CHAPTER 2

Scope and Contributions of Plant Pathology

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I. Introduction

Plant pathology sweeps across most of the sciences in botany. It dips into zoology when animals cause disease. It must deal with soils, meteorology, physics, chemistry. This is precisely the same situation as prevails in medicine and veterinary science.

The chemist must deal with a wide range of science, but it is hardly to be compared with the wide ranging scope of plant pathology.

In this chapter we hope to suggest how the other sciences impinge on plant pathology and how it impinges on some of them. Also the importance of plant pathology for several aspects of human life will be discussed.

II. Plant Pathology among the Sciences

A. Scope of Plant Pathology

For a good understanding of the scope of plant pathology, we must go back to the middle of the 19th century, when this science began. At that time, the theory of spontaneous generation of microbes and fungi was still accepted by many scientists. Botany, including plant taxonomy, physiology, and mycology, was gradually evolving from the merely descriptive stage into the more dynamic one of experimentation. In Germany, old erroneous ideas about the causes of parasitic plant diseases began to tumble down mainly as a result of the excellent work of the brilliant young mycologist Anton De Bary and the critical writings of Julius Kühn, who published the first book dedicated to plant pathology as a whole in 1858. In 1853, De Bary wrote his first paper on plant diseases proving by experiment, that smuts and rusts of cereals are due to pathogenic fungi. He showed that the fungi are not exudates of diseased tissue and that they are not spontaneously generated. This was quite revolutionary, as at that time leading scientists believed that fungi on diseased plants derived from waste material of the plant whereas diseases were thought to be due to a general inner disease predisposition present in all crop plants but absent in wild species. Thus arose experimental plant pathology.

As the science of plant pathology partly evolved from plant physiology it is not surprising that all abnormal growth of plants belonged to its field of study, independent of the primary cause of the abnormalities. Plant galls due to mite infestation or deformations resulting from the presence of insects, such as gall midges, were just as important to the first pathologists as diseases due to fungus attack or unfavorable weather conditions such as heavy frost or abnormal drought.
Probably the early development of the science of plant pathology in Germany is responsible for the fact that descriptions of damage due to insect pests still are found in German handbooks such as the well known six-volume "Handbuch der Pflanzenkrankheiten."

Many disturbed physiological processes of the plant result from adverse environmental conditions either in the soil (e.g., mineral deficiencies or excess of certain elements, lack or excess of water) or in the atmosphere (e.g., too low or too high temperatures, presence of poisonous industrial gases).

In many other cases a living pathogen is responsible for the disease. Fungi were the first living pathogens to be recognized. Bacteria, the most dangerous germs for men, were discovered much later as plant pathogens. Although they may cause severe diseases in plants especially when the climate is hot during the growing season, the number of diseases caused by fungi is far greater. More recently, viruses were recognized as the cause of many diseases, and also eelworms (nematodes) were found to cause serious damage to crops. The importance of the latter group is gradually being recognized. Within the near future nematology will probably develop to such an extent that it will be impossible to treat this subject in a handbook like the present one. Of course, specialization is necessary but one should never forget that the disorders in plant life are complicated physiological phenomena in which more often than not several organisms and the environment play an important role.

In the following paragraphs an attempt will be made to discuss those disciplines which impinge on plant pathology and on which plant pathology impinges.

B. Relation between Plant Pathology and Other Sciences

1. Physiology of Healthy and Diseased Plants

Plant physiology is the science most closely related to plant pathology. A disease has been defined as an abnormal physiological process. Hence, plant pathology is concerned with abnormal physiology.

Plant physiology has contributed greatly to plant pathology. Plant pathology makes use of essentially all that the plant physiologist has learned. This may be illustrated with some examples.

Nutrition is basic to the life of plants as well as of animals. A shortage of trace elements such as manganese, zinc, and boron induces disease symptoms and application of the right fertilizers may reverse the process and bring the plants back to normal. Thus, it has been
possible to cultivate new lands by adding trace elements and phosphates, e.g., in southern Australia, which hitherto were too low in fertility to allow a profitable crop production.

Photosynthesis and the distribution of assimilation products influence and are influenced by pathogenic infections as shown in more detail in Chapter 8 of this volume. Recent investigations suggest an increase in photosynthesis during the first few days after infection (Sempio, 1950) and a subsequent decrease especially in heavily infected plants (Allen, 1942). In the earlier literature, too little attention was paid to the trend in photosynthesis with time, some investigators measuring photosynthesis at an early stage of infection whereas others used plants with an established infection (Yarwood, 1957). However, photosynthesis always decreases within a few days after infection.

The chemical constitution of healthy leaves changes during the growing period and simultaneously the susceptibility for diseases alters. For example, only young apple leaves of a certain age are attacked by Venturia. The older leaves remain free from the disease even after artificial inoculation, and according to Grümmer (1955) there is a correlation between the infectivity of potato leaves by the late blight fungus Phytophthora infestans and protein decomposition in the leaf tissues. This decomposition takes place as a result of initial tuber formation. This fascinating subject is treated in Chapter 12 of this volume.

Many diseases increase transpiration in plants, often in combination with an increase in permeability (Thatcher, 1939). Whether this increase in permeability is responsible for the mobilization of substances from adjacent healthy tissue or whether such a mobilization is due to metabolic changes is not quite clear.

Pathological wilting may occur, e.g., as a result of the action of vascular parasites attacking the roots and lower parts of the plant. These parasites (fungi or bacteria) may produce toxins which according to Gaumann (1951) have a coagulating effect on the protoplasm of the host cells resulting in water release, and an excessive rate of transpiration. In Section 8, we shall see that other workers hold another opinion, with respect to the biochemical background of wilting.

Not only does the plant pathologist depend on the plant physiologist for a better understanding of the pathological processes going on in a diseased plant, the physiologist may also gain understanding of normal physiological phenomena by using "abnormal" (i.e., diseased) plants (Suchorukov, 1957). Thus, Bennett (1937) studying curly top (a virus disease) of sugar beets, contributed substantially to our general knowledge about translocation of food in plants. Another example is dormancy.
Braun cites an interesting effect of witches' broom on dormancy (see Chapter 6 of this volume). The elucidation of this effect should be valuable in normal plant physiology. But unfortunately such reciprocal features of plant pathology are often ignored by the physiologist.

2. Pathological Anatomy and Morphology

The histologists, anatomists, and morphologists have contributed their share to plant pathology. Various histological and morphological characters of the plant influence and are influenced by disease. These matters are subject to detailed analysis in Chapter 11 of this volume and in Chapter 6 of Volume II. A few examples suffice to outline the subject for our purposes here. Many infections induce local necrosis of tissue, e.g., in the case of hypersensitivity of a host for a pathogen (see Chapter 13). The pathogen dies when the adjacent cells are induced to divide forming a protective meristem, often consisting of corky cells (peri­derm). Potato leaves become brittle in case of leaf roll infection. This virus disease produces typical changes in the cells of the phloem that prevent a normal downward stream of assimilation products.

Several instances of pathological plant growth and monstrosities are mentioned in the Report of a Symposium on Abnormal and Pathological Plant Growth (1953) including tumors due to the crown gall bacterium (Agrobacterium tumefaciens) and to virus infection. The former will be treated more in detail in Chapter 6 of this volume. Abnormalities range from the formation of "giant cells" (e.g., caused in potato roots by Heterodera rostochiensis, the potato root eelworm) to leaf enations, green protrusions mostly on the underside of the leaves, as in the case of rasp leaf virus disease of cherries, and cup-like outgrowth of the veins, being a symptom of the so-called "kroepoek" virus disease of tobacco (Kerling, 1933).

Witches' brooms are also common disease symptoms that arise from the forcing of dormant buds. Rubus stunt virus of raspberries (Prentice, 1950) induces phyllody which means a change of floral organs (sepals, petals, carpels, and stamens) into leafy structures; they are sometimes of exactly the same shape as normal leaves, e.g., with clover. Strangely enough in many cases the stamens are not altered. A recent survey of the literature on this subject is given by Bos (1957). Although these peculiar pathological forms have been known for a long time, it is only recently that viruses have been found to be the causal agents in many cases. This type of disease is not just a teratological rarity, but it may spread epidemically causing severe losses to the growers (Rhind et al., 1937; de Fluiter and van der Meer, 1953).
Here also we find reciprocal contributions of plant pathology. The crown gall disease has contributed greatly to the knowledge of differentiation. It has also been valuable to students of human cancer. Floral morphology was elucidated by the study of phyllody.

3. Genetics, the Basis for Breeding Resistant Varieties

Little as we may know of the physicochemical processes that prevent a pathogen from establishing itself in plant tissues, there are nevertheless many examples of successful breeding of disease resistant varieties of our agricultural and horticultural crops. Modern plant breeders have provided us with an increasing number of valuable crop plants that are resistant to some or all the major diseases. Stakman treats these problems in Chapter 14 of Volume III.

Unless the etiology of the disease-causing agent is known, the chances of obtaining resistant varieties are limited. Admittedly, some very successful resistant varieties have been produced without knowing anything of the causal agent of the disease. One of the classic examples is sugar cane resistance to the so-called sereh disease on Java. Much later it was found that sereh disease is caused by a virus.

