are therefore a cause of malnutrition, starvation and poverty. They also deplete our food reserves by spoiling stored produce and ruin our environment by destroying vegetation.

'Know your enemy' is a good adage in most walks of life and is particularly apposite to that of the plant pathologist. The range of organisms which cause plant disease and the techniques for their identification are therefore introduced in the first two chapters of this book together with accounts of some of the worst epidemics they have caused. Those with an historical inclination may know that a disease of potato was the cause of a great famine in the 1840s in which Ireland lost over a quarter of its population through starvation and emigration. Similarly, death by starvation of an estimated two million people living in Bengal (now the Province of West Bengal in India and Bangladesh) is thought to have been caused by a disease of rice in the 1940s. As an example of the devastation of a cash crop, the growing of coffee in Sri Lanka became uneconomic in the last part of the 19th century owing to coffee rust; in consequence, the farmers turned to growing tea – and the British, obligingly, to drinking it! With regard to the environment, parents and grandparents of today's students may remember that elm trees were a distinctive and attractive feature of parts of the USA and the southern part of England but that in the 1970s they rapidly died out owing to 'Dutch Elm Disease'. Finally, of the many organisms that cause spoilage of produce in storage, fungi of the *Aspergillus flavus* group are perhaps the most notorious; not only are the infected or infested plant products such as maize and peanuts toxic, they are also highly carcinogenic.

Once the identity of a pathogen is known and there are adequate techniques for its rapid identification (Chapters 1 and 2), the study of its dissemination and the losses it causes become practicable (Chapter 3 and 4, respectively). Chapter 5 addresses the control of inoculum of the pathogen since prevention is not only better than cure but is also, apart from growing resistant plants, virtually the only feasible option for poorer parts of the world. Richer countries may be able to afford pesticides but concerns about their adverse effects on human health and the environment have led to several of them being phased out. Emphasis is therefore placed on biological control as a potentially less hazardous and more environmentally friendly way of reducing inoculum.

Plant pathogens have evolved many ingenious ways of locating and effecting entrance into their hosts, often involving the recognition of host topography or chemical signals. In some instances, entrance is achieved through natural openings and wounds, but in others direct penetration of the cell wall is achieved by the secretion of enzymes or the development of high turgor pressure in special organs (appressoria). Enzymes are also required by many pathogens for the colonization of the host and the release of metabolizable products and their action may give rise to a considerable amount of cell death (necrosis). Location, penetration and colonization are the topics discussed in Chapter 6.

Some pathogens subvert the metabolism of their hosts by altering hormone levels, the ultimate level in sophistication in this regard being species of *Agrobacterium*. These organisms are genetic engineers since they insert genes into plants that encode enzymes for the synthesis of two important plant hormones, as well as other genes that harness the metabolism of infected plants to produce compounds which can only be used by the pathogen (Chapter 7). Some pathogens influence the metabolism of their hosts and may kill them by the production of phytotoxic compounds (Chapter 8).

Faced with this onslaught from pathogens, it is not surprising that plants have developed mechanisms for fighting back. Some of these are constitutive (Chapter 9) while others are induced by the challenging organism (Chapter 11). The induced responses are often triggered by recognition of the invader, the genetic elements responsible on the part of the plant and the pathogen being termed resistance and avirulence genes, respectively. This gene-for-gene relationship is discussed in Chapter 10 together with structures of the genes involved and the means by which their products may be brought together and interact.

Finally, in Chapter 12, the material of the six previous chapters is viewed from the perspective of developing control measures that are environmentally friendly.

A number of people deserve my thanks for help in producing this book, those who sent illustrations and who are acknowledged in the legends, Andy Slade and his team at John Wiley and Sons Ltd., and especially John Mansfield who kindly read an earlier version of the manuscript. Any mistakes that remain are mine.

