PRINCIPLES OF PLANT PATHOLOGY

STAKMAN ◇ HARRAR

Principles of Plant Pathology

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PREFACE

In this book we have attempted to develop and illustrate the fundamental principles and conccpts of plant pathology as we have seen them validated by observation, experimentation, and research. We deal with the nature and classification of plant pathogens, the ecologic and physiologic relationships between host and pathogen, the nature and development of epidemics, and with the international aspects of plant disease control. We hope we have given the reader the basis for an understanding of the broad interrelationships between plants as economic resources and the diseases which limit their productivity. In a sense, the book attempts to answer questions that have been asked by several generations of our students, and some questions that we have had to ask ourselves while trying to contribute to agricultural improvement programs in several countries of the world. It is our hope that this volume may be valuable for students specializing in plant pathology and also, as a reference, for scientists and specialists concerned with the critical problem of increasing the world's food production.

There are thousands of kinds of host plants and thousands of different pathogens that attack them under every kind of climatic condition. The resulting diseases are scientifically interesting and economically important. The services of many specialists are required in learning what we need to know in order to control the multitude of diseases on innumerable plant species. But the specific results obtained by specialists must be woven together into a general order of procedures for producing healthier plants. Our emphasis is on the pathogens which afflict food-producing plants because of the importance of these plants to society and to the growing demand for increased production of basic foods throughout much of the world.

This problem of plant protection is by its very nature international in scope. However, the great diversity of special interests in diseases of tropical crops, subtropical crops, temperate-zone crops, and all the subdivisions within each must be unified into a coherent pattern of understanding and effort. We have tried to show that there is a real unity in the great diversity of information regarding plant diseases and their control, and that principles and concepts can be universal in their application. Indeed, the test of their validity is the extent of their applicability.

The literature in the field of plant pathology is rich in journal articles, bulletins, and books that deal with specific and general aspects of the science. We hope that this book, concentrating as it does on the principles

of plant pathology, may make these publications even more meaningful. Selected references follow the chapters. The important literature in plant pathology has become so voluminous that increasing dependence must be placed on good review articles; therefore we have tried to include them in the reference lists, and we suggest that students acquire as many of them as possible. A list of important books is given in Appendix A.

Definitions, terms, and concepts are not, as yet, fixed in plant pathology. Until there is general agreement regarding the language of the science there will be differences of opinion and some flexibility in usage. We ask the indulgence of those who do not agree with some of our terms, but hope that we at least have precedent for using them.

The problem of scientific names is always with us, and some names have even been changed while the book was being written. In summarizing some investigations we have used the names that were generally used at that time. We hope that Appendixes B and C will be useful in contributing to clarification.

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INTRODUCTION

The health of plants is vital to society and human progress, and this volume is essentially a discussion of the problems and principles involved in protecting the health of domestic plants. It deals principally with those species which are of greatest significance as food crops on a world-wide basis and with the diseases which are limiting factors in their production.

The classic approach to disease through the study of the pathogen on individual hosts has undergone much modification, and this is even more true with plant diseases than with diseases of animals and man. Although it is still possible to deal with man and his diseases on an individual basis to a considerable degree, more and more it is realized that the major health problems are, by nature, public rather than personal. Diseases of individual plants usually are relatively unimportant, and plant pathology is therefore essentially a community, or "plant public health," science.

In undisturbed nature the community aspect of plant disease is evident though less conspicuous than among cultivated crops. Under natural conditions plants usually occur in mixed stands in which there is a rather well-established biological balance among the several plant types relative to competition for space, light, moisture, and nutrients. This ecological arrangement tends to minimize the attack of specific pathogens of a single species. However, upon examination, evidence of disease is readily found within natural plant communities. Some common examples are rusts of wild grasses, cedars, pines, and currants; leaf spots of indigenous tree species such as the oak, poplar, and wild cherry; mildews on wild legumes and other hosts; and cankers of many woody species. There is clear evidence that these diseases vary in incidence and severity from year to year with environmental influences, yet they rarely become truly epidemic. Most of the devastating outbreaks of plant diseases among indigenous and noncultivated plants are the result of the introduction of exotic pathogens. Classic examples include the pathogens causing chestnut blight, the white pine blister rust, citrus canker, and Dutch elm disease, which were introduced into the North American continent.

The greatest need for plant disease control is in connection with those crops that are artificially cultivated. When several hundred human beings dwell within a single square mile, the area is said to be crowded,

and great care is taken to prevent the development of serious public health problems. In comparison, one acre of wheat may contain approximately a million individual plants, all more nearly identical than individuals in any group of human beings; and the plant pathologist is concerned with the fact that the crowding together offers optimum conditions for the development of epidemic diseases. This crowding is a deliberate modern agronomic technique designed to promote maximum agricultural production through the use of improved varieties and soil management, but it provides highly favorable conditions for the devastating attacks of plant pathogens. Thus, agriculture takes the form of plant urbanization in which tremendous populations are abnormally concentrated in a relatively small area, and in a sense each cultivated field becomes a gigantic culture medium for pathogens. Every successful effort to improve yield by adding to the carrying capacity of the soil intensifies disease problems which must be met if agriculture is to progress.

The plant pathologist must seek methods to prevent or control plant diseases under conditions of high epidemic potential. Unless plant diseases are contained, the world's efforts to feed itself cannot be successful. Every loss from disease reduces the average yield per unit of cultivated area, and these losses increase the pressure upon the land available for agricultural production and make even more acute the problem of feeding a growing world population.