Originally, breeders used only mass selection. They picked out the healthy plants in a heavily infested population and there was some risk that such plants had escaped infection. Subsequent testing demonstrated whether or not a resistant strain had been obtained. An early example of this procedure is the success of L. R. Jones (1914) in selecting yellows resistant cabbages.

Mass selection is less promising than formerly, however, because our agricultural and horticultural crop varieties are usually more homogeneous than before and comprise fewer biotypes than the old indigenous breeds of crops.

Because of this, the potential danger of a serious outbreak of disease is greater today than it used to be. Plant breeders are well aware of this menace.

The rediscovery of Mendel's laws of heredity in 1901 greatly facilitated the use of genetics in plant pathology.

Biffen (1907), during his studies on wheat genetics at Cambridge, was the first to discover that resistance and susceptibility to yellow rust (Puccinia glumarum) are inherited characters following the same rules as the inheritance of morphological characters. When his rust resistant varieties turned out to be susceptible in Australia there was much disbelief in genetically bound disease resistance. However, with the discovery of physiological races of the pathogen, Biffen's conclusion was generally accepted.
Often, the species or variety carrying the resistant gene is of no value as a crop plant. One must then make several back crosses to the valuable but susceptible cultivated variety, thus combining the genes for resistance with valuable market qualities. Such a procedure is a time consuming business. A period of 10 years is quite normal before an acceptable new variety is obtained.

In order to prevent disappointments, a knowledge of the disease and its causal agent is imperative in deciding on the inoculation methods, and the best ways of establishing a local epidemic (Coons, 1953). The breeder should be aware of the great variations in pathogenicity within the races of the pathogen (fungus, bacterium, or nematode). The study of the genetics of pathogens, therefore, is of the greatest importance for breeder and plant pathologist alike. While the geneticist or mycologist may study the inheritance of any given property of a pathogen such as color, spore morphology, or biochemical reactions (for details see Beadle, 1945, and Catcheside, 1951), the plant pathologist is especially interested in its pathogenicity to the host plant.

A complication in the plant pathologist's work is the fact that the races of the pathogen seldom differ morphologically but only in virulence toward the host plant. Therefore, these races can only be distinguished by their behavior toward different varieties of the host plant. For many diseases such differential varieties are being used with success, e.g., in the case of stem rust of wheat (Stakman et al., 1944), rust of flax (Flor, 1954), anthracnose of beans (Andrus and Wade, 1942; Hubbleing, 1957). More details on this subject will be given in Volume III, Chapter 14.

Plant pathology has contributed to genetics with studies on the sexual reproduction of pathogenic fungi and on the genetic background of pathogenicity (e.g., Keitt et al., 1943; Keitt and Boone, 1954: Venturia inaequalis; Flor, 1955: flax rust). As an example of the complications met with in this work, the outstanding contribution of Flor (1955) may be mentioned. He explains host-pathogen interaction in flax rust by assuming a gene-for-gene relationship between rust reaction in the host and pathogenicity in the parasite. In flax and the flax rust fungus Flor has been able to identify 25 such pairs of genes.

Comparable results have been obtained by Black et al. (1953) using races of Phytophthora infestans on potato.

How the so-called Fungi imperfecti form physiological races has long been obscure. It was mostly thought to be due to mutation, but recent work of Pontecorvo et al. (1953; Pontecorvo and Sermonti, 1954) and Buxton (1956) throws some new light on this phenomenon. It seems that heterokaryosis as found by Buxton for Fusarium oxysporum f. pisi (a cause of pea wilt) is not uncommon and it is not at all improbable
that a parasexual system as described by Pontecorvo and Sermonti (1954) is responsible for the formation of new physiological races in many of the Fungi imperfecti. On culture media, anastomoses between adjacent hyphae of different strains of a fungus are quite common and there is no reason why this should not occur in nature.

From the foregoing, the fundamental mutual importance of genetics and plant pathology will be clear. Both disciplines should be obligatory in the training of students in plant pathology. This is already the case in almost every university in the United States. The important role that American plant pathologists play in the development of so many disease resistant varieties of crop plants in the United States may be due to the fundamental knowledge of genetics present with the student in plant pathology in that country.

4. Plant Taxonomy and Plant Geography

Plant geography and taxonomy have also contributed to the science of plant pathology. Vavilow (1935, English translation 1949–50) first realized that cultivated crops had probably lost important genes and that these could be recovered only by collecting taxonomically related species and genera from the centers of origin of our crops. In such work, expertness in taxonomy and plant geography is important.

Vavilow and others traveled to all eleven regional centers of origin of our crops throughout the world and collected more than 300,000 samples of seed and seedling material. Enormous unknown varietal resources even of such crops as wheat, potato, corn, legumes, rye, and flax were discovered. As Vavilow says: "In the case of certain plants such as the potato, the newly discovered species and varieties literally revolutionized our conception of the source materials."

Careful plant geographic studies had to precede the expeditions and finally the large collections had to be studied taxonomically. Vavilow concludes his chapter on the phytogeographic basis of plant breeding as follows: "The enormous plant potentials discovered in the centres of primary origin of forms and species of cultivated plants, should be subjected to investigation not only by the taxonomist, but also by the physiologist, the biochemist, and the pathologist. In the field of genetics, which aims at new creations through the most rational combinations of parents, an immense field of the most fascinating and urgent work is opened up."

Many of the species collected by the Russians are of an endemic type. This means that their biochemical constitution may be entirely different from that of the commonly used cultivated varieties, thus providing a new base for resistance to pests and diseases to which they
have not been exposed in their original habitat. This so-called preadaptational resistance seems of great importance (Harland, 1955).

It is not surprising that Vavilow's publications aroused much interest all over the world. American, German, and other expeditions were sent to the promising gene centers. Large collections of as many varieties, related species, and genera as could be found, were planted in experimental plots to be used as a gene reservoir. In order to prevent introduction of dangerous new diseases or pests, such plants had to stay in quarantine before they were released to the breeding stations. There these stocks are being tested for resistance to the major diseases. The interregional potato introduction and preservation project at Sturgeon Bay, Wisconsin, for instance, is testing the reactions of all collected material to *Verticillium* wilt, *Fusarium* spp., common scab, late blight, early blight, Southern bacterial wilt (brown rot), ring rot, black leg, virus A and X, and leaf roll (Stevenson and Akeley, 1953). Similar work is done at the Max Planck Institute for Plant Breeding at Köln/Vogelsang, Germany, where immunity from viruses X, B (closely related to X), Y, A, and leaf roll was found in a number of wild potato species (Ross and Baerecke, 1950).

5. **Mycology, One of the Important Foundations of Plant Pathology**

Mycology is the science that fathered plant pathology. That is because fungi are bigger than bacteria and viruses and could be seen first with primitive microscopes. Plant pathology could not become a science as long as etiology was lost in a haze of spontaneous generation. Originally, mycology was a purely descriptive science devoted to the classification of fungi. One of the outstanding early mycologists was E. M. Fries, of Sweden, who published his "Systema Mycologicum" over the years 1821–29. This work forms the basis for systematic mycology in much the same way as Linnaeus' "Species Plantarum" became the classic for plant taxonomy. However, Fries' ideas on plant parasitic fungi, which he brought together in a section called Hypodermii, because they were found under the skin of plants, were fully in accordance with the opinion of his contemporaries. He stated: "These fungi depend on a diseased condition of the plant rather than vice versa. From the study of many examples, we have learned that they are hereditary and that they depend on the composition of the atmosphere. Every fear of their propagation by sporidia is superfluous" (cited by Brown, 1951).

The idea of the independent existence of microscopic fungi became generally accepted only after the appearance of the epoch-making publications of the Tulasne brothers (1861–65) in France and of De Bary (1853, 1866) in Germany.
The development of synthetic sterile media for the cultivation of fungi was a seven-league step for mycology and plant pathology. It converted etiology to a scientific reality. It enabled an ever increasing number of scientists to study the physiology, sexuality, sporulation, nutritional wants, and genetics of countless saprophytic and parasitic fungi.

In the meantime, systematic mycologists went on describing new species compiled in Saccardo's well known "Sylloge Fungorum" (1882–1931), now containing no less than 80,000 names! After the beginning of the 20th century, it became evident that the species limits for many of these fungi were too narrow since most of them had been described without taking into account the influence of environmental conditions on morphology. Each species contains many strains, and the range of characters shown by the sum of strains is wider than that of the original strain. For us as plant pathologists, physiological strains are of even greater importance than morphological ones as the virulence of one strain may differ greatly from that of another, e.g., with the rust fungi on cereals.

A special group of mycologists study those fungi living symbiotically in the roots of trees where they give rise to morphological changes called mycorrhiza. It is interesting that Basidiomycetes, are particularly important in this role. They include toadstools, such as *Boletus* and *Amanita*. Their role seems to be very specific, one *Boletus* species being associated only with one type of tree.

6. *VIROLOGY, A STUDY OF THE BORDERLINE BETWEEN LIVING AND DEAD SUBSTANCES*

**MOTTO: Nature makes so gradual a transition from the inanimate to the animate kingdom, that the boundary lines which separate them are indistinct and doubtful** (Aristotle, cited from K. M. Smith, "Beyond the Microscope").

