JOHN A. LUCAS

PLANT PATHOLOGY AND PLANT PATHOGENS

FOURTH EDITION

with website

WILEY Blackwell

Plant Pathology and Plant Pathogens

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Fourth Edition

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Contents

Preface

Plant pathology is an applied science concerned primarily with practical solutions to disease problems in agriculture, horticulture, and forestry. The study of plant disease and the development of methods for its control continue to be vital elements in the drive to improve crop productivity and ensure global food security. Projected world population growth and the impacts of climate change make this a priority. From a more strategic perspective, the experimental analysis of the interactions between plants and pathogens has become fertile territory for scientists interested in emerging areas of plant biology, including recognition and response systems, signal pathways, and innate plant immunity. The use of molecular genetic techniques has provided new insights into how pathogens cause disease and how plants defend themselves against attack. In turn, this new understanding is suggesting novel ways in which plant disease might be controlled.

This book provides an introduction to the main elements of plant pathology, including the applied aspects of disease identification, assessment and control, and fundamental studies of host–pathogen interactions. The aim is to place the subject not only in the context of agricultural science but also in the wider spheres of ecology, population biology, cell biology, and genetics. The impact of molecular biology and genomics on the diagnosis and analysis of plant disease is a recurrent theme.

A large number of people have helped me in the production of this new edition. First, I should acknowledge the invaluable help of many of my colleagues at Rothamsted Research who have generously provided advice, assistance, and materials for use in the book. They include Kim Hammond-Kosack, Jason Rudd, Kostya Kanyuka, Nicola Hawkins, Ana Machado, Bart Fraaije, Jon West, Stephanie Heard, Anastasia Sokolidi, Kevin King, John Jenkyn, Roger Plumb, James Bell, David Hughes, Mike Adams, Graham Shephard, and Sally Murdoch. Joe Helps advised on mathematical modeling as well as replotting data. The library staff, Tim Wales, Catherine Fernhead, and Chris Whitfield, helped with tracing publications and scanning figures. Special thanks are due to Lin Field and Sheila Bishop who supported me as a visiting worker in the Biointeractions and Crop Protection department. Numerous others in the plant pathology and crop protection community have also supplied images, articles, advice, and data for use in figures and tables, including Bruce McDonald, Mike Coffey, George Sundin, Pamela Gan, Richard O'Connell, Petra Boetink, Yaima Arocha-Rosete, Geert Haesaert, David Cooke, Paul Birch, Diane Saunders, Judith Turner, Moray Taylor, Sarah Holdgate, Nicola Spence, Ana Lopez, Hans Cools, Mike Davey, Jurriaan Ton, Stephen Rolfe, Paul Bowyer, Clive Brasier, Joan Webber, John Mansfield, Lili Huang, Victoria Routledge, Lucy Carson-Taylor, Jason Pollock, Dierdre Haines, David Whattoff, Graham Matthews, Haydn Beddows, Dennis Gonsalves, and Malcolm Briggs. Thanks go to Holly Regan-Jones for her skilful copy editing and Dave Gardner who re-drew many of the Figures. Vimali Joseph provided vital support during the final production process. My appreciation should also be extended to previous colleagues at the University of Nottingham, especially Alison Daniels and the late Brian Case, who took many of the studio photos featured in this edition. Space does not allow me to acknowledge the many other colleagues who agreed to the use of published results.

Finally, thanks are also due to my daughter Maria Gabriella, whose grasp of digital technology greatly exceeds my own, and my wife Adélia, not only for her forbearance throughout the time taken to complete this project but also for her active contribution searching out all manner of useful information on the internet.

John A. Lucas
January 2020

List of Abbreviations

ABA	Abscisic acid
AUDPC	Area under disease progress curve
BCA	Biological control agent
CDA	Controlled droplet application
CDPK	Calcium-dependent protein kinase
CK	Cytokinin
CWDE	Cell wall-degrading enzyme
DAMP	Damage-associated molecular pattern
DSS	Decision support system
EHM	Extrahaustorial membrane
ELISA	Enzyme-linked immunosorbent assay
ETI	Effector-triggered immunity
GA	Gibberellic acid
GLA	Green leaf area
GPS	Global positioning system
GWAS	Genome-wide association studies
HGT	Horizontal gene transfer
HIGS	Host-induced gene silencing
HLB	Huanglongbing disease of citrus, also known as citrus greening
HR	Hypersensitive response
HRGP	Hydroxyproline-rich glycoprotein
Hrp	Hypersensitive response and pathogenicity
HST	Host-specific toxin
IAA	Indole acetic acid
IPPC	International Plant Protection Convention
ISR	Induced systemic resistance
JA	Jasmonic acid
LAMP	Loop-mediated isothermal amplification assay
LGT	Lateral gene transfer
LPS	Lipopolysaccharide
LYD	Lethal yellowing disease of coconuts
MAMP	Microbe-associated molecular pattern
MAPK	Mitogen-activated protein kinase