Richard Strange
January, 2003

1 The Causal Agents of Plant Disease: Identity and Impact

Summary

Eleven groups of organisms cause plant disease: parasitic angiosperms, fungi, nematodes, algae, Oomycetes, Plasmodiophoromycetes, trypanosomatids, bacteria, phytoplasmas, viruses and viroids. Pathogenicity is normally established by the application of Koch's postulates, modified in the cases where culture of the causal organism is not feasible. Individual members of all 11 groups cause severe diseases of important crops with consequent significant economic and social impact. Their ability to reproduce prolifically and survive transportation and long periods of inactivity as dormant propagules has ensured that they continue to present a formidable threat to the health of our crops and therefore to the world's food security.

1.1 Introduction

Plants, through their ability to fix carbon dioxide by photosynthesis, are the primary producers of the food that feeds the world's human population as well as the many animals and other organisms that are heterotrophic for carbon compounds. It is not surprising, therefore, that among the latter there is a considerable number which, in order to have first call on these rich pickings, have adopted the parasitic mode of life. They range from higher plants themselves, the parasitic angiosperms, to viroids, naked fragments of nucleic acid, in some instances less than 300 nucleotides in length. Between these extremes of size, there are plant pathogenic organisms among the fungi, nematodes, algae, Oomycetes, Plasmodiophoromycetes, trypanosomatids, bacteria, phytoplasmas and viruses. In almost all of these categories there are organisms that cause catastrophic plant diseases, affecting the lives of millions of people by competing for the plant products on which they depend for food, fibre, fuel and cash. In this chapter all 11 classes of plant pathogenic agent will be introduced and those that are particularly destructive will be highlighted together with the impact that they have had on the people who have been most seriously affected. However, the first imperative of a plant pathologist is to establish unequivocally the cause of disease.

1.2 Establishing the Cause of Disease

The correct diagnosis of a plant disease and its cause is not always an easy task. In the first instance symptoms may be ill defined which make their association with any organism problematic (Derrick and Timmer, 2000) and, secondly, plants grow in environments which are notably non-sterile. In particular, besides supporting a microflora on their aerial parts, the phylloplane, they are rooted in soil which may contain in excess of 1 million organisms per gram. The plant pathologist is therefore faced with trying to determine which, if any, of the organisms associated with the diseased plant is responsible for the symptoms. This is normally achieved by the application of the postulates of Robert Koch, a German bacteriologist of the 19th century, which for plant pathogens may be stated as follows:

(1) The suspected causal organism must be constantly associated with symptoms of the disease.

(2) The suspected causal organism must be isolated and grown in pure culture.

(3) When healthy test plants are inoculated with pure cultures of the suspected causal organism they must reproduce at least some of the symptoms of the disease.

(4) The suspected causal organism must be reisolated from the plant and shown to be identical with the organism originally isolated.

Clearly, these criteria can only be met with organisms that can be cultured, ruling out all obligate pathogens which include a number of important fungi, many phytoplasmas and all viruses and viroids. Establishing these organisms as causal agents of disease usually involves purification of the suspected agent rather than culture and the demonstration that these purified preparations reproduce at least some of the disease symptoms.

1.3 The Range of Organisms that Cause Plant Disease

1.3.1 Parasitic angiosperms

The parasitic angiosperms are higher plants which are parasitic on other higher plants. They number more than 3000 species and are found in nine families (Stewart and Press, 1990). *Striga* and *Orobanche* are two prominent genera which

Figure 1.1 (a) *Striga hermonthica* flowering on sorghum (reproduced courtesy of Dr Chris Parker and CAB International); (b) *Orobanche foetida* flowering on *Vicia faba* (reproduced courtesy of Dr Diego Rubiales, University of Cordoba). A colour reproduction of this figure can be seen in the colour section

are said to be parasitic weeds. On germination of their seeds, they attach themselves to the roots of their host plants by a structure termed a haustorium (Section 6.6) and abstract nutrients, causing losses of yield which may be total (Figure 1.1(a)) (see plates between pages 32–33 and 240–241). The use of the term weed is perhaps unfortunate since, until relatively recently, it seems to have diverted the attention of plant pathologists from this important group of plant pathogens! Species of *Striga* are particularly notorious as they infect more than two-thirds of the 73 million hectares of cereals and legumes grown on the African continent, affecting the lives of over 100 million people living in 25 countries. Losses may be total and infestation of some areas may be so great that continued crop production becomes impossible (Estabrook and Yoder, 1998). It seems likely that these diseases will continue to exact a high toll of crops in Africa since the pathogens responsible seed prolifically and the seed remains viable in the soil for at least 10 years. However, with regard to *S. gesnerioides*, which infects cowpea, two advances were made in 1996: the discovery of races of the pathogen and the clustering of the races in discrete geographical areas in West Africa (Lane *et al.*, 1996). These exciting results raise the possibility of breeding resistant cultivars and distributing them to areas where their resistance will be effective.