Disease control measures, whether successful or not, increase the costs of production. Individual or local losses from plant disease are of relatively minor importance in the aggregate. Those diseases responsible for the greatest percentage of total damage are world-wide in distribution and involve parasites whose hosts are the important food crops of the world, such as wheat, rice, corn, and potatoes. Without minimizing the over-all importance of local diseases of dozens of secondary food crops, it is nevertheless true that plant health is basically an international problem. This problem must be attacked on an international basis, and the experience and research of workers in many countries are necessary to its solution.

Important research already accomplished in the field of plant pathology has often been the product of efforts in many different areas. As transportation has become more rapid and extensive, treatment of plant diseases as strictly local phenomena has become impossible, and concentrated effort on an international scale to prevent and control important diseases is the only feasible approach to this phase of the problem of food production. In the chapters which follow, hosts, pathogens, and the factors that govern their interaction are dealt with. The several aspects of plant public health on an international basis are treated and an attempt

made to lay the groundwork for a general understanding of the development of disease. An effort is made to place the problem of plant disease control in the proper setting, bring out the international aspects of the science, and suggest methods by which world progress might be made toward the solution of some of these problems which are vital to all mankind.

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THE IMPORTANCE OF PLANTS

Man occupies this planet as a guest of the plant kingdom. In fact, he is completely dependent upon plants, since they feed the world and provide much of the shelter and many of the conveniences and luxuries demanded by society. Lumber, drugs, beverages, spices, fibers, and chemical extracts are only a few of the many plant products besides foodstuffs which benefit man. Fossil plants are the basis of the world's fuel reserves and thus its principal current source of energy.

Plants are of greatest significance as synthesizers of foods vital to the health and well-being of man and animals. Plants alone among living forms are capable of capturing minute quantities of solar energy and, by photosynthesis, of synthesizing elementary substances into organic compounds essential for animal metabolism and growth. Man and animals are transformers, rather than synthesizers, of the basic food materials, and therefore their numbers must in the foreseeable future be governed by the availability of appropriate plant species.

The variety of plants useful to man is enormous. Each major taxonomic group contains from several to many economically important species. Bacteria, fungi, mosses, ferns, and seed plants are all represented, with the seed plants greatly outranking all others in importance. Not only does this group produce approximately 99 per cent of the total direct food supply of the world, but it occupies nearly all of the world's cultivated area. Although vast land areas are planted to nonfood crops, more than 80 per cent of the world's agricultural effort is directed toward food production. Of the more than 200,000 known plant species, approximately 3,000 have been used for food. Only about 300 are widely cultivated, and 95 per cent of the world's annual food production is derived from fewer than a dozen crops—wheat, rice, corn, potatoes, sweet potatoes, sugar cane, cassava, beans, coconut, and bananas.

Three fourths of the total world food supply is drawn from a single plant family, the grasses. Wheat, rice, millet, sorghum, and barley (known for more than 5,000 years) were among the earliest-known cultivated grasses, and these were later joined by corn, oats, rye, and sugar cane (known for more than 2,000 years). Today wheat, one of the two most important crops in the world, is planted annually to more than 430

Figure 1–1. Hybrid corn is rapidly becoming a major source of food and feed throughout the Americas. The upper photo shows a crossing block in El Salvador. Below, hybrid corn in production in Mexico is pictured, along with a wheat rotation.

million acres. Rice occupies approximately 220 million acres of land each year but has a total production from 10 to 15 per cent greater than the production of wheat. This represents the difference in average yields of the two cereals, that of wheat being approximately 15 bushels an acre and rice nearly 34 bushels. Wheat is grown to some extent in nearly every country, while rice, although widespread, is more limited in range by climate than wheat. Next in importance to wheat and rice are corn and sorghum. Corn is typically a crop of the Western Hemisphere, whereas sorghum has been used traditionally in Asia and Africa. Both are now widely grown for food and for industrial purposes. Sugar cane is the most important known source of sucrose, and since it is especially productive in the tropics and subtropics, cane is most intensively cultivated in the West Indies, East Indies, Hawaii, India, the Philippines, Mexico, and Brazil.

All of the other economic species of grasses are important as direct sources of human food or as animal feed, or both. Because of their variety, distribution, adaptability, and productivity, forage grasses are the basis for successful animal husbandry. This fact is dramatically evident in range areas in the United States, Mexico, and Australia, in the pampas of Argentina, Uruguay, and Brazil, and wherever cattle raising is a major industry.

The legume family has numerous representatives, ranging from small succulent plants to enormous trees; and various types of legumes occur both naturally and under cultivation throughout the world. Some types of beans and peas, principally soybeans, broadbeans, lentils, and chickpeas, have been cultivated for more than 5,000 years in Egypt and Asia. Kidney beans and peanuts have been cultivated in the Western Hemisphere for more than 2,000 years. Because of their habit of symbiotic nitrogen fixation, legumes are excellent sources of protein and, in consequence, they are important in dietary patterns almost everywhere. Peoples whose major food source is wheat, rice, corn, potatoes, bananas, or cassava have learned to balance these high-carbohydrate foods with one or more legumes; some type is found in nearly every diet, in primitive societies as well as in the more sophisticated sectors of society.

Potatoes and sweet potatoes, indigenous to the Western Hemisphere, are now widely cultivated. They have become the principal item of the diet in many areas and are of secondary importance in others. Bananas and plantains have long been staple foods in much of the humid tropics, and the coconut is a well-known multipurpose food throughout the coastal tropics. Each of these is a major food source for millions of people in areas to which they are adapted and where they are intensively cultivated.

Supplementing the food plants are those that satisfy other human needs. Chief among these are medicinal plants, which have served