NDVI	Normalized difference vegetation index
NGS	Next-generation sequencing, also known as high-throughput sequencing
NLR	Family of receptor proteins characterized by nucleotide-binding site and leucine-rich repeat domains
NO	Nitric oxide
NRPS	Nonribosomal peptide synthase
PAL	Phenylalanine ammonia lyase
PAMP	Pathogen-associated molecular pattern
PCD	Programmed cell death
PCR	Polymerase chain reaction
PG	Polygalacturonase
PGIP	Polygalacturonase-inhibiting protein
PKS	Polyketide synthase
PRA	Pest risk analysis
PRR	Pattern recognition receptor
PTI	PAMP-triggered immunity
QTL	Quantitative trait locus
REMI	Restriction enzyme-mediated integration
RIP	Ribosome-inactivating protein
RLK	Receptor-like kinase
RLP	Receptor-like protein
ROS	Reactive oxygen species
RT-PCR	Real-time polymerase chain reaction
RUE	Radiation use efficiency
SA	Salicylic acid
SAR	Systemic acquired resistance
SIGS	Spray-induced gene silencing
SNP	Single nucleotide polymorphism
T3SS	Type 3 secretion system
UAV	Unmanned aerial vehicle
WRKY	(pronounced *worky*) Family of transcription factors containing a WRKY amino acid domain

About the Companion Website

This book is accompanied by a companion website:

The URL is **www.wiley.com/go/Lucas_PlantPathology4**

The website includes:

Figures from the book

Part I

Plant Disease

We see our cattle fall and our plants wither without being able to render them assistance, lacking as we do understanding of their condition.

(J.C. Fabricius, 1745–1808)

The health of green plants is of vital importance to everyone, although few people may realize it. As the primary producers in the ecosystem, green plants provide the energy and carbon skeletons upon which almost all other organisms depend. The growth and productivity of plants determine the food supply of animal populations, including the human population. Factors affecting plant productivity, including disease, therefore affect the quantity, quality, and availability of staple foods throughout the world. Nowadays crop failure, due to adverse climate, pests, weeds, or diseases, is rare in developed agriculture, and instead there are surpluses of some foods. Nevertheless, disease still takes a toll, and much time, effort, and money are spent on protecting crops from harmful agents. In developing countries, the consequences of plant disease may be more serious, and crop failure can damage local or national economies, and lead directly to famine and hardship. Improvements in the diagnosis and management of plant disease are a priority in such instances. Furthermore, the pressures on plant productivity are increasing. The area of cultivated land available per person on the planet declined from around 0.4 ha in the 1960s to less than 0.3 by the year 2000 (FAO data), and as the human population continues to multiply the area will further decrease.

As well as supplying staple foods, plants provide many other vital commodities such as timber, fibers, oils, spices, and drugs. The use of plants as alternative renewable sources of energy and chemical feedstocks is becoming more and more important, as other resources such as fossil fuels are depleted and the need to mitigate climate change becomes a priority. Finally, the quality of the natural environment, from wilderness areas to urban parks, sports fields, and gardens, also depends to a large extent on the health of plants.

Healthy plants provide a series of benefits for the farmer, food chain, and the environment (Table 1). The yield and quality of crop products are ensured, and healthy plants are more efficient at using precious resources such as water and nutrients. In doing so, they

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Table 1 Benefits of healthy plants

- Greater yield
- Superior quality
- More competitive with weeds
- Easier harvesting
- Fewer residual nutrients, reduced pollution
- Improved control of soil erosion
- Lower carbon footprint

also prevent losses of nitrogen and other nutrients to the wider environment, and reduce pollution of rivers and ground water, which in many areas is a potential problem for drinking supplies. Vigorous, healthy plants are more competitive with weeds, and are easier to harvest than crops that are stunted or collapsed. Plant root systems play an important role in reducing soil erosion, and thereby help to conserve another precious resource. Finally, given the mounting concerns about climate change, it should be noted that healthy crops have a lower carbon footprint than diseased crops, due to their greater productivity and more efficient use of inputs per area of cultivated land.

The science of **plant pathology** is the study of all aspects of disease in plants, including causal agents, their diagnosis, physiological effects, population dynamics and control. It is a science of synthesis, using data and techniques from fields as diverse as agriculture, microbiology, meteorology, engineering, genetics, genomics, and biochemistry. But first and foremost, plant pathology is an applied science, concerned with practical solutions to the problem of plant disease. Part of the appeal of the subject is to be found in this mixture of pure and applied aspects of biology.

The scope of plant pathology is difficult to define. On a practical level, any shortcoming in the performance of a crop is a problem for the plant pathologist. In the field, he or she may well be regarded in the same way as the family doctor – expected to provide advice on all aspects of plant health! A distinction is often drawn between **disease** caused by infectious agents and **disorders** due to noninfectious agents such as mineral deficiency, chemical pollutants, or adverse climatic factors. The main emphasis of this book is on disease caused by plant pathogenic microorganisms such as fungi, oomycetes, bacteria, and viruses. Under favorable conditions, these pathogens can multiply and spread rapidly through plant populations to cause destructive disease **epidemics**. Many of the principles discussed apply equally well, however, to other damaging agents such as insect pests and nematodes.

A fundamental concept in plant pathology is the **disease triangle** (Figure 1) which shows that disease results from an interaction between the host plant, the pathogen, and the environment. This can be enlarged to include a further component, the host–pathogen complex (Figure 1), which is not simply the sum of the two partners, as the properties of each are changed by the presence of the other.