Species of *Orobanche* cause serious losses of plants belonging to the families Solanaceae, Fabaceae, Apiaceae and Asteraceae. They produce large numbers of

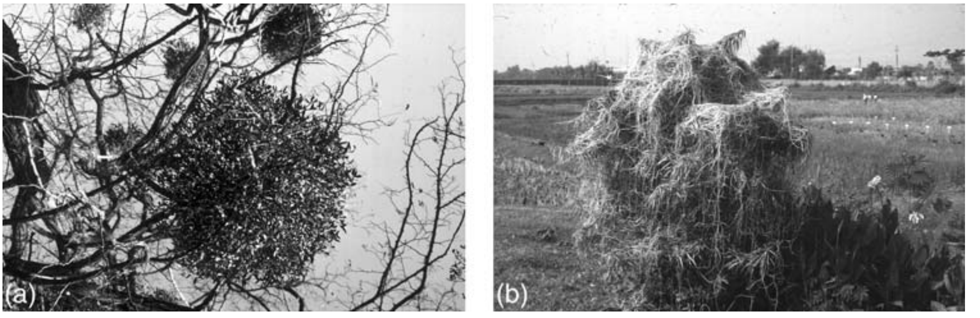

Figure 1.2 (a) *Viscum album* subsp. *album* on *Robinia pseudoacacia* (courtesy of Dr Doris Zuber, Swiss Federal Institute of Technology, Zurich); (b) *Cuscuta reflexa* on an unidentified shrub (reproduced courtesy of Dr Chris Parker and CAB International). A colour reproduction of this figure can be seen in the colour section

seed but relatively small numbers are required to harm the crop. For example, fewer than 1000 and 250 seeds/kg of soil reduced yields of faba beans and peas, respectively, to zero (Linke, Sauerborn and Saxena, 1991; Bernhard Lensen and Andreasen, 1998). As a consequence, in some areas such as North Africa, farmers have been forced to abandon growing these crops (Figure 1.1(b)).

Other genera of parasitic angiosperms such as mistletoe (*Viscum* spp.), dwarf mistletoe (*Arceuthobium* spp.) and dodder (*Cuscuta* spp. and *Cassythia* spp.) also cause diseases which have profound economic and social consequences (Figure 1.2). In the Intermountain Region of the USA, *Arceuthobium americanum* was estimated to cause losses of ca. 500 000 m^3 of lodgepole pine per annum, equivalent to more than 80 per cent of the annual harvest (Hoffman and Hobbs, 1985) and a more recent estimate puts the annual loss at more than 3.2 billion ‘board feet’ of lumber in the USA as a whole (Parker and Riches, 1993).

1.3.2 Fungi

There are at least five reasons why fungi may cause catastrophic plant disease.

(1) They sporulate prolifically, the spores providing copious inoculum which may infect further plants.

(2) Their latent period, i.e. the time between infection and the production of further infectious propagules, usually spores, may be only a few days.

(3) The spores, if they are wettable, may be spread as high-density inoculum in surface water or in droplets by rain-splash. Alternatively, non-wettable spores may be carried long distances by the wind.

(4) They may produce compounds that are phytotoxic and/or a battery of enzymes that destroy the plant’s structure.

(5) Biotrophic pathogens, such as the rusts and mildews, draw nutrients away from the economically valuable part of the plant by the production or induction of growth regulators such as cytokinins and consequently depress yields.

These points will be reviewed in later chapters.

