Breeding Plants for Disease Resistance
Concepts and Applications

Breeding Plants For Disease Resistance

Concepts and Applications

Edited by R. R. Nelson

The Pennsylvania State University Press
University Park and London

Library of Congress Cataloging in Publication Data

Nelson, Richard Robert, 1926-
Breeding plants for disease resistance.

1. Plants—Disease and pest resistance. 2. Plant-breeding. I. Title.
SB750.N44 631.5'3 71-128175
ISBN 0-271-01141-6

Library of Congress Catalog Card Number: 71-128175
International Standard Book Number: 0-271-01141-6

Printed in the United States of America
Designed by Maria DeFebo

Preface

The old adage that "nations swarm for food" bodes ill to civilizations unable to sustain themselves. Food-deficient nations house a majority of today's people, and their starving millions attest to the urgent need for greater quantities of quality food throughout much of the world.

A number of proposals have been suggested as means to alleviate the world's food problem. Some, such as population controls, would necessitate what many consider to be impossible changes in moral, religious, and philosophical ethics. Others, such as "a meal in a pill" and "down to the sea for algae," undoubtedly would test the psychological fiber of many of us to the breaking point.

There are some viable alternatives. The reclamation of nonarable land currently is converting deserts into farmlands and abandoned mining tracts into orchards. The continued development and increased use of synthetic materials will lessen the need to devote arable land to fiber crops.

Productivity may be the prime scientific key to the world's food needs. A greater yield of better quality food per acre of arable land is the avowed mission of agricultural sciences. That mission remains undiminished despite the tendencies of urban societies to provide fewer funds and less encouragement to the "wetbacks" of science. And yet, if we don't swim, they won't eat. Agricultural research on food productivity is a composite of science, sense, and society. It is time for society to acquire more sense about science.

This book focuses attention on and extols the virtues of what many believe is the key of all keys to greater food production. Disease resistance in plants is well documented as a spectacular means of increasing productivity, as well as an able, if not consistent, defender against epidemic losses. Many of its prime credentials are assembled herein.

Part I summarizes my general considerations of the concepts, principles, and terminology that are germane to controlling plant diseases by resistance. Some of the concepts and several of the terms are controversial in their interpretation, and my treatment of them may well be deemed the same. I firmly believe that the principles and concepts pertinent to disease resistance are applicable to the control of most diseases of most crops. That the amount of scientific facts doubles every seven years while the number of concepts and principles remains fairly constant lends credibility to that belief. Part II treats many of the world's important crop species and ably demonstrates the role that resistance has played in their continued prominence. Each of the crop chapters has been written by one or more of the world's recognized leaders in the field. Their names and contributions to science are well known to many. My thanks go to each of them for their contributions and their patience with me during the editing phase. The authors were asked to restrict the number of their citations. Any omissions by them of pertinent references should not be construed as a minimization of their importance, or as an oversight on the part of the authors. If this book is a worthy contribution, it is because of them. In fact, some of my colleagues who followed the book from its inception refer to it as one "where the fiction comes first and the facts last."

Certain important crop species are not treated here; the reasons for their absence are varied.

This book is dedicated to Dr. C. C. Wernham. In a very real sense, it is his book. His entire professional career was dedicated to the proposition that disease resistance in plants was essential to the well-being of man. With that dedication to guide him, he set out to compile this book upon his retirement. His untimely death left it in its incipient stages. It was finished out of respect for him.

R. R. Nelson

University Park, 1973

Contents

Part I

General Considerations, Concepts, and Terminology

1 Introduction

R. R. Nelson[1]

The Past

> *If men could learn from history, what lessons it might teach us. But passion and party blind our eyes and the light which experience gives is a lantern on the stern, which shines only on the waves behind us. . . .*
>
> *Coleridge*

Plant diseases have been one of the greatest hazards to crop production almost since man began to domesticate plants. Diseases became epidemic and inflicted serious losses in ancient times, as evidenced by Biblical references to severe blasting, blighting, and rusting of plants.

Man has attempted to explain the occurrence of plant diseases for thousands of years. The accepted thinking and philosophies of the times tempered such explanations along certain lines. Prior to 1800, for example, the theory of spontaneous generation was accepted generally to explain the origin and occurrence of most living things, including plant diseases. This theory was advanced by Hebrew writers before 600

1. Professor of Plant Pathology, The Pennsylvania State University.

B.C. The idea of Aristotle (384-322 B.C.) that living organisms were formed by the union of a passive principle "matter" with an active principle "form" influenced the minds of men and scholars for more than 2000 years. During the Greek and Roman empires, the occurrence of plant diseases was thought to be punishment for displeasing the gods, and elaborate ceremonies were held to regain their favor. From then until early in the 19th century, beliefs concerning the causes of plant diseases were not appreciably different from those of the Greeks and Romans. The 50 years preceding the acceptance of the germ theory were dominated by the autogeneticists, who believed that fungi were the products of morbid sap produced by the living cells of the host.

Numerous achievements prior to 1850 appreciably aided the transition from the general ignorance of the Dark Ages to an awareness of the causes of plant diseases. The invention and later improvement of the microscope, the systematic treatment of the fungi by Fries and Persoon, the early work on the infectious nature of diseases of wheat by Tillet and Fontana, and the brilliant research of Prevost in 1807 on the cause of bunt of wheat are some of the milestones in the development of the germ theory. Despite these scientific facts and tools, general acceptance of the germ theory still was lacking by 1850.