A comprehensive analysis of plant disease must take all four components into account. Obviously, one needs to be familiar with the characteristics of the host and the pathogen in isolation. The successful establishment of a pathogen in its host gives rise to the host–pathogen complex. Unraveling the dynamic sequence of events during infection, the

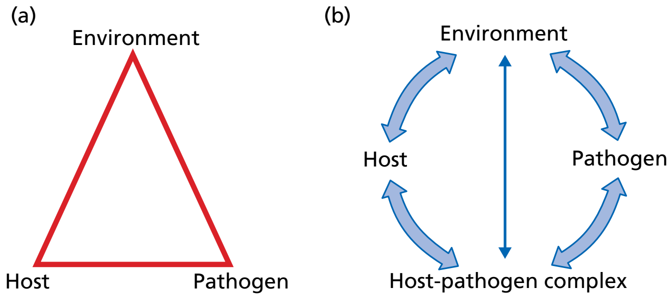

Figure 1 The disease triangle (a) incorporating the host–pathogen complex (b).

molecular "cross-talk" taking place between the partners, is one of the most challenging problems in experimental biology. In addition, the effects of the environment on each of other components must be understood. This includes not only physical and chemical factors but also macro- and microbiological agents. The two-way arrow between the host and the environment in Figure 1b should not be overlooked, as populations of crop plants often have important effects on their surrounding microclimate. For example, the relative humidity within a crop canopy is higher than that outside and this will favor the development of some microorganisms. Plants attacked by pests and pathogens often produce volatile compounds that can act as signals sensed by neighboring plants. Effects of pathogens on the environment are more subtle but may be significant; some fungi, for instance, produce the volatile hormone ethylene, which can in turn affect the development of adjacent host plants.

This book is intended to provide an outline of the main elements of modern plant pathology. The approach is designed to achieve a balance between laboratory and field aspects of the subject, and to place the phenomenon of plant disease in a wider biological context. Research in plant pathology can be broadly divided into **tactical** and **strategic** aspects. The former is concerned with providing solutions to disease problems by identifying causal agents and evaluating the most cost-effective options for their control. The latter is longer term and aims to understand fundamental aspects of plant disease such as pathogen ecology, population biology, host–pathogen interactions, and plant immunity. This knowledge can then be applied to devise improved methods of disease control.

The book is divided into three parts. The first focuses on the problem of plant disease, the causal agents and their significance, disease diagnosis, and the development of epidemics in plant populations. This account highlights the influence of environmental factors on the multiplication and spread of pathogens, and the use of climate data in disease prediction. The second part deals with host–pathogen interactions: how pathogens gain entry to the host, how their growth and development in the plant lead to disease symptoms, and how the plant responds. The outcome of any host–pathogen confrontation depends on a dynamic interplay between factors determining microbial pathogenicity and the active mechanisms of plant immunity. This interaction ultimately determines host–pathogen specificity, whereby any pathogen is able to cause disease in only a restricted range of host plants. Plant and molecular biologists are studying host–pathogen systems as experimental models to probe the mechanisms of gene expression and regulation, and to reveal details of the evolutionary "arms race" taking place between plants and pathogens. Part III deals with the practical business of disease control, often described as **crop protection**. This covers the management of disease by means of chemicals, breeding for resistance, and alternative biological approaches. Finally, the combined use of cultural practices and all these other measures to provide sustainable, integrated systems for disease control is described.

A comprehensive treatment of individual diseases and the methods used in their control is beyond the scope of a text of this length. For the sake of brevity, specific pathogens or the diseases they cause are often mentioned without further explanation. This approach may be likened to that adopted in many ecology texts, in which the reader is expected to be familiar with most of the higher plants or animals discussed therein. There is, however, an appendix listing all the pathogens and diseases mentioned in the book, together with brief details which will enable the reader to obtain further information about particular diseases. More detail concerning specific aspects of pathology may be obtained by consulting the recommended further reading.

Further Reading

Books

Agrios, G. (2005). *Plant Pathology*, 5e. Amsterdam: Elsevier Academic Press.

Schumann, G.L. and D'Arcy, C.J. (2009). *Essential Plant Pathology*, 2e. St Paul, Minnesota: American Phytopathological Society Press.

Strange, R.N. (2003). *Introduction to Plant Pathology*. Chichester: Wiley.

Reviews and Papers

Foley, J.A., Ramankutty, N., Brauman, K.A. et al. (2011). Solutions for a cultivated planet. *Nature* 478: 337–342.

Godfray, H.C.J., Beddington, J.R., Crute, I.R. et al. (2010). Food security: the challenge of feeding 9 billion people. *Science* 327: 812–818.

Savary, S., Bragaglio, S., Willocquet, L. et al. (2017). Crop health and its global impacts on the components of food security. *Food Security* 9: 311–327. https://doi.org/10.1007/s12571-017-659-1.

Scientific Journals

Many scientific journals contain reviews and research papers relevant to plant pathology. One especially useful source is the Annual Review of Phytopathology. Others include:

Advances in Botanical Research
Annals of Applied Biology
Crop Protection
European Journal of Plant Pathology
Fungal Genetics and Biology
Journal of Phytopathology
Molecular Plant–Microbe Interactions

Molecular Plant Pathology
Mycological Research
New Phytologist
Pest Management Science
Plant Disease
The Plant Cell
The Plant Journal
Physiological and Molecular Plant Pathology
Phytopathology
Plant Pathology
PLOS Pathogens
American Phytopathological Society: www.apsnet.org
British Society of Plant Pathology: www.bspp.org.uk
European Foundation for Plant Pathology: www.efpp.net
Review of Plant Pathology, an abstracts database of plant pathology research: www.cabi.org/publishing-products/online-information-resources/review-of-plant-pathology

1

The Diseased Plant

Since it is not known whether plants feel pain or discomfort, and since, in any case, plants do not speak or otherwise communicate to us, it is difficult to pinpoint exactly when a plant is diseased.