Fungal taxonomy and identification was traditionally based on morphology but, since many fungi are poorly endowed with distinctive morphological features, this approach has led to error and confusion. For example, Marasas and co-workers (1985) reported that about 50 per cent of a collection of 200 *Fusarium* strains reported to be toxigenic in the literature were incorrectly named on the basis of the taxonomic concepts current at the time. Fortunately, DNA sequence data are becoming the norm in fungal classification (see Section 2.5.5) and although these often uphold traditional classifications for higher taxa they frequently do not do so at the species level. All data support the view that fungi may be separated into the four classes originally defined on the basis of the morphology of their sexual structures and the sporulating organs formed after sexual reproduction. These are the Chytridiomycetes, Zygomycetes, Ascomycetes and Basidiomycetes. A further class, the Deuteromycetes, alternatively known as the Fungi Imperfecti, is reserved for those fungi for which no sexual phase is known. Organisms that are highly destructive to plant life are found in all five classes.

Oomycetes, which contain such important plant-pathogenic genera as *Phytophthora, Peronospora* and *Pythium*, have, until recently, been classified as fungi but are more properly placed well away from the fungi in the kingdom, Chromista (Cavalier-Smith, 1998; Baldauf *et al.*, 2000) and are considered separately (Section 1.3.5). Similarly, the Plasmodiophoromycetes, which are sometimes referred to as slime moulds, are not fungi and are therefore also given a section of their own Section 1.3.6). In the following paragraphs we shall only be concerned with plant pathogens which are true fungi.

Chytridiomycetes

Synchytrium endobioticum is the cause of potato wart disease (Figure 1.3). It is an obligate pathogen consisting only of two types of sporangia, winter and summer. Winter sporangia germinate in the spring and release zoospores, which are propelled by a single flagellum, enabling them to move in soil water and reach the living host. Penetrated host cells enlarge and the fungus forms within them the evanescent summer sporangium. Numerous zoospores are rapidly discharged from the summer sporangium and reinfect surrounding cells. Under favourable conditions further summer sporangia are produced, inducing swelling of penetrated cells and those surrounding them and giving rise to the cauliflower-like appearance which is characteristic of the disease (Figure 1.3). Under conditions of stress, zoospores fuse in pairs and form a zygote from which the thick-walled

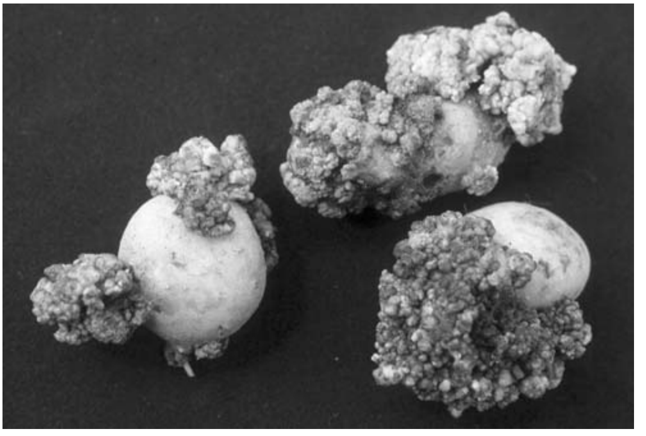

Figure 1.3 Cauliflower-like symptoms of potato wart caused by the Chytridiomycete fungus, *Synchytrium endobioticum* (reproduced courtesy of Dr Hans Stachewicz and CAB International). A colour reproduction of this figure can be seen in the colour section

winter sporangium develops. These are released from rotting warts and may remain viable for at least 30 years, providing a long-term source of inoculum for succeeding crops.

Other members of this class of fungi, while causing little damage themselves, may serve as vectors for viruses (Section 3.3.2). For example, *Olpidium brassicae* may transmit lettuce big vein virus (LBVV) and tobacco necrosis virus (TNV, Figure 1.4).

Zygomycetes

Rhizopus is one example of a genus in the Zygomycetes which causes significant losses of many disparate crop plants such as cassava, groundnuts, sorghum and cucurbits. *Rhizopus stolonifer* is an important cause of postharvest disease in soft fruit (Michailides and Spotts, 1990) and sweet potato (Holmes and Stange, 2002) and *R. oryzae* causes damping off of cotton (Howell, 2002).