After many centuries of disbelief, this 2000-year-old remark of the famous disciple of Plato is gradually being accepted by more and more scientists.

Without going into further detail on this philosophical concept, one may say that only viruses possess characteristics partly specific for living organisms and partly inherent in dead substances. Mycology may have whelped plant pathology, but plant pathology has done much toward developing the science of virology.

The first virus to be isolated in a para-crystalline form was the tobacco mosaic virus (Stanley, 1935). This accomplishment eventually
won a Nobel Prize for Stanley. Even to this day the tobacco mosaic virus continues to contribute importantly to knowledge of virus and even to knowledge of genes and their function.

Virology has very rapidly grown into a separate discipline because viruses of man, plants, livestock, insects, and bacteria have many properties in common. Results obtained in one group are as a rule of great interest to the virus workers in the other specialties.

Isolation of the virus in as pure a form as possible is essential for further studies. Only recently through the use of the ultracentrifuge, electrophoresis, chromatography, and electron microscope, a number of viruses have been obtained in a relatively pure state. This engenders admiration for Stanley (1935) and his co-workers, who had to crystallize tobacco mosaic virus by using ordinary chemical methods. The tobacco mosaic virus now appears to be a nucleoprotein with a molecular weight of about 40,000,000. It has been possible to measure the size of the virus particles by ultrafiltration or X-ray application. Later, these data were confirmed when the virus particles were visible with an electron microscope at a magnification of 10,000 to 30,000 times.

In order to understand fully the biological activities of a virus, it is desirable to know the special configuration of the virus molecule. This seems at the moment still a superhuman task (Thung, 1957). Nevertheless, recently considerable progress has been made in this field (Perutz, 1958).

One of the general virus problems is the attachment to and penetration of cell walls by viruses. Here, the workers with bacteriophages of the T system have got the lead (Tolmach, 1957).

Another and perhaps the most important general problem is that of virus multiplication in the host cells. This will be considered in detail in Chapter 3 of Volume II.

Animals develop resistance to viruses by producing antibodies in the blood. Since plants do not form antibodies, the methods used with animals to stimulate antibody formation are useless in treating plant virus diseases. However, for diagnostic purposes, serology is used on a large scale in plant virus work. Rabbits and other animals are used for the production of antibodies by injecting the purified plant virus into their veins. A whole range of antisera have been prepared in this way, and these are used by the General Netherlands Inspection Service for Seeds of Field Crops and for Seed Potatoes (N.A.K.) for the production of healthy seed potatoes free from viruses X, S, and M. The antisera are prepared by the Laboratory for Bulb Research at Lisse, where the mass-testing techniques also have been developed (van Slogteren,
1955). It is interesting to note that the presence of potato virus S was discovered during serological research at Lisse. This virus may cause 15% yield reduction and now that it has been discovered, it seems to be widespread in Europe and the United States.

7. Applied Entomology, an Indispensable Help to the Plant Pathologist

During succeeding decades, plant pathology began to neglect insects as pathogenic organisms and drifted into mycology, bacteriology, and virology. The role of insects as causes of plant diseases and injuries was left to entomologists who founded the science of applied entomology.

Plant pathologists have, however, also contributed to applied entomology by their studies of symbiosis between insects and microorganisms.

A typical example of a mutualistic symbiosis is the case of bacterial soft rot affecting many vegetable crops. This disease is spread by the seed-corn maggot, *Hylemyia cilicrura* (Rond.) and other dipterous insects. The maggots can develop normally only in plant tissues decayed by the bacteria. The soft rot bacteria, in turn, cannot penetrate uninjured plant tissues, but grow abundantly once the plants have been wounded, e.g., by maggots (Leach, 1952). In this respect, it is interesting to note that the bacteria survive within the intestinal tract of the insect in all stages of metamorphosis including the eggs.

Much more common is the spread of diseases by insects which apparently do not benefit from this transmission at all but merely act as vectors. The first report of such an insect transmitted plant disease was given by Waite (1891), who proved that the bacteria causing fire blight of pears are transported by bees and wasps while visiting blossoms in search of nectar. This subject is treated in considerable detail by Broadbent in Chapter 4 of Volume III.

The Japanese entomologist Takami discovered as early as 1901 that the dwarf disease of rice in that country developed as a result of the feeding of the leaf hopper, *Nephotettix apicalis* Uhl. He did not know, however, that this leaf hopper acted as a vector of an infectious disease. This was established by other Japanese workers in 1908. It was many more years before the virus nature of the disease could be proved.

If one realizes how long ago leaf hoppers have been indicated as vectors of virus diseases in Japan, United States, and Russia, it is surprising that no leaf hopper transmitted virus disease has been reported from Western Europe before 1953 when de Fluiter and van der Meer (1953) found the leaf hopper *Macropsis fuscula* Zett. to be the vector of rubus stunt, a virus disease of raspberries. This may be due to the fact that the leaf hoppers are more frequently vectors of virus diseases, in subtropical and tropical climates than in cooler climates.
There is another interesting problem in relation to the transmission of virus diseases. Why are some viruses nonpersistent (allowing the insect carrier to transmit the pathogen soon after feeding on a diseased plant) whereas with others—the persistent viruses—an interval of up to several weeks may be necessary before the insects can infect healthy plants? The latter case seems to be the rule with viruses transmitted by leaf hoppers. Here apparently the virus multiplies in the insect body as the insects remain infective through several successive generations (Black, 1950; Black and Brakke, 1952). Other instances are reported where the nymph of a leaf hopper can pick up a virus but is not able to transmit it until the adult stage is reached. This also points in the direction of virus multiplication in the insect body. Still different is the case of a thrips (Frankliniella insularis), transmitting spotted wilt virus of tomato. Here, the adults become infective only after the larvae have sucked on a plant diseased by virus (Bald and Samuel, 1931).

8. Biochemistry and Plant Diseases

Biochemistry is a rapidly rising science which is contributing very fundamentally to our knowledge of the abnormal processes in disease.

In many ways the advances in science are derived from advances in technique. Biochemical techniques are developing so fast that they almost tumble over each other's heels and every new technique is soon reflected in advances in plant pathology.

The more that is known about the biochemical processes taking place at the foci of infection the more it becomes clear how complicated pathogenesis is. This fascinating and most fundamental section of plant pathology is getting more and more attention from the modern research worker. The difficulties he faces are tremendous, but important achievements attained thus far have stimulated yet more research aimed at a better understanding of pathogenesis.

The possible role of toxins in the development of disease symptoms is a typical biochemical problem. This is especially the case with wilt diseases. Many plant pathologists still adhere to the theory that toxins induce the wilt diseases (Gäumann, 1954). Others however, have recently questioned the role that toxins such as lycomarasmin, vasinfuscarin, and fusaric acid play in the syndrome of wilt diseases, etc., because such phytotoxic compounds isolated from culture filtrates of a pathogen have not been detected in or isolated from diseased plants (Dimond, 1955). A possible exception is ethylene. The epinasty and leaf-yellowing symptoms of wilt diseases seem to result from the action of ethylene formed by the pathogen and possibly to some extent by the host.
It would, therefore, be wrong to regard all toxin formation of pathogenic fungi and bacteria as unimportant in pathogenesis. Wildfire disease of tobacco caused by the bacterium *Pseudomonas tabaci* may serve as another example. The biochemistry of this disease has been studied in detail. It produces localized chlorotic halos surrounding central brown necrotic leaf spots. In this case, a characteristic toxin has been isolated. It is a structural analogue of methionine, one of the amino acids essential for plant growth.

The wildfire toxin owes its biological activity in one and perhaps in all susceptible plant species to its antimetabolite properties, i.e., the toxin molecule is able to replace the structurally related essential metabolite, thus causing the development of pathological symptoms (Braun, 1955). Toxins are discussed in much more detail in Chapter 9 of Volume II.

Much biochemical work has been done with the aim of elucidating the cause of disease resistance. Biochemists have, in the first place, tried to isolate chemicals which were only present or occurred in a much higher concentration in the nonsusceptible than in the susceptible variety. Classic examples of such chemicals are protocatechuic acid and catechol isolated from the dry outer scales of pigmented onions (Link and Walker, 1933). Such onions are highly resistant to *Colletotrichum circinans* (Berk.) Vogl. and several other pathogens. Resistance depends on the presence of the dry outer scales, as here the toxic substances are easily accessible in a water soluble form and prevent germination of the fungus spores.

The biochemistry of enzyme activity has also advanced our knowledge of pathogenicity.

Thiourea, 2,4-dinitrophenol, and sodium fluoride break down resistance in several plant species. Substances having this effect are all inhibitors of the activity of respiratory enzymes. These enzymes seem to play an important role in disease resistance (Walker and Stahmann, 1955; Fuchs and Kotte, 1954; Hessebrauk and Kaul, 1957). It has been found for instance that the activity of the ascorbic acid oxidase system was higher in wheat plants resistant to brown rust (*Puccinia triticina*) than in susceptible wheat varieties (Hessebrauk and Kaul, 1957). In wheat affected by stem rust (*Puccinia graminis tritici*) the activity of other enzymes (e.g., glycolic acid dehydrase and glutaminic acid decarboxylase) was much reduced. Since at the same time ascorbic acid oxidase is stimulated the normal enzymatic balance of the healthy plant is shifted to new metabolic chains in the diseased plant (Farkas, 1957).