(George N. Agrios, 1936–2010)

The significance of disease in plants varies depending upon biological, agricultural, and socioeconomic factors. At one extreme, disease may be so severe that the farmer is faced with total crop failure, and the need for control measures is immediately obvious. In other cases, it may be difficult to define disease symptoms, the cause of the problem is not initially clear, and any benefits obtained from control measures are not easy to predict. This chapter discusses the nature of disease and surveys the range of pathogens, pests, and other agents which adversely affect plants. The impact of disease, both in natural plant communities and in agriculture, forestry and horticulture, is then considered.

Concepts of Disease

To fully understand the nature of disease, one must first identify the processes occurring during the growth and development of the healthy plant. Such an analysis may be done at three levels:

- the sequence of events comprising the normal plant life cycle
- the physiological processes involved in plant growth and development
- the metabolic pathways and molecular reactions underlying these processes.

Seed germination, maturation of vegetative structures, the initiation of reproduction, and the formation and dispersal of fruits and seeds are all critical phases of the life cycle at which disease may occur (Figure 1.1). At each stage in this developmental sequence, the integration of several physiological processes is essential for the continued development of the plant. Cell division and differentiation, the fixation and utilization of energy (photosynthesis and biosynthesis), transport of water and nutrients (transpiration and translocation), and storage of reserve compounds are all necessities for growth. Each of these functions involves a complex series of molecular events which comprise the overall metabolism of

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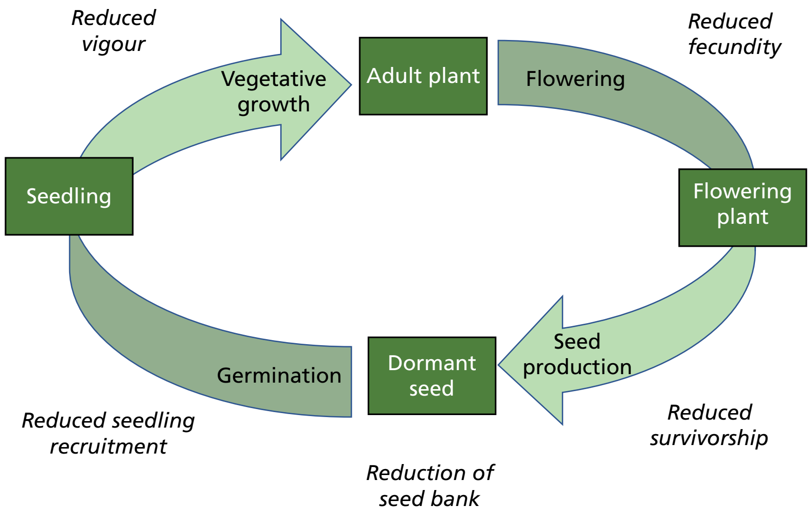


Figure 1.1 A plant life cycle and some effects of disease.

the plant. The nature and regulation of metabolism are themselves determined by the genetic make-up of the plant, interacting with the environment in which it is growing.

Disease may disrupt the activities of the plant at one or more of these levels. Some disorders involve subtle alterations in metabolism which do not affect the successful completion of the life cycle. Certain diseases caused by viruses have only slight effects on the growth of the plant; in such cases, it may be difficult even to recognize the existence of a disease problem. For instance, potato virus X was known as potato healthy virus until virus-free seed potatoes became widely available. Comparisons with infected plants then showed the virus to be capable of causing a 5–10% loss in yield. Other more destructive diseases may interfere with numerous molecular, cellular, and physiological processes and lead to premature death of the plant.

While everyone is familiar with the idea of disease, in practice there may be difficulties in drawing a precise distinction between healthy and diseased plants. No single definition of disease has found universal acceptance; the most widely used involves some reference to the "normal" plant, for instance "a condition where the normal functions are disturbed and harmed" (Holliday 1989). However, there is no consensus as to the exact extent of deviations from this norm which may constitute the diseased state. The problem of defining normality, in terms of the processes outlined above, is further complicated by the variation inherent in all plant populations. Such variation is particularly common in natural populations, especially where hybrids occur, but even within apparently uniform populations of crop plants, there may be differences between individuals. Such differences either have a genetic basis or are due to environmental factors operating during the growth of the crop. If, for instance, one sows seed of an old cereal variety alongside that of a modern, improved cultivar, one will observe major differences between the two crops. In particular, the modern cultivar will be shorter, form much larger seed heads and heavier grains, and the final yield will be greater. The difference in this case is due to intensive selection and genetic improvement rather than to any disease in the old variety, but this example highlights the importance of understanding the initial potential of the plant before accurate estimates of disease can be obtained.

Damage or Disease?