Ascomycetes

Many plant pathogenic fungi are Ascomycetes and several fungi that were originally classified as Deuteromycetes are now placed in this class owing to the discovery that they form asci (singular ascus). These are the characteristic sack-like structures of the group which are the result of sexual reproduction, each ascus usually containing eight ascospores, the products of meiosis and one round of mitosis. Normally the Deuteromycete name is retained but the Ascomycete name is also used, particularly when sexual reproduction, leading to the produc-

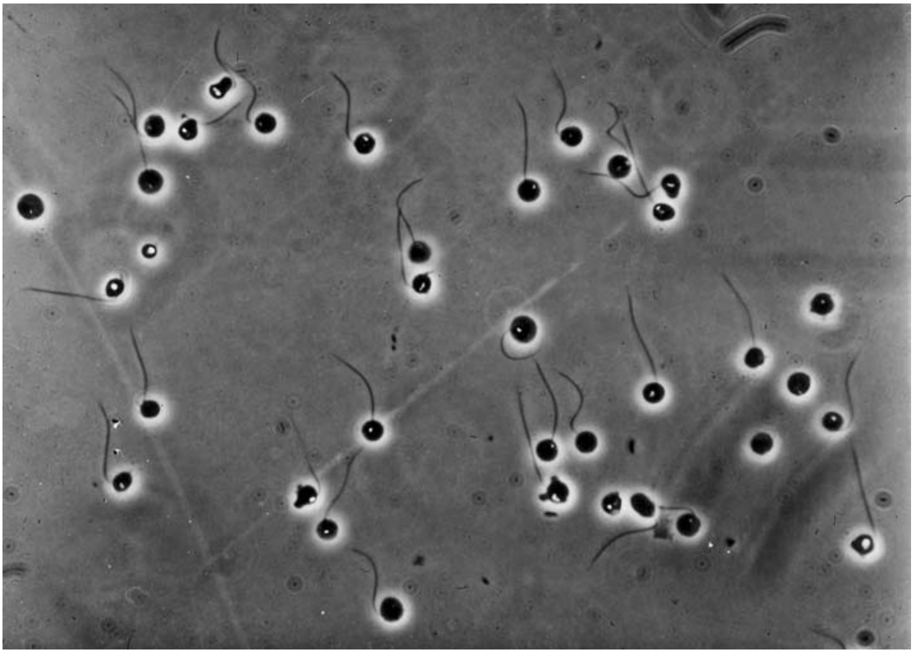

Figure 1.4 Zoospores of *Olpidium brassicae*; these may act as vectors for virus diseases such as lettuce big vein virus and tobacco necrosis virus (courtesy of Ian Macfarlane and Rothamsted Research, Harpenden, Herts., UK)

tion of asci, is common. The Deuteromycete form is known as the anamorph and the Ascomycete form as the teleomorph. For example, the greatest recorded epidemic of a plant disease was that caused by a fungus originally referred to as *Helminthosporium maydis*, the anamorph name. The teleomorph of the same organism is *Cochliobolus heterostrophus* (Figure 1.5).

The fungus was first found on ears and stalks of samples from a seed field in Iowa, USA, in October 1969 where it caused a greyish-black rot but it was not until the next year that the epidemic struck. Then it caused a severe epidemic, particularly in the Midwest and South of the USA, with some areas reporting losses of 50 to 100 per cent. In monetary terms at today's (2003) prices this represents about $\$ 4 \times 10^9$.