In this respect it is interesting that hypersensitive reactions occurring in resistant varieties of various crops have been attributed to nonspecific
"defense bodies" which are formed some hours after infection of the host cell has taken place. The name phytoalexin has been proposed for these substances (Müller, 1957). They can be isolated from the host tissues and are toxic to several nonrelated pathogenic fungi. The fact, stressed by Müller, that they are formed only after infection has taken place seems of particular importance, also in connection with the statements made by several investigators that fungitoxic materials isolated from healthy noninfected plants may not be responsible for resistance. The apparently easy transport of many chemicals to the site of infection as described by Shaw and Samborski (1956) may be better understood in the light of recent cytophysiological and cytochemical studies which led to considerable doubt on the presence of a membrane of high resistance outside the cytoplasm of the cell. Instead, the theory of apparent "free space" has been put forward. According to this concept, the cytoplasm has water-filled spaces continuous with the water-filled spaces of the cell wall and the intercellular space systems allowing free diffusion between the aqueous phases of the cytoplasm and an external solution, e.g., of intermediates of metabolism (Robertson, 1957).

In the case of plant virus diseases, the great stimulus to biochemical research was given by Stanley's isolation of tobacco mosaic virus (Stanley, 1935). The following years revealed that several plant viruses, including tobacco mosaic virus (TMV) consist of ribonucleoproteins (Bawden and Pirie, 1937, 1938; Stanley and Knight, 1941). In fact, up till now, no plant virus has been found which does not contain proteins and nucleic acids (Markham, 1953).

Modern isolation techniques such as chromatography and electrophoresis enabled research workers to separate the amino acids of the proteins and the various constituents of the nucleic acids. Recent investigations, both with respect to the amount of purines and pyrimidines present in the nucleic acid part of the virus and analysis of the amino acid composition of the proteins, revealed marked differences between various viruses (Schramm and Kerékjártó, 1952; Black and Knight, 1953).

Much more biochemical work must be done in relation to pathogenesis and for diagnostic purposes. We can see only the beginning.

9. Chemistry, One of the Pillars of Modern Plant Protection

That the title of this paragraph is not an overestimation of the important role chemistry plays today in plant protection may be illustrated by some examples. Seed treatments with fungicides, now being a common practice, e.g., with cereals and vegetable crops, is the cheapest insurance the farmer can take against certain plant diseases, especially
those caused by "damping-off" fungi. Before seed treatment came into use, many crops had to be replanted at considerable cost. Treatment of spinach seed at a cost of only 30 cents yielded a $300 gross return according to McNew et al. (1951). New very potent seed protectants such as thiram and captan have been added to organic mercury and inorganic copper compounds which were the favorites before World War II.

Recently, new antibiotics (e.g., rimocidine) have been isolated from certain *Streptomyces* species. They have shown a systemic action, penetrating through the seed skin thus killing internal pathogens such as *Ascochyta pisi* in peas (Dekker, 1957).

In the United States, the yield of potatoes per acre doubled from 1939 to 1952 as a result of combined spraying of the foliage with DDT and ethylene bisdithiocarbamates (Dimond and Horsfall, 1955).

Control of soil-borne fungus diseases, other than damping-off, is still difficult to obtain, although some new approaches (e.g., with sodium N-methyldithiocarbamate) look rather promising. Soil treatments with nematicides such as DD have given excellent results against plant parasitic nematodes.

As the potential market for pesticides is enormous, the great interest in plant protection shown by chemical companies is not surprising. More than 25,000 organic compounds have been tested as possible fungicides, and this number is still increasing daily. Less than 0.1% ever reaches the stage of practical application (Dunegan and Doolittle, 1953). The development of such a promising compound needs large investments ranging from $250,000 to over $1,000,000. Still, the prospects seem to be attractive. In the last 3 years, the average annual production of copper sulfate for fungicidal use amounted to 145,000,000 lb. in the United States. Total United States exports of pesticides increased to a value of $85,909,000 in 1957 (Shepard, 1958). For the control of Sigatoka disease of bananas in Central America more than 45,000,000 lb. of copper compounds are applied each year! In fact, crop protection forms the highest cost in present day banana production.

As it is clear that it would be impossible to test every chemical compound in field trials, research must primarily be carried out by chemists and plant pathologists in the laboratory. Modern industrial research laboratories have been built for this purpose.

While the mode of action of fungicides is not yet fully understood, the search for new active chemicals will be more or less on a "trial and error" basis. Clearly, the ideal would be to predict the fungitoxic activity from the structure of a chemical compound just as the modern chemist working with plastics can now design new compounds with the desired
properties at his desk, and then prepare them in the laboratory. With the “trial and error” method we do not mean, however, that one should take all the available chemicals from the shelve and just screen them on their biological activity. As van der Kerk (1956) said: “Rather has one to admit that discoveries of new fungicides usually are based on knowledge also of distant domains of the natural sciences, on a keen intuition, and on the ability to make cross-links between apparently unrelated fields.” As an example, he mentions the development of the dialkyldithiocarba-

mates as fungicides.

Gradually, a stage of knowledge is reached where one scientist of genius, capable of surveying the whole subject and finding time for constructive imaginative thinking, may detect the still lacking fundamental natural law lying at the very base of the most divergent physico-chemical interactions of the living organisms and their inanimate environment.

We now must face the practical implications connected with the use of fungicides. The laboratory techniques necessary for the development of new fungicides will be treated later (Chapter 14, Volume II). Clearly, in plant disease control it is not sufficient to find a chemical with strong fungicidal activity. The product also should not be harmful to crop plants; moreover, it must be rain resistant. This sounds simple, but disappointments have been the reward of industrial chemists because in the field, some products have behaved differently from laboratory and greenhouse tests, both on phytotoxicity and on rain resistance.

The final product ready for marketing does not contain only the active ingredient and some inert material, but as a rule stickers and/or spreaders (wetters), and stabilizers are also added. This so-called “formulation” of the product, done by special chemists, is more an art than a science although gradually out of experience and knowledge some general principles are evolving.

Both for insecticides and fungicides there is at present a certain trend toward biocides which kill the noxious organisms but save the beneficial ones. An example is the selective action of thiram used as a soil fungicide, in which case the antagonistic fungus *Trichoderma viride* was not affected (Richardson, 1954). The most specific fungicide known at present is hexachlorobenzene, discovered in France for wheat bunt (*Tilletia caries*). In general, the organic fungicides seem to be more specific than the inorganic ones (Lilly and Barnett, 1951).

The chemist who develops new fungicides may have to deal with resistance of a fungus against the fungicide. Spraying of insecticides has frequently resulted in the development of resistant strains of the pest, and the use of antibiotics both in medicine and agriculture has led to
acquired resistance of pathogenic bacteria. Until recently, there was not much evidence that the same occurred with fungi, but Horsfall (1956, p. 96) gives some literature citations which undeniably demonstrate the possibility of the development of resistance of certain fungi with respect to such fungicides as copper compounds, organic mercury compounds, thiram, and tetrachloronitrobenzene. Recent German work on the differences in resistance between various strains of wood attacking fungi toward wood preservatives points in the same direction (Gersonde, 1958; Schulz, 1957).

Undoubtedly, the ideal chemical treatment of crops against fungus attack is chemotherapy, also called internal therapy, contrary to the conventional method, where the chemical is used as a protectant. In the case of chemotherapy, the fungus is killed after it has penetrated the plant tissue. Organic mercury compounds, for instance, can be used as therapeutants (eradicants) up until several days after infection of apple scab has taken place. Many promising laboratory and greenhouse experiments have been carried out with chemotherapy, but so far only a few practical applications of this method are known. Chemotherapy also includes the use of antibiotics, e.g., as seed dressings, and the control of deficiency diseases. In the latter case good results have been obtained by the application of the deficient trace element either to the soil or as a foliage spray. Chemotherapy will be treated in detail in Chapter 15 of this volume.

10. Technology Comes to the Rescue

Much of the art of plant pathology requires engineering technology and the engineers have contributed their share. This is particularly true in the technology of spraying and dusting.

Bordeaux mixture was first applied to plants by sprinkling with a brush. This is not a very economical way of engineering. Gradually, mechanical sprayers were developed, beginning with knapsacks and passing on to larger power equipment. Originally it was thought essential to go on with spraying until "run-off," but doing so one usually wastes 95% of the liquid and even then one does not completely wet the plant (Fraser, 1957). This so-called high volume spraying, originally carried out with hydraulic sprayers reached its limit in the powerful speed-sprayers with air-propellers, carrying an arc of nozzles and discharging as much as 100 gallons/min. at a pressure of 55 lb./sq. inch. Only by making use of air, was it possible to let the liquid pass through a rather wide orifice, thus avoiding clogging and providing sufficient penetration. Although such a machine functions excellently (the fan making 2100 revs./min.) and although it can be operated by one man, the drawback
remains that one or more large tank wagons have to ride to and fro for filling purposes.