It can be argued that short-term harmful effects on plants, such as injury due to grazing, do not constitute disease. Indeed, some plants, such as the grasses, are well adapted to regular grazing and respond with increased growth if so affected. In cases where damage is sustained over a longer period of time, such as progressive destruction of roots by migratory nematodes or distortion of aerial shoots by exposure to persistent herbicides, the outcome is clearly within the scope of pathology. However, these fine distinctions are of limited use in arriving at a working definition of disease. Such a definition will depend in part on the situation in which it is intended to be used. For example, the biochemist may well be concerned with a malfunction involving a single enzyme and hence view disease as a specific metabolic lesion, whereas the farmer is normally only interested in changes which affect the overall performance of the crop and reduce its value.

Although at present, definitions of disease lack precision, it may ultimately be possible to describe all malfunctions in terms of biochemical changes. To date, this has been achieved in only a few exceptional cases, notably in diseases caused by fungi which produce host-specific toxins, where all the symptoms are due to a single toxic compound acting at a specific target site (see Chapter 8).

Symptoms of Disease

A doctor diagnoses illness in a patient by looking for visible or measurable signs that the body is not functioning normally. Such signs are known as **symptoms** and they may occur singly or in characteristic combinations and sequences. For example, someone suffering from influenza may have a sore throat, fever, and muscular aches and pains. Such a group of symptoms occurring together and in a regular sequence is termed a disease **syndrome**. For many diseases, the occurrence of a particular combination of symptoms is sufficient to arrive at an accurate diagnosis. Alternatively, symptoms may be common to a wide variety of diseases (for instance, fever is a generalized response to both infection and certain types of injury). In such cases, detailed microbiological and biochemical analyses will be necessary to detect other diagnostic symptoms.

Similar considerations apply to the diagnosis of disease in plants. Just as with doctors and human disease, plant pathologists must be aware of the range of visual disease symptoms, the organs affected (Figure 1.2) and what these suggest as the cause of the problem.

The major symptoms of disease in plants are listed in Table 1.1 on the basis of the functions affected. This approach is used because it directs attention to the underlying nature of the disorder. For instance, the presence of galls or other cancerous growths immediately suggests some malfunction in the control of cell division; this in turn implicates a hormonal imbalance and/or genetic change in host cells. It should be realized that this classification of symptoms is to some extent arbitrary and nonspecific. Permanent wilting provides

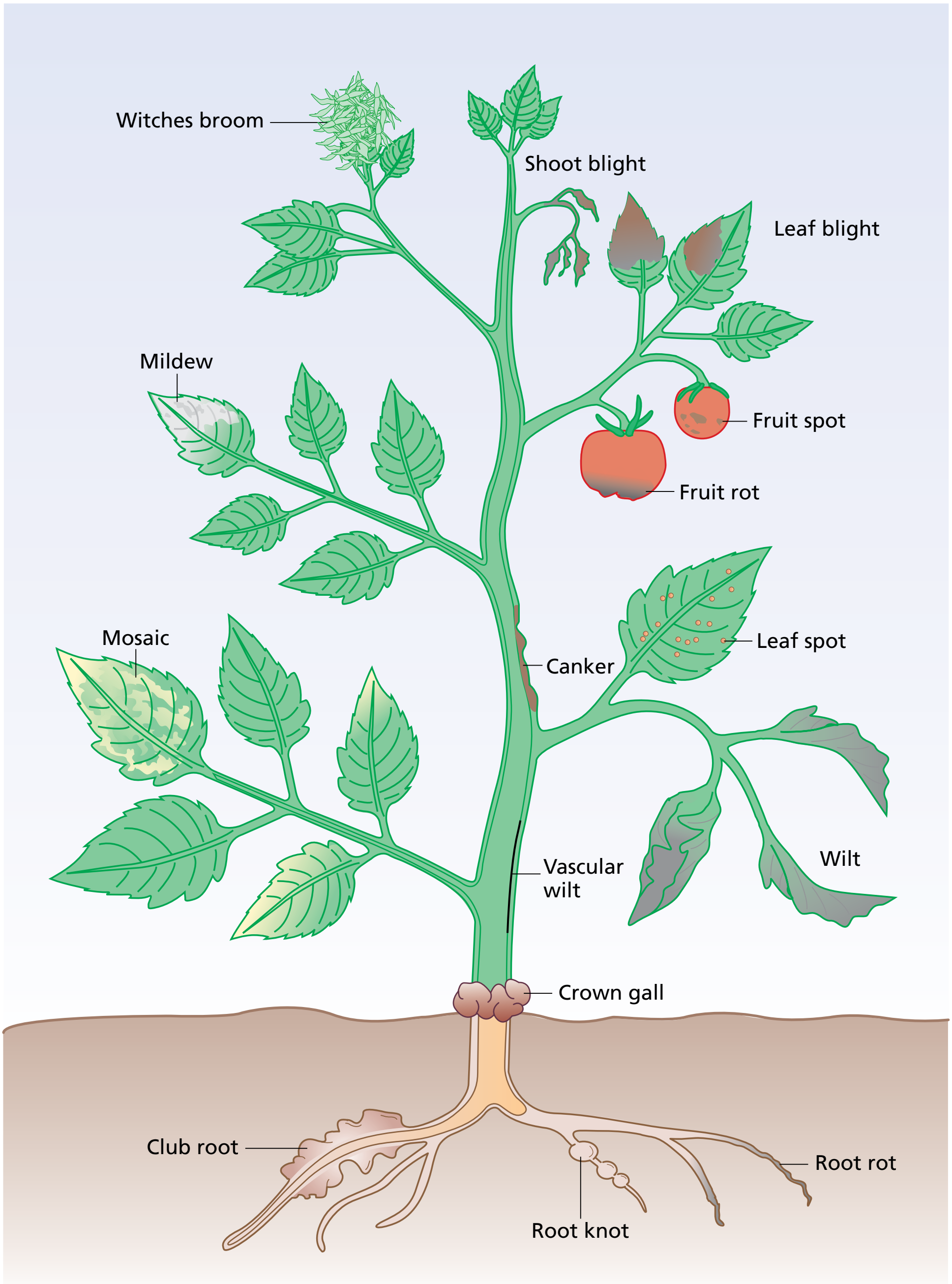


Figure 1.2 Some disease symptoms caused by pathogens infecting different plant organs.