The reason for the devastation lay in the widespread use of a gene in the crop for breeding purposes that had the unfortunate pleiotropic effect of conferring acute susceptibility to a variant of the fungus which, up to that time, had caused little damage. The gene concerned was cytoplasmically inherited and conferred male sterility. As it originally came from Texas it was known as the *T*exas *c*ytoplasmic *m*ale *s*terile gene or the *Tcms* gene for short. Plant breeders used the gene in developing high-yielding hybrids as it prevented self-pollination and obviated the need to remove the pollen-bearing structures, the tassels, from the plant destined to be the female parent, a tedious and costly process. A field

Figure 1.5 Symptoms of Southern Corn Leaf Blight (SCLB) caused by *Cochliobolus heterostrophus* (reproduced courtesy of Dr M. Listman, CIMMYT). A colour reproduction of this figure can be seen in the colour section

planted exclusively with *Tcms* maize sets no seed as there is no pollen capable of fertilizing the ovules. To overcome this problem, the farmer either buys a blend, made of *Tcms* seed and seed with normal cytoplasm, or seed which is a hybrid between a *Tcms* parent and a pollen parent containing a restorer gene. Such a gene, as its name implies, restores the fertility of the pollen to the hybrid. The advantages of using *Tcms* in hybrid seed production ensured that the gene became widely distributed and, by 1970, it was present in about 85 per cent of the American maize crop. Ironically, therefore, a technique used to broaden the genetic base of the crop by the production of hybrids had resulted in the uniformity of one part of the cytoplasmic genome – that containing a gene conferring male sterility. Remarkably, this gene had the pleiotropic effect of conferring acute susceptibility to a disease which had previously been of minor importance. The virulent pathogen, which was the cause of the disease, was a variant of *C. heterostrophus* and was specifically aggressive for maize with *Tcms*. It was therefore designated race T to distinguish it from the less virulent race O. Subsequent work showed that race T produced a family of compounds which are specifically toxic to maize bearing the *Tcms* gene. These toxins and the reasons for their specific toxicity to *Tcms* maize are discussed in Chapter 8 (Section 8.4.2).

Claviceps is one of the most notorious plant pathogenic genera in the Ascomycetes. The fungus parasitizes the developing cereal grain and supplants it by a sclerotium, called an ergot, consisting of a hard mat of fungal hyphae, usually somewhat larger than the grain itself. The sclerotia are rich in a number of alkaloids which cause the contraction of smooth muscle. This property has been exploited in childbirth in which the mother is often given an injection of one of the compounds, ergometrine, to aid parturition and to promote the return of the uterus to its normal size after birth. However, in uncontrolled doses, as may occur when grain contaminated with ergot is consumed, horrific symptoms ensue. In the Middle Ages these were regarded as divine punishment for misdeeds and were known as ‘St Anthony’s Fire’. They have been graphically described by Large (1940) as follows: ‘Ergot, through its constrictive action on blood vessels, not only caused abortion in women, it cut off the blood supply to the extremities of the body; hands and feet became devoid of sensation and then rotted most horribly away. In the progress of the ergot gangrene whole limbs fell off at the joints, before the shapeless trunk was released from its torments.’

Sorghum, *Sorghum bicolor*, is the world’s fifth most important cereal crop. Since the 1960s the development and use of F_1 hybrid seed has boosted yields to between 3 and 5 tonnes/hectare under high-input farming conditions but much lower yields, averaging less than 1 tonne/hectare, are obtained when farming inputs are low. Unfortunately, production of F_1 hybrid seed is jeopardized by ergot caused by the fungi, *Claviceps sorghi* and *C. africana*. They enter the host principally through the pistils of unfertilized gynoecia. When pistils are fertilized the fungus grows slowly or fails to grow altogether. The production of hybrids from male sterile lines is therefore particularly hazardous since pollen from the restorer line (which restores fertility to the progeny) may not synchronize with flowering of the male sterile line, thus leaving the pistil unfertilized and susceptible to infection. Production of copious amounts of honeydew oozing from florets is an early symptom of infection (Figure 1.6). Later in the season sclerotia are produced which contain alkaloids but their presence and toxicity has not been as well-established as those of *C. purpurea* (Bandyopadhyay *et al.*, 1998).