Eventually, the engineers developed methods whereby the large amount of water could be abandoned. Nozzles had to be designed for distributing very small quantities of liquid uniformly. Here the experience obtained by engineers in the combustion of liquid fuels was tapped. This led to the development of hydraulic low volume spraying. Quite another type of low volume equipment is the air-blast low volume sprayer, the so-called mistblower or atomizer. A large variety of low volume sprayers was constructed, taking into account the crops that had to be sprayed and also the method of application. For application of chemical sprays from the air, for instance, the droplet size must not be too small (MMD* > 100 \( \mu \)) otherwise they drift away in the wind and never reach the leaf surface. Moreover, very small droplets (MMD < 10 \( \mu \)) will not adhere to plants even if they are applied by ground equipment.

The first blowers for low volume spraying were developed as early as 1934 (French, 1934). At that time it was thought necessary to use oil as a carrier instead of water because one feared that water would evaporate too rapidly. Later it became evident that this is not the case unless the climate is too dry.

It is interesting to note that the development of low volume spraying for agricultural purposes followed different ways in the various countries. In the United States, England, and Holland for instance, the cold method was mainly used, whereby the liquid was atomized into tiny particles by means of a very fast centrifugal fan or by using compressed air. In Germany on the other hand, attention of the research workers has long been concentrated on aerosols, i.e., a dispersion of liquid with a mass median diameter (MMD) of less than 40 \( \mu \). They started with the so-called hot method, already known in the United States, whereby superheated steam or exhaust gases were used as atomizers and propellents for material dispersal. In the latter case particles are so small that they are carried a long distance by even low wind velocities. Therefore, up to now this method has mainly been successfully applied in woods (e.g., for the control of cockchafers) or in barns. In the laboratory, it has also been possible to use fungicides in this way but no practical field controls have been obtained because spray drift takes the fungicidal clouds over too large a distance, and it does not settle well. In Germany, Stobwasser (1953) especially investigated the possibilities of this method.

Engineers have been studying the behavior of the liquid sheet pro-

* MMD = mass median diameter.
duced by different designs of nozzles but up to now there is no connecting theory to enable them to predict the performance and to guide them in their design (Fraser, 1957). Nevertheless, the postwar development of low volume machines has been amazing (Ripper, 1955; van den Muijzenberg, 1957).

A new and promising engineering development is electrodusting, whereby the dust is given a charge (Bowen et al., 1952). Thus, two to three times as much dust settles on the leaves as compared with non-charged dusts. There is little or no clogging of dust particles and deposits are much more uniform; moreover, there is a good deposit at the underside of the leaves. Tenacity is much better against wind and mechanical movements but rain resistance is only slightly better than with uncharged dusts (Göhlich, 1957). This type of dusting looks very attractive for areas with a poor water supply.

Interesting machines have been built for the application of chemicals to the soil, e.g., for the control of nematodes.

11. Physics, Providing Essential Tools and Methods of Control

At the very dawn of plant pathology as a science the great importance of physics for the study of plant diseases was realized. In the first handbook on plant pathology, Kühn (1858) dedicates more than 30 pages to the description and use of the compound microscope, an invaluable tool to the plant pathologist. Without this instrument it would have been impossible to distinguish the morphological characters of the causal agents of parasitic diseases and to study their life cycles. By using the polarizing microscope, Takahashi and Rawlins (1933) got strong evidence of the shape of tobacco mosaic virus before it could be observed with the electron microscope.

Another optical tool is the ultraviolet spectrophotometer. Ultraviolet absorption spectra contribute to the study of nucleoproteins (Fraenkel-Conrat and Williams, 1955) and make possible the determination of concentrations of highly purified virus preparations (Takahashi, 1951). However, this method is not very specific. Ultraviolet fluorescence is used for diagnostic purposes, e.g., in the case of boron deficiency in celery called brown checking. While normal young growing petioles appear a dull reddish green, early brown checking symptoms on the inside of the petiole exhibit a bright light blue fluorescence even at a time when no symptoms are visible on the outside (Spurr, 1952). A disadvantage of the use of blue fluorescence may be that with other crops the same change of color is obtained if necrosis is due to different causes. Tubers of potatoes having internal necrosis initiated by the dry rot fungus Fusarium caeruleum display a blue fluorescence under ultra-
violet light, but the same color can be seen if they are attacked by *Corynebacterium sepedonicum*, the ring rot bacterium. Moreover sprain, probably a virus disease, gives about the same fluorescence. Yellow fluorescence, as also described by Spurr for brown checking of celery, may be more specific. The type of color of the fluorescence enabled chemists to identify some of the causal agents. Frequently, coumarins have been found. They may play a role in the development of necrosis. The sterilizing effect of ultraviolet light, especially on bacteria, has led to the frequent use of ultraviolet tubes in sterile transfer rooms.

The other side of the spectrum, the infrared, has also been used in plant pathology, e.g., for the disinfection of chestnuts imported into France from countries where the dangerous chestnut blight (*Endothia parasitica*) occurs (Busnel et al., 1951). The advantage of using heat treatment obtained by infrared irradiation over heating by convection in dry air is obvious in this case: 80 seconds in an apparatus heated with infrared radiation (12,000 Å), killed all spores of *Endothia*, whereas a normal heat treatment of 10 minutes at 100° C. gave only a very incomplete sterilization of the fruit surface.

X-ray radiation has been used in virus research, e.g., for investigations of the structure of some viruses; it can also produce new mutants of either plants or fungi.

Several of the latest developments in physics are being investigated for their possibilities for research in the field of plant pathology or for the control of plant disease, e.g., the effect of ultrasonic waves and more recently of atomic energy.

Ultrasonic treatment using special equipment has been successful for the control of plant pathogenic bacteria (*Bacterium michiganense* in tomato seed) and fungi present under the seed coat (*Phoma betae, Cercospora beticola*, etc., in beet seed), if the treatment was combined with special fungicides (e.g., 8-oxyquinoline sulfate) which alone proved ineffective (Jaenichen and Heimann, 1955). High intensity ultrasonic waves changed the physical structure and infectivity of tobacco mosaic virus (Newton, 1951).

Another interesting use of ultrasonic energy was recently described by Waid and Woodman (1957). It appears that the transmission of ultrasonic waves through wood is considerably reduced in case of even very slight inner decay. Fungal infections such as heart rot often remain invisible on the outside of a tree; so they may be destructive for years. Through this new technique, inner diseases of trees and wood can be detected in an early stage and measures can be taken, leading to a marked reduction in economic loss of timber.

Use of beams of electrons was made by plant pathologists, more
particularly virologists, when they started using the electron microscope in their studies. Magnifications of 10,000 to 30,000 times (now even up to several hundred thousand times) made virus particles visible for the first time; the instrument is now indispensable for diagnostic purposes in virus research and for studies on the behavior of virus particles inside the cell.

The latest and most fascinating developments in physics are concerned with the structure of atoms and the possibilities of mastering the immense forces being liberated by atomic fission. From nuclear reactors, radioactive isotopes are readily available and are of special interest for research in medicine, biology, and agriculture. They can be incorporated into chemical compounds such as fungicides and these so-called labeled fungicides can easily be followed on their way in plants and fungus tissues, in extremely minute amounts. It appears that all fungicides tested, with the exception of sulfur, are accumulated by fungus spores (Miller and McCallan, 1956). Radioactive fungicides and nutrients have shown a marked accumulation at infected sites of leaves, especially if obligate parasites were used in the experiments (Miller, 1956).

In plant pathology and plant breeding radioisotopes are useful as a source of ionizing radiation. As a source of gamma rays, Co$_{60}$ is convenient for the induction of inherited changes in germ plasm and for sterilizing biological tissues (especially in food preservation). With this mutagenic agent the plant breeder can produce resistant varieties of valuable crops more efficiently than with the usual plant breeding methods (Myers et al., 1956). Also, one can produce more virulent races of the pathogen. Under controlled conditions, the breeder could use such races to breed adequate resistance prior to the appearance of new strains of the pathogen in the field (Anonymous, 1956).

Electrophoresis and the ultracentrifuge are complementary physical tools essential for the study of the basic properties of size, shape, and electrical charge of viruses.

These few examples clearly demonstrate the important contribution physics has made to a better understanding of the causes and backgrounds of plant diseases and the ways by which they may be controlled.

12. Meteorology Necessary for Epidemiology, Ecology, and Phenology

There is hardly any parasitic disease that is not influenced by the climate, and many diseases derive directly from adverse weather conditions. In warm continental regions crop failures due to drought or heat are common, whereas in the temperate zone late frost may do a lot of damage. Thus, meteorology is another science that is intimately related
to plant pathology. These relations will be developed further in Chapter 14 of this volume and in various chapters of Volume III.

Since L. R. Jones and his colleagues in Wisconsin carried out their classic experiments on the influence of soil temperature on cabbage yellows, plant pathologists have paid considerable attention to the influence of environmental conditions on the development of plant diseases. Literature on this subject comprises about one-tenth of all phytopathological papers (Foister, 1946).

As "weather" is a complicated phenomenon, most plant pathologists investigate its influence under laboratory conditions, e.g., the influence of temperature and humidity on the disease syndrome and on the pathogen, while keeping other environmental factors constant. Afterwards they translate their findings into actual field conditions. Thus, many important results have been obtained which have led to a better understanding of pathogenesis and the epidemiological spread of the diseases under investigation.