Table 1.1 Symptoms of disease in plants

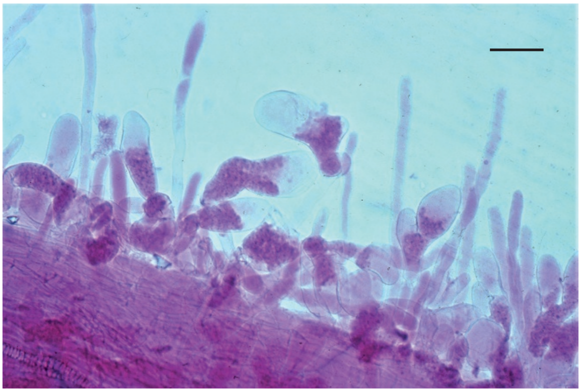
Symptom	Function affected	Examples
Stunting	General development	Take-all of cereals, barley yellow dwarf, Napier grass stunt (phytoplasma)
Necrosis (cell death)	General	Whole plant – damping off of seedlings
		Leaf tissues – potato late blight, botrytis gray mold of vegetables and ornamentals
		Storage tissues – *Erwinia* and *Dickeya* rot of potatoes and vegetables
		Woody tissues – apple canker, fireblight, chestnut blight
Chlorosis	Photosynthesis	Cereal rusts, beet mild yellowing virus, halo blight of bean, cassava mosaic diseases
Wilting	Water relations	Panama disease of bananas, *Verticillium* wilt of tomatoes, bacterial wilt of cucurbits
Hypertrophy	Growth regulation	Club root of brassicas, maize smut, peach leaf curl
Hyperplasia	Growth regulation	Crown gall, cocoa witches broom, peach leaf curl
Leaf abscission	Growth regulation	Leaf blight of rubber, coffee rust, black spot of roses
Etiolation	Growth regulation	Bakanae disease of rice
Inhibition of flowering and fruiting	Reproduction	Choke of grasses
		Ergot of grasses, cereal smut diseases
Abnormal coloration	Pigment synthesis	Grapevine leaf roll virus, citrus greening, tulip breaking virus

a useful example. Although this symptom suggests that something is interfering with the uptake and transport of water, the symptom itself tells us little about the actual site or cause of the interference. The problem could be due either to a blockage in the vascular system, as in vascular wilt diseases, or to a general destruction of root tissues. It is also possible that the problem has little to do with water uptake or transport; in some diseases, such as infections of leaves by rust fungi, wilting is a sign of excessive water loss due to increased transpiration.

The symptoms listed in Table 1.1 will also interact in numerous ways. In club root of cabbage, the basic symptoms are hypertrophy (abnormal enlargement of cells) and hyperplasia (uncontrolled cell proliferation) in root tissue (Figure 1.3), but the first visible symptom is often wilting of the aerial parts of the plant. Any disruption of normal root development inevitably affects other functions such as water and nutrient transport. In view of the highly integrated nature of life processes, it is hardly surprising that attempts to define symptoms often lack precision.

The relative importance of any symptom will vary, depending not only upon its duration and severity but also on the habit or life form of the plant affected. Hence,

(a)



(b)

Figure 1.3 Club root disease of brassicas. (a) Primary infection causes distortion of root hairs, which contain plasmodia of the pathogen *Plasmodiophora brassicae*. Bar = 50 μm (b). Secondary infection of the main root leads to division and enlargement of cortical cells to produce the typical "clubbed" root symptom. Photo by Brian Case.

(a) (b)

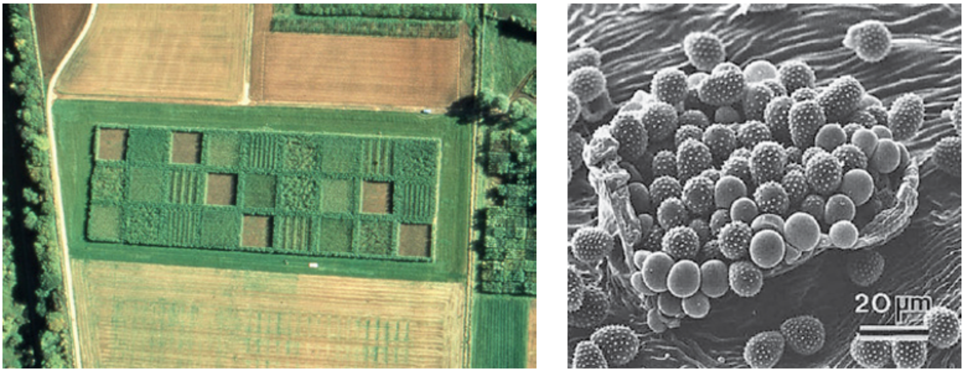


Figure 1.4 Rust of willows caused by *Melampsora* species. (a) Aerial view of experimental trial of willow clones in summer. Plots which appear empty have lost their leaves due to severe rust infection. *Source:* Courtesy of D.J. Royle. (b) Scanning electron micrograph of rust pustule on willow leaf showing spiny urediospores of the fungus. *Source:* Spiers and Hopcroft (1996).

necrosis in the stem of an herbaceous seedling will probably lead to the death of the whole plant, while necrotic lesions (known as cankers) in the stem of a woody perennial may only result in the loss of a twig or branch. If, however, such a lesion girdles the trunk of a tree, then translocation will be disrupted to the extent that the plant will die.