A third Ascomycete, *Cochliobolus miyabeanus* (teleomorph name; anamorph = *Helminthosporium oryzae*), is a destructive disease of rice which, under favourable conditions, causes severe losses (Figure 1.7). In 1942, an epidemic occurred in Bengal (now the Province of West Bengal in India and Bangladesh), an area that was normally deficient in both wheat and rice. In 1942, the winter rice crop, reaped in November and December, was exceptionally poor with late cultivars being particularly badly affected. Yield reductions recorded at research stations varied from nearly 40 per cent to over 90 per cent (Padmanabhan, 1973). As a consequence of the shortages, prices escalated early in 1943, putting them beyond the means of ordinary people. Many, who lived in rural areas, left their villages and travelled to the larger cities in search of work and rice. There, ‘finding neither, they slowly died of starvation’ (Padmanabhan, 1973). They numbered two million. However, some scientists remain unconvinced that *C. miyabeanus* was the cause of the disease in West Bengal and suggest that high levels of iron or high aluminium may have been responsible while others suspect that the problem was actually a brown planthopper outbreak (R. S. Zeigler, personal communication).

Figure 1.6 Honeydew on sorghum caused by infection with the fungus *Claviceps africana* (courtesy of Dr F Workneh, Texas Agricultural Experiment Station). A colour reproduction of this figure can be seen in the colour section

Basidiomycetes

Some members of this class of fungi such as the rusts and smuts are highly destructive plant pathogens. Rusts are obligate pathogens and therefore cannot normally be grown in pure culture as demanded by Koch's second postulate. However, since they often produce massive numbers of spores, usually of the rust colour that gives these fungi their name and which, at least under the stereoscan electron microscope, are distinctive, their causal relation to disease is relatively easy to prove – the spores may simply be collected and used as inoculum on test plants. Production of the same type of spores on these plants is clear evidence that the fungus is the cause of the disease. A more stringent test would be to adopt one or more of the serological or nucleic acid procedures detailed in Chapter 2 (Sections 2.5.4 and 2.5.5).

The rusts and smuts are highly specialized with regard to their host ranges but their prolific production of aerially borne spores ensures their continuation as threats to our crops (Figure 1.8). Although the rusts produce small, although abundantly sporulating lesions on their hosts, other members of the Basidiomycetes produce their prolific numbers of spores from large structures known as sporopohores. These are often tree pathogens such as *Ganoderma* and, because of

Figure 1.7 Lesions on rice leaves caused by *Cochliobolus miyabeanus*, often cited as the cause of rice crop failures in 1943 that led to the great Bengal famine in which an estimated 2 million people died (courtesy of Dr. R. S. Zeigler). A colour reproduction of this figure can be seen in the colour section

the shape of their sporophores, they are commonly known as bracket fungi (Figure 1.9).

Deuteromycetes

The Deuteromycetes contain many important pathogens such as species of *Alternaria, Fusarium* and *Helminthosporium*, some of which produce powerful toxins which kill plant cells (Chapter 8) and mycotoxins, compounds of fungal origin that are toxic to people or domestic animals. For example, *Alternaria alternata* f. sp *lycopersici* causes stem canker of tomato on susceptible lines of the plant and produces a host selective toxin (AAL toxin) which is essential for pathogenicity. Remarkably, a number of *Fusarium* species synthesize compounds known as the fumonisins which are structurally related to AAL toxin and are mycotoxins (Section 8.4.1). Other Deutermoycetes produce mycotoxins, the most notorious being those of the *Aspergillus flavus* group which synthesize aflatoxins. Aflatoxin B_1 has high mammalian toxicity and is also extremely carcinogenic,

Figure 1.8 Stripe rust of wheat caused by *Puccinia striiformis*; the orange colour of the lesions on the leaves is given by the copious numbers of spores which they contain. A colour reproduction of this figure can be seen in the colour section

causing liver tumours (Figure 1.10). *A. flavus* and its toxins are frequently found in maize and peanuts (groundnuts).

1.3.3 Nematodes

Nematodes are an important group of plant parasitic organisms, causing crop losses directly by their parasitic activities on the plants they infect and also indirectly by acting as vectors for plant viruses. There are 17 orders of nematodes but only two contain plant pathogens, the Tylenchida and the Dorylaimida with virus vectors found only in the latter (Wyss, 1982). As an example, *Ditylenchus dipsaci* attacks over 450 different plant species, including many weeds (Goodey, *Franklin and Hooper*, 1965) and is one of the most devastating nematode species