One typical example may be cited. In the Fall of 1949 turnips, a common catch crop on the sandy soils in the eastern part of The Netherlands, were severely damaged for the first time by a disease which appeared to be caused by the nonpersistent turnip virus 1. Beemster (1957) proved that severe symptoms developed only at 20-25°C. Plants grown at 15°C. did not show any reaction, but after transferring such plants to 20-25°C. necrotic symptoms appeared within 3 days. Temperature data from the Royal Netherlands Meteorological Institute showed that September 1949 had been the warmest September since daily temperature measurements were started more than 200 years ago. Because of this, work on this disease was stopped, since it was extremely improbable that the disease would again be of economic importance in the near future.

High temperature, on the other hand, may mask symptoms of other virus diseases (e.g., the effect of cauliflower mosaic virus; Walker et al., 1945).

With most fungus diseases both temperature and humidity are of major importance for disease development. In the case of apple scab infection, for instance, there is a close correlation between temperature and the time that the leaves must be wet.

Only careful investigation of each separate disease can lead to the establishment of optimum temperature and humidity conditions for infection. These conditions in many cases are quite distinct from the optimum for fungus growth on cultural media.

Damage to plants as a result of industrial air pollution is also depen-
dent on meteorological conditions, the wind direction being responsible for the place where damage occurs, fog or drizzle often increasing severity of symptoms.

Hail storms, wind, and frost may cause considerable damage not only directly but also indirectly as several weak pathogens may become destructive once they have been able to enter plant tissues through mechanical lesions. Miss Kerling (1953) was able to demonstrate in laboratory trials that young pea plants treated with an air stream containing fine sand particles with or without water, were much more severely affected by *Fusarium avenaceum* than plants treated with a water stream only.

![Fig. 1. Circular experiment field for the study of the spread of a disease in relation to weather conditions: Diseased plants are planted in the center. Temperature and humidity are registered by the instruments to the right.](image)

Wind, carrying spores of fungi, is often responsible for the spread of such diseases as stem and yellow rust of cereals even over large distances, thus leading to real epidemics. Van Doorn and Post (unpublished) designed a circular experiment field—divided into 16 sectors and separated by narrow open strips (see Fig. 1)—in order to investigate the relation between spread of a disease and wind direction. Thus, a correlation could be established between wind direction during a period critical for infection and the sector in which disease outbreak was most severe. The method has been successfully used in The Netherlands for experiments with downy mildew in onions, late blight of potato, and apple mildew.
Annual records of phenological data, such as the first discharge and germination of ascospores of *Venturia inaequalis*, are of great value for disease-warning services on which the growers rely with their spraying scheme.

The best and most reliable analysis is obtained if plant pathologist and meteorologist work closely together. The development of epidemics and the possibilities of forecasting them will be treated in Chapter 8 of Volume III.

13. **Soil Microbiology and Soil Chemistry and Their Importance to Soil-Borne Plant Diseases**

The study and the control of soil-borne plant diseases is one of the most difficult subjects in plant pathology, for one reason because “soil” is a very complex substrate largely differing from one place to the other as to physical, chemical, and biotic properties.

With respect to physical properties, the following quotation of Sir John Russell (1957) is of interest to the plant pathologist: “It seems incredible but nevertheless it is true that in an apparently solid clod of earth only about half is usually solid matter, the other half is simply empty except for the air and water it contains.” If this is the case, one can easily understand why microorganisms, nematodes, insect larvae, etc., thrive in inconceivably large numbers in most soils. These organisms are not only influenced by the chemical constitution, the pH, the texture, and the water-content of the soil, but also by such environmental conditions as soil temperature and by the presence or absence of antagonistic fungi or bacteria and, in the case of nematodes, by the number of predators (e.g., other eelworms) or parasites [e.g., amoebae (*Thra-tromyxa weberi*, van der Laan, 1954), nematode catching fungi such as *Arthrobotrys oligospora* and *Dactylella* spp. (Deschiens et al., 1943)].

Another complication arising for the soil microbiologist is the influence of growing plant roots on microbial life in the direct vicinity of such roots. In this so-called rhizosphere, the microbial flora differs from that of soil remote from the roots, not only quantitatively (100 times more bacteria were present near the root than in the adjacent soil) but also qualitatively (Garrett, 1955a).

Root exudates are responsible for the hatching of the cysts of highly specific parasitic nematodes such as *Heterodera rostochiensis* and *H. schachtii* and for the positive chemotaxis found with several other eelworms. In some cases the root secretions are nematicidal, e.g., with African marigold (*Tagetes erecta*). The chemical responsible for this nematicidal action has been isolated and was identified as alpha ter-
thienyl (Uhlenbroek and Bijloo, 1957). Root secretions of tulips and other plants have been found to be fungitoxic (Winter and Willeke, 1951). It is highly probable that these secretions prevent parasitic fungi from passing through the rhizosphere.

Not only do parasitic nematodes, fungi, and bacteria stay over in the soil, either in a resting stage or as mycelium, but during the past few decennia it has been found that several viruses also remain virulent in the soil during the dormant season when no crop plants are present. How these viruses (nucleoproteins) remain unchanged in such an active microbiological and chemical medium is not quite clear. They may be adsorbed to clay minerals like montmorillonite (van der Want, 1951) or they may overwinter in plant material either derived from the previous year’s crop or in the roots of surviving weeds (Noordam, 1956). It has also been suggested that they bridge unfavorable periods inside some kind of vector (McKinney et al., 1957). Recent unpublished investigations support this hypothesis. Eelworms as well as fungi have been found to act as vectors for such viruses.

It is a well-known phenomenon that in general disease symptoms are more severe and that the pathogen develops more rapidly and intensely in sterilized soil than in normal untreated soil. This led Garrett (1955b) to the conclusion that the normal microflora of the soil exert a natural biological control of most, if not all, soil-borne diseases of plants. In several cases, the parasitism of certain soil-inhabiting fungi or bacteria toward plant pathogens has been proved experimentally, e.g., with *Rhizoctonia solani* being destroyed by *Trichoderma viride* (Weindling, 1932). From this fungus the antibiotics gliotoxin and viridin could be isolated. *Penicillium expansum* and *Pullularia pullulans* exerted a strong antagonistic effect against *Pythium volutum* and *P. debaryanum*, causing root decay of grasses (van Luyk, 1938).

These complex interactions among soil organisms are discussed more fully in Chapter 8 of Volume II.

Soil chemistry is mentioned in the heading of this paragraph because lack or unavailability of certain elements in many cases induces nutritional diseases in plants. Even lack of so-called trace elements can be, and in fact often is, very harmful to our crops. Because soil is a very complex substrate, the mere presence of an element does not at all guarantee its availability to plants. Iron deficiency for instance may be the result of toxic amounts of heavy metals or an excess of calcium carbonate. It produces typical chlorotic symptoms. The application of high amounts of potassium fertilizers may block the availability of magnesium, symptoms showing especially in plants with a low nitrogen content (Russell, 1957). Not only does the amount of available elements
essential for plant nutrition determine whether nutritional diseases will
develop, but also the ratio of these elements is of great importance for
the predisposition of crop plants towards parasitic diseases.

From the soil scientist the plant pathologist derives his ideas for the
solution of all these diverse problems.

14. Conclusions

From the preceding paragraphs it will be clear that our knowledge
of plant pathology and the control of plant diseases has grown greatly
since the foundation of this science a century ago. Our basic insight into
what really happens in a diseased plant remains still very limited, but
we now know for certain that biochemical processes are involved which
seem to be responsible for pathological physiology and pathological
morphology.

Biochemistry, plant physiology, and plant morphology have all prof­
ited from the work of plant pathologists. Tobacco mosaic virus, being
responsible for typical disease symptoms, is today one of the favorites
of the biochemist from which he obtained considerable information on
the structure of proteins. Moreover, these studies have contributed to
our knowledge of nucleic acids, most essential substances in the protein
synthesis in general.

Plant pathologists were the first to be interested in the study of
chemical activities of fungi, a rather new field of research of major
importance for fundamental biochemistry (Foster, 1949) and for the
development of antibiotics to which mankind owes so much.

Basic studies on the translocation of virus in sugar beets (Bennett,
1937) led to a better understanding of translocation of food in plants.

Some virus diseases causing phyllody and proliferations have fur­
nished valuable facts for the solution of morphological problems, e.g., for
the interpretation of floral morphology. They supported Goethe’s theory
that the flower must be regarded as a modified leafy branch (Bos, 1957).

The plant pathologist knows how to make use of genetics, plant
taxonomy, and plant geography for the production of resistant varieties.
Breeding for disease resistance in its turn has had a stimulating effect,
not only on many breeding programs, but also on the accumulation of
basic knowledge of the genetics both of higher plants and of fungi. The
study of mycology and virology led to a better understanding of
pathogenesis and enabled us to employ chemical and physical control
measures which otherwise would have been impossible. Plant pathol­
ogists have described many new fungus species and their life cycles;
they also contributed to fungus physiology, genetics, and biochemistry.
Chemists and technologists furnished many powerful weapons in man’s
fight against such enemies as insects, nematodes, bacteria, and fungi. But did not the plant pathologist, the applied entomologist, the nematologist, and the bacteriologist by their discoveries initiate this whole new field of chemical activities resulting in huge chemical industries with an annual turnover of several hundred million dollars?