Pathogens which actually kill plants are the exception. More commonly, disease symptoms indicate an impairment of the efficiency of plant physiological and metabolic processes (Table 1.1). Some symptoms, such as local changes in pigmentation, may be trivial in terms of overall plant performance. Often, the most important consideration is the stage in the life cycle at which symptoms first appear. Severe chlorosis or even necrosis of the first-formed leaves of a cereal may have little effect upon the final yield, as these leaves senesce naturally during crop growth, and most of the photosynthetic products required for grain filling are provided by the top three leaves and ear tissues. Accelerated abscission of leaves is unlikely to be a problem in annual herbaceous plants but in perennials, it may exert a severe drain on the food reserves of the plant. For instance, Figure 1.4 shows defoliation of some willow clones due to infection by the rust fungus *Melampsora*. Loss of photosynthetic tissue reduces the biomass produced by the crop. A similar symptom can be seen in coffee bushes affected by another rust, *Hemileia*, or in rubber trees affected by the leaf blight fungus *Microcyclus ulei*. In both these evergreen crops, early leaf fall is often followed by the production of a second flush of leaves. If these are also prematurely lost due to further infection then the plant loses vigor and may eventually die.

While visual symptoms are still routinely used to diagnose diseases and disorders in crops growing in the field, in recent years a range of molecular assay techniques have become available to directly detect the agents causing the symptoms. Such molecular diagnostics are discussed in more detail in Chapter 4.

Causes of Disease

Any agent capable of adversely affecting green plants may be regarded as lying within the scope of plant pathology. The principal agents involved in plant disease are shown in Figure 1.5. Partial or total crop failure may be due to one or more agents. Where more than one agent is responsible, each may act independently, or they may interact. In the latter instance, there may be **synergism**, that is, two or more agents acting in combination to cause symptoms that are more severe than those produced by either agent alone. Synergism has been demonstrated to occur with several combinations of viruses. For example, tobacco mosaic virus and potato virus X each cause relatively mild mottling symptoms in tomato. But if by chance they both occur together in the same host, then severe necrosis develops and this may even result in the death of the plant.

A useful distinction can be drawn between animate (**biotic**) and inanimate (**abiotic**) causes of disease (Figure 1.5). Many of the animate agents, including the microbial **pathogens**, the parasitic angiosperms, and some of the animal pests, are infectious. Due to their capacity for growth, reproduction, and dispersal, these agents spread from one host plant to another. Under particularly favorable conditions, they may be dispersed rapidly over wide areas and even entire continents.

Pests

Among the animals exploiting plants are many pests which cause damage to roots, leaves, shoots, flowers, and fruits. Usually these pests, which include insects such as aphids and leafhoppers, and some nematodes, spend relatively brief periods on individual plants

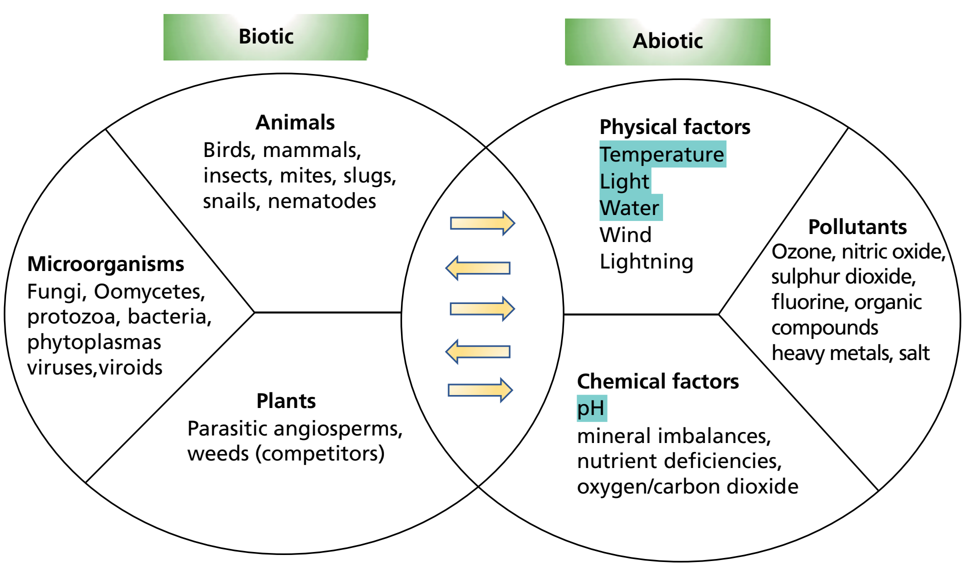


Figure 1.5 Agents responsible for plant disease, disorders, and damage. Highlighted factors are damaging when extremes occur.

before moving on to explore new food supplies. Other pests, such as leaf miners, gall-forming sawflies, and endoparasitic nematodes, spend their entire life cycle, or a major part of it, on one plant. Pest attack may result simply in a drain on host nutrients or, alternatively, in extensive destruction of tissues. Aphids and whiteflies on leaves and stems extract sap from the phloem with almost clinical efficiency. Many caterpillars are simply small herbivores; nevertheless, they can consume large areas of the leaf lamina.

Other pests cause more complex host responses or symptoms. Developing gall wasp larvae induce the formation of morphologically characteristic and often pigmented galls on leaves, while nematodes such as *Meloidogyne* spp. cause swellings, termed “knots,” on the roots of tomatoes and potatoes. When these root-knot nematodes and the related endoparasitic cyst nematodes penetrate root tissues, host cells adjacent to the vascular system become enlarged and provide a specialized feeding site where nutrients are transferred to the sedentary worm. Such pests often show highly specialized adaptions to their respective hosts and, conversely, the plants mount defense reactions in response to attack which are similar to those induced by pathogenic microorganisms. Nematodes are of particular importance in the tropics where they damage numerous crop species, but some are also serious pests on temperate crops; for instance, cyst nematodes are the number 1 pest problem on potatoes in the UK and have infested around two-thirds of the land on which the crop is grown.

Larger animals such as birds or mammals can also be destructive pests. Winter grazing by rabbits can seriously reduce the final yield of autumn-sown crops such as wheat and oilseed rape. In Europe, pigeons also cause damage to oilseed rape, while in parts of Africa flocks of seed-eating finches, such as *Quelea*, are a major threat to crops of sorghum and millet.

Parasitic Plants and Weeds

Higher plants may cause disorders of or damage to other plants, either by acting directly as parasites diverting nutrients and water or as vigorous competitors or antagonists within mixed populations. Parasitic angiosperms are rare enough to be curiosities in many cool temperate countries, but elsewhere they are nuisances or economically important parasites (Table 1.2, Figure 1.6). The dwarf mistletoes, *Arceuthobium*, can kill or deform pines and other conifers, and even minor attacks reduce the quality of timber by causing the production of numerous large knots and irregularly grained, spongy wood. These parasites spread their sticky seeds by an explosive dispersal mechanism, leading to patches or foci of infestation within a plantation. By contrast, root parasites such as *Orobanche* and witchweed, *Striga*, produce numerous tiny seeds which lie dormant in the soil. The seeds are triggered to germinate by a stimulant from host roots. The parasite then attaches itself to the root by means of a specialized organ and diverts water and nutrients, leading to wilting, chlorosis, and stunting of the host. These parasites are difficult to control due to the large number of seeds they produce (in the case of *Striga*, as many as 200 000 per plant) and the long periods over which they remain viable.

On a world scale the most important angiosperm parasite is *Striga hermonthica* which attacks cereals such as maize, sorghum, millet, and rice. In many of the agricultural areas where it is most prevalent, for example sub-Saharan Africa, there are insufficient resources

Table 1.2 Angiosperms parasitic on other higher plants

Family, common name, genus	Geographic area	Crops attacked
Convolvulaceae		
Dodder (*Cuscuta*)	Europe, North America	Alfalfa, clover, potatoes, sugar beet
Lauraceae		
Dodder (*Cassytha*)	Tropics and subtropics	Citrus trees
Loranthaceae		
Dwarf mistletoe (*Arceuthobium*)	Worldwide	Gymnosperms
American true mistletoe (*Phoradendron*)	North America	Angiosperm trees
European true mistletoe (*Viscum*)	Europe	Angiosperm trees, especially apple
Orobanchaceae		
Broom rape (*Orobanche*)	Europe	Tobacco, sunflower, beans
Scrophulariaceae		
Witchweed (*Striga*)	Africa, Asia, Australia, North America	Maize, sorghum, rice, cowpea

to support expensive control measures and infested land may eventually be abandoned. Recently, cultivation systems have been developed that reduce *Striga* infestation by intercropping the cereal host with a different crop, usually a legume, that suppresses infection by the parasite (see later in this chapter). *Orobanche* is a significant problem in sunflower, tobacco, tomato, and especially faba bean, with a substantial proportion of the crop area in the Mediterranean region affected.

The deleterious effects of other higher plants are due to competition for space, light, water, and nutrients. Species which are vigorous competitors with crop plants are usually described as **weeds**. As well as affecting crop development, weeds may interfere with harvesting and their seeds can contaminate grain samples. They may also be important as alternative hosts for pests or pathogens which can subsequently spread to crops. In addition to direct competitive effects, some plants produce chemicals which inhibit the growth of neighboring plants. This phenomenon, analogous to microbial antibiosis, is known as **allelopathy**. Plant roots release a diverse range of chemicals which can act as potential inhibitors or defense compounds, but it is difficult to determine the extent to which these interactions operate in nature. Allelopathy is believed to influence plant succession and distribution in natural communities, and may also have significant effects in agricultural systems. The chemicals involved are of interest both as potential herbicides and as signal molecules affecting the growth and behavior of other organisms. The suppression of *Striga* by some legumes, described earlier, has been shown to be due to a combination of compounds that stimulate "suicidal germination" in the absence of the host and inhibitors that interfere with infection of roots.