Modern, most ingenious physical instruments stand at the disposal of the plant pathologist today. On the one hand this provides him with better possibilities than his ancestors, but on the other hand it also increases his responsibilities: he has less excuse for not finding control measures for serious plant diseases. In the meantime it may be wise to remember that it is hard to change weather conditions which have such a strong influence on pathogenesis and epidemiology.

The practical plant pathologist should take great care not to overlook the experience gained by countless generations of farmers in the course of many centuries. Prevention is better than cure and good crop husbandry (including plant hygiene) will forever remain a cheap and promising basis for the growing of healthy crops. But it is by no means always successful nor are control measures known against all diseases. This leaves us with some serious problems. However, we may hope to solve many of them in the future if we are prepared to cooperate with specialists from the most divergent disciplines. This seems an absolute necessity because of the growing interrelationships between all natural sciences.

As the world population increases rapidly and as already an alarming percentage of our contemporaries are underfed or starving it is our duty to intensify our efforts to increase crop yields, amongst others by controlling plant diseases. Only if scientists from all over the world have a free exchange of their results and ideas may we ever hope to reach our goal: sufficient food for every human being living on the surface of the earth.

It is our intention to give an impression of some aspects of the fight against plant diseases, their influence on human society and history in the next pages.

III. PLANT PATHOLOGY AND HUMAN SOCIETY

Outbreaks of plant diseases have greatly influenced human society since the beginning of the cultivation of crop plants by man. Sometimes they have resulted in famines. Even today, losses may be tremendous. In the United States alone, losses due to plant diseases are estimated at about $3 \times 10^9$ dollars a year (Wood, 1953); i.e., the equivalent of 7% of the total potential production.

Already about two-thirds of the world's population is underfed,
hungry, or starving, and it is impossible to enlarge the area of cultivated land sufficiently to provide enough food for the existing millions. And still, the world population is increasing by about 30,000,000 people a year, or the equivalent of a new Australia to feed every 4 months (Stakman, 1957). Therefore we must raise the production per acre and here the plant pathologist has an important task to fulfill.

A. Influence of Plant Diseases on the Production of Food and Raw Materials

Plant diseases have wiped out or seriously threatened many flourishing tropical plantations. Coffee rust caused by *Hemileia vastatrix*, toward the end of last century, destroyed the culture of Arabian coffee on Ceylon (see also Section III, B, 4) and *Dothidella ulei*, causing South American leaf blight of rubber (*Hevea brasiliensis*), made the cultivation of this native tree impossible until an ingenious multiple grafting technique was adopted (private communication by Dr. Lee Ling, F.A.O.).

In order to establish a soft wood industry the Forest Department of Kenya started plantations of cypress (*Cupressus macrocarpa*). Growth was abundant until the trees were about 20 years old. Then, *Monochaetia unicornis*, causing severe cankers of the trunk, spread rapidly either killing the trees or making the timber worthless (Watts Padwick, 1956).

Tobacco plants on Sumatra, producing the world famous cigar wrappers, suffered frequently from an unknown top necrosis, until Mes (1930) revealed that this disease was a result of boron deficiency.

Leaf spot or Sigatoka disease of bananas caused by *Cercospora musae* has become so serious in Central America that without the use of fungicides (15–17 sprayings per year) the banana industry could not survive in that area.

Breeding of resistant varieties has saved a tropical crop in other cases. One of the oldest examples is the breeding of sugar cane varieties resistant against sereh-disease and mosaic, both caused by viruses (see also Section II, B, 3). Sugar beet varieties resistant to curly top (also a virus disease) saved the sugar beet crop for the western United States. Following the introduction of these resistant varieties the sugar beet area in California increased from 53,000 to 170,000 acres and the yield from 8.3 to 16 tons per acre, whereas before, several sugar factories had to be closed down as a result of the disease.

Bacterial blight or black-arm, a cotton disease caused by *Xanthomonas malvacearum*, has been particularly destructive in several cotton producing countries in Africa. In Uganda the introduction of seed dressing with a copper fungicide combined with the use of a more resistant
cotton variety resulted in a doubling of the yield if compared with the previous 27 years (Pottie, 1953).

The risks taken by the farmer in producing a crop and how he can combat them are familiar to all plant pathologists. The ratio of benefit received to cost of a control measure determines how far the farmer can go in applying control measures. Although the diseases are different, the food merchandising organization is confronted with the same problem, because their commodity is perishable and marketing diseases take their toll of produce in transit and storage.

B. Social Effects of Plant Diseases

1. Reduction of World Food Supplies

Since, as we have already seen, two-thirds of mankind have not enough to eat, it is a deplorable fact that weeds, diseases, and pests take about 20% of the food production of the world. This is a low estimate since it is based on figures provided for the United States, a country with high agricultural standards and extensive crop protection. From this 20% loss, 7% is due to plant diseases.

Every plant pathologist who has been working in the tropics, will agree that crop losses are much higher there, partly as a result of primitive farming and inadequate disease control, partly because a humid hot climate favors epidemics of many fungus diseases. Moreover, losses during storage are much higher in less developed countries.

Although Asia produces about as much food as Europe and the United States together, the people of many Asiatic countries are very vulnerable with respect to their food situation. A sudden outbreak of a serious disease in an essential food crop may soon cause a famine, for food reserves are very limited or nonexistent.

White stripe (hoja blanca) is a destructive virus disease of rice, resembling rice stripe, known for a long time from Japan. Since about 1954, this disease has been found in the Western Hemisphere where it caused a reduction of rice yields of 25 to 50% in countries like Cuba and Venezuela. Recently it has been reported also from Panama (Lasaga, 1957) and Florida.

Another serious disease of an essential food crop is maize rust (Puccinia polysora) which fungus disease has spread very rapidly over large parts of the world since the last World War. It is especially serious in West Africa where loss in corn grain amounted to 40% in 1951 (Watts Padwick, 1956). It is a tropical rust and does not occur under cool conditions.

The devastating effect of rust epidemics in wheat is well known.
As wheat, rice, and maize produce the bulk of the world's food one can imagine what damage is done by such diseases as have just been mentioned.

There is not much chance for a sufficient expansion of the agricultural area of the earth. To a small extent this may be done by irrigation of desert areas (Middle East, United States, North Africa), reclamation of inland seas (Holland) or deforestation, but this never will suffice to feed the rapidly increasing population of the world. The only alternative is a higher yield per acre. This may be reached by using better producing varieties (hybrid corn), virus free seed stocks (potatoes), fertilizers, disease resistant crops, and disease control through plant hygiene and the application of chemicals, such as fungicides, herbicides, insecticides, and nematicides.

2. Local Famines in Past and Present

On the basis of information in the scarce literature of ancient times it seems highly probable that famines as a result of rust and mildew epidemics on wheat were not uncommon in the Roman empire. The serious famine resulting from the failure of the potato crop in Ireland in two successive years (1845 and 1846) is so well known, that we hardly need mention it here. Some consequences will be dealt with in Section III, C of this chapter. The fungus that caused this disaster, Phytophthora infestans, is still responsible for heavy losses. In some years it may destroy over 10% of the world's potato crop. As the annual world production of white potatoes is estimated at 8 billion bushels, this means a loss of no less than 800,000,000 bushels or about 22,500,000 tons of valuable food.

However, not the potato, but cereal crops are the most important ones for human subsistence throughout the world, providing roughly 80% of man's food. Among the cereals, the production of wheat ranks highest. It has been estimated that for the world as a whole the annual average losses caused by rust fungi amount to about 600,000,000 bushels. In the center of a stem rust epidemic susceptible varieties may even have a yield reduction of 80%. If no food is supplied from elsewhere, this may easily initiate a famine.

A rice crop failure in Bengal due to Helminthosporium oryzae has actually led to famine conditions.

Cassava, although not nearly as valuable a food as rice, nevertheless is an important subsistence crop in the tropics. Mosaic, a virus disease, frequently occurring in African cassava, may cause a severe reduction in yield. Cassava is a vegetatively propagated crop and, e.g., in Uganda it was totally infected with mosaic, yielding 2 tons an acre, whereas
selected virus free stocks yielded 14 tons to the acre. This means that in
the Uganda district where the virus free stock was introduced, each
man, woman, and child now gets one extra pound of food a day (Int.

The sudden outbreak of maize rust has in some areas (West Africa)
reduced the yield by 40%, thus endangering the local food position.

3. Poisoning of Food Due to Plant Diseases

Poisoning of man and livestock animals as a result of plant diseases
does not occur frequently today. In the Middle Ages, however, due to
eating ergot-poisoned rye bread thousands among the poorer classes of
Europe have suffered terribly from ergotism or St. Anthony’s fire as it
was often called. In severe cases of gangrenous ergotism the patients
lose fingers, toes, or even whole limbs, the flesh gradually rotting away.
Another type called convulsive ergotism, is characterized by nervous
symptoms which in severe cases led to convulsions of the whole body
and finally various mental derangements such as epilepsy and dementia
(Barger, 1931).

Not before the first half of the 17th century was the cause of this
disease discovered; that is to say it was then that a connection was
found between the occurrence of many large kernels (so-called ergots)
in rye fields and the outbreak of ergotism after eating bread, made from
ergot-contaminated flour. But it was not until the middle of the 19th
century that the cause of the ergot-formation was identified and the
life cycle of this parasitic fungus (*Claviceps purpurea*) was unraveled
by the well-known French mycologist Tulasne. He also proved that the
ergot was the sclerotium of this fungus and not an abnormal outgrowth
of the ovary of the rye kernel.

Less severe poisoning of man may result from eating bread made
from rye heavily infected with *Fusarium* spp. or *Phialea temulenta*.
Symptoms are general weakness, vertigo, nausea, and headache.

*Claviceps purpurea* is not restricted to rye; it may infect at least
150 different grasses and thus cause ergotism in cattle with symptoms
similar to those described for man. It frequently leads to abortion (Hardi-
son, 1953).

Barley seed infected with *Gibberella zeae*, is often found in the
eastern and central United States. It is called “scabby” grain and, when
fed to pigs, it appears to be poisonous.

Crown rust (*Puccinia coronata* var. *lolii*) renders perennial rye grass
(*Lolium perenne*) unpalatable to sheep in New Zealand (Cruickshank,
1957).

The nematode *Anguina agrostis* is a common parasite of grass seed,
particularly of chewings fescue (*Festuca* sp.). Fatal poisoning of sheep, cattle, and pigs has occurred in western Oregon from feeding screenings of this grass seed containing nematode galls (Hardison, 1953).

Also mineral deficiencies in forage crops and grasses may lead to abnormalities or diseases in animals. Seeds from manganese deficient oats fed to poultry induced cannibalism, perosis, and bad hatching of eggs. Copper deficiency of meadow grasses is manifested by unthriftiness, depraved appetite, anemia, and diarrhea in cattle. Applying copper sulfate to the deficient meadow or directly to the animal causes disease symptoms to disappear.

4. *Why the English Drink More Tea Than Coffee*

In England consumption of coffee was about equal to that of tea in the middle of the 19th century (Ordish, 1952). At that time, Ceylon was one of the world's greatest coffee producing countries, followed immediately by India, Malaya, and Java.

In 1867, a pathogenic leaf fungus, later known as coffee rust (*Hemileia vastatrix*), was found in one coffee plantation of Ceylon. This pathogen was spread with alarming rapidity by the monsoon winds, favored by the uninterrupted monoculture of coffee over large areas.

While in 1871 the average annual yield was still about 4.5 cwt. (= 228.6 kg.)/acre it had dropped in 1878 to 2 cwt. (= 101.6 kg.)/acre. This, for Ceylon alone, meant a monetary loss of about $5,000,000. Between 1879 and 1893 exports of coffee dropped to less than 7% of the pre-rust epidemic shipments (see Wellman, 1953). No wonder, then, that *Hemileia* ended coffee growing on a large scale, not only in Ceylon, but also in other East Asiatic countries. "The planters (on Ceylon) were ruined and the Oriental Bank went smash in the general confusion" (Large, 1946).

After this catastrophe Brazil gradually became the main coffee producer of the world. Fortunately for that country, coffee rust is not known in the Western Hemisphere, but with modern rapid transportation there is always the very real danger of importation, just as maize rust is now spreading with alarming speed all over the world.

Coffee rust is also present in British East Africa, but there it produces serious losses only occasionally. By spraying with copper and other fungicides, leaf fall can be reduced by 10 to 40% (Watts Padwick, 1956).

After shifting from coffee to tea, the Ceylon plantations gradually became profitable once more, until blister blight threatened them again. However, very effective chemical control measures have been developed against this disease.

Since the coffee rust disaster, tea has become much more important
in Great Britain and Ireland. While coffee and tea consumption were about equal in the middle of the last century, there is now a 6:1 ratio in favor of tea (Ordish, 1952). That the British did not import coffee from Brazil on a large scale, but changed their drinking habits, is probably due to the favorable trade relations existing within the British Empire and, in more recent times, between the partners of the Commonwealth.

5. Development of Chemical Industries, Dusting and Spraying Equipment Firms, and Spraying Contractors

Especially during and after the Second World War the number of potent crop pesticide products increased tremendously. It is estimated that the annual world sale of these products amounts to approximately $280,000,000 at wholesale prices, or an on-farm value of $420,000,000 (Ordish, 1952). How much of this money is spent for fungicides is not known. But also, without this knowledge it will be clear that many people find a living in the production, distribution, and sale of such chemicals.

In Section II, B, 10 of this chapter a short survey was given of the newer types of machines developed for the application of pesticides. Like the chemical plants, the machine manufacturers employ many people.

For the designing of new sprayers, blowers, and dusters and for the search for new fungicides, insecticides, etc., industrial firms have invested large sums in laboratories, their staff, and equipment.

Spraying, especially with the more poisonous chemicals, must be done with great precaution and skill and can best be carried out by specialists. As a result more and more acres are treated by contract sprayers.

A special kind of contract spraying is carried out by aerial spraying companies, well known for instance from locust campaigns in the Middle East and elsewhere. This type of spraying is suitable only for larger areas and in most countries where it is employed its use is limited to insect control, weed control, or the aerial application of fertilizers. Recently it became clear that fungicides could also be distributed successfully this way, e.g., on potato fields for the prevention of late blight.

6. Potential Dangers in the Use of Poisonous Chemicals on Food Crops

"Many of us look with growing concern at the chemical warfare which farmers and horticulturists are forced to wage today against insects and diseases if they want to secure their share in the markets and make a success of their chosen profession" declared F. T. Wahlen, of the Food and Agriculture Organization, in an address at the opening session of the 7th International Botanical Congress (1950).
It is in a way gratifying for the plant pathologist that the fungicides he prescribes are, generally speaking, far less poisonous to man and livestock animals than many modern insecticides and weed killers.

But some fungicides, such as organic mercury compounds, can also be dangerous for public health when used as foliage sprays. They remain on the leaves and young fruits for weeks, are easily absorbed by the waxy layers of the fruit skin and may persist there until after harvest. Because they are cumulative poisons, Public Health Authorities in most countries do not allow even traces of mercury residues on fruits and vegetables. This practically will prohibit their use as foliage sprays, e.g., against apple scab, where they have certain advantages as eradicants.

Whether or not a new pesticide will be accepted for general use, therefore, depends not only on its effect against the noxious organism, but also on its toxicity for man and livestock animals. This is investigated in many countries by Public Health Institutes and approval or disapproval is finally decided by such organizations as the Food and Drug Administration (United States) or by special Committees in which both Public Health Administrators and Officers of Plant Protection Organizations participate (England and Western European countries).

Danger for the consumer can be reduced to acceptable limits by either prohibiting the use of certain chemicals or by restricting their use to certain periods. Although there have been some incidental cases of poisoning of consumers none is known to have been fatal.

The man who applies the chemicals to the crop runs more risks, but if he is careful and keeps to the instructions given he need not be worried too much.

Adverse effects on livestock animals have been observed, e.g., if spray drift brought arsenic weed killers on adjacent meadows.

A danger of quite another type is poisoning of the soil by too frequent uses of pest control chemicals. Up to now this has been observed in orchards in western United States where manifold applications of arsenic insecticides made replanting of apple trees impossible. Arsenic compounds used as weed killers may poison arable land. Oats sown after such treatments of a previous crop have shown a marked reduction in growth and yield.

Too frequent spraying of copper fungicides on the foliage of crops has also resulted in unfavorable effects on plant growth.

C. Plant Pathology and Human History

Plant diseases never had such a direct bearing on human history as those epidemic diseases of man in which insects played a major role. "Applied entomology and human history" therefore would yield more impressive facts.
What happened in ancient times we do not know. It is quite possible that famines resulting, for instance, from losses of wheat by rusts have had influence of historic importance.

In more recent times the most striking example of how a plant disease may influence history is the case of the great famine in Ireland toward the middle of the last century. In 1845 and 1846 late blight almost wiped out the whole potato crop in that country. This together with the very backward social and political situation not only led to the Irish famine and the emigration of hundreds of thousands of Irishmen to the United States, but also it was a decisive factor in the subsequent social and economic policy in Ireland itself. It ultimately led to the separation of Ireland from the United Kingdom.

The Irish famine has greatly stimulated research in the field of plant diseases and may be seen as the start of the modern era of plant pathology, which since has yielded so many results of great economic and social importance.

Epidemics of plant diseases in the tropics have often had political repercussions, especially if the threatened crop is the one of greatest economic importance to the community. A typical example is the swollen shoot disease of cacao, reducing the production in the eastern region of the Gold Coast from 128,000 tons in 1936–37 to 47,583 tons in 1951–52. In some areas production was reduced by as much as 80%. In 1953 there were about 50,000,000 infected trees. By cutting out the diseased trees, the rural industry of the Eastern Province of the Gold Coast was upset, and the expensive cutting out program has had serious political repercussions (Watts Padwick, 1956).

Good control of plant diseases is essential for the maintenance of a better standard of living, especially in the underdeveloped countries.

Thus, by helping to increase the world’s food supplies, plant pathologists may have some influence on human history in underdeveloped regions. It must be admitted, however, that this influence will only be very small as long as the people of such regions do not wholeheartedly cooperate in our fight against plant diseases and insect pests.

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