The Irish famine, which resulted from 5 epidemics of potato late blight, may well have been the final contributor to a general acceptance of the germ theory of plant disease. Rapid increases in population, dependence on one crop for food, and widespread starvation resulting from plant diseases dictated that man must acknowledge the germ theory or die. The classic work of de Bary proved the validity of the germ theory once and for all.

Progress on the cause and control of plant diseases during the last 100 years has been spectacular. Yet the heavy toll that diseases still reap in all areas of the world and the approaching problem of feeding the world's expanding population clearly illustrate the immediate need for additional knowledge of the nature and control of plant diseases.

The impact of plant diseases on crops is still grossly underestimated in most agricultural areas. This is particularly true of those crops that are rarely, if ever, subjected to severe epidemics of a plant disease. The dramatic losses from stem rust of wheat, coffee rust, late blight of potatoes, and black shank of tobacco; the near elimination of the American chestnut; the ever-increasing losses from oak wilt; and the 1970 epidemic of southern corn leaf blight in the United States are graphic examples of the effect of plant disease epidemics. Spectacular losses create spectacular concern about diseases, although intense concern may be short-lived. In most crops, however, reductions in yield and quality are brought about in less spectacular fashion by diseases that occur annually or nearly so in less than epidemic proportions. Total losses from these diseases over a period of years can more than equal the losses incurred during a single epidemic year.

There are many methods of effective disease control. Such measures as chemotherapy, cross-protection, and systemic fungicides are of recent origin. Others came into play only after the acceptance of the germ theory, which postulated that organisms can cause disease. Seed treatment of cereal grains preceded this era, but it was used empirically. Disease control by resistance probably was the first method used to combat plant pathogens. The selection and use of disease resistant plants may have been a conscious or unconscious part of man's philosophy from the time he began to cultivate crop plants: he certainly must have been concerned with plant improvement at an early date. There is no reason to assume that the tendency to select the most productive types of plants is the singular prerogative of modern man. Indeed, the ancient civilizations of Greece and Rome recognized differences among plants in their susceptibility to diseases. Natural selection and survival of the fittest probably provided early man with some base of resistance in the wild plants that served as the progenitors of cultivated crops.

Recent history and our understanding of basic differences between wild and cultivated species provide excellent insight into many of the reasons for man's early confrontation with diseases of crop plants as he began to domesticate plants for convenience and for greater quantities of food and fiber. Wild species typically are comprised of populations of plants exhibiting considerable genetic diversity for many traits; man tends to emphasize homogeneous and uniform populations of cultivated or domesticated plant species to facilitate cropping and harvesting practices. Wild species typically exhibit a variety of traits or characteristics which may be beneficial or necessary to survival, but which definitely are not desirable to man in his domesticated crops. Wild species typically grow at random in nature as single plants or groups of few plants. For convenience and to preserve land, man crops his domesticated species as large populations of plants in relatively small areas.

Recent attempts commercially to domesticate wild rice in northern Minnesota illustrate the significance of these basic differences between wild and cultivated species. Wild rice plants grow randomly in scattered groups along banks of streams or in wet, boggy areas. Most of the plants shed their kernels at maturity as a natural response to wind or rain, a trait that man refers to as "shattering." The obvious benefit to the plant of quick release of seed is that the species sows its seed for reproduction. The obvious disadvantage to man of shattering plants of domesticated species is loss of yield. One of the first steps in domesticating wild rice in Minnesota was the selection of nonshattering plants that occurred in low frequencies among natural populations. Necessary as this selection was, it served to reduce the genetic diversity of the populations. The domestication of wild rice proceeded with the intensive cropping of the species in prepared rice paddies. Almost immediately the cultivated wild rice was subjected to a leaf spot disease which rapidly reached epidemic proportions and now threatens the domestication of wild rice until resistance or some other appropriate control measure is obtained. The domestication of coffee and bananas in large plantations created a situation of intense cropping which no doubt contributed significantly to epidemics of coffee rust and banana wilt. Early man probably faced similar instances of disease problems as he domesticated wild species. To what extent early man selected for disease resistance and how efficient he was in doing so are not known.

Precisely when the use of disease resistance as a means of controlling plant diseases had its modern beginning depends largely on how one defines the term "modern." For example, Foex is credited with saving the grape industry of France a century ago by importing American varieties resistant to downy mildew. Considering that significant progress in selecting for disease resistance occurred near the beginning of this century, it may be appropriate to designate the era around 1900 as the modern beginning of disease control by hereditary methods. Certainly the belated appreciation about 1900 of Mendel's contributions provided a firm scientific basis for exploiting the inherent resistance present in most crop species to a multitude of causal agents.

Initial efforts to identify and obtain disease resistant plants utilized the process of selection from already available lines or varieties. In the United States Orton initiated a program of selecting cotton for resistance to fusarium wilt. Plants were tested in heavily infested soil; from those that appeared healthy, seed was saved for testing in the same soil the following season. Persistence in this method of selection and progeny testing led to the production of several varieties of Sea Island and Upland cotton. Success with the cotton wilt program was paralleled by progress with cowpeas resistant to wilt and to the root knot nematode. In each of these efforts Orton selected resistant cultivars from varieties already in cultivation.

The technique of within-variety selection was used by Bolley in North Dakota to seek resistance against fusarium wilt of flax at about the same time Orton was working with cowpeas and cotton. Flax grown in successive years in the same soil showed such a high incidence of *Fusarium lini* that only a few plants of a tested variety managed to survive. Progeny testing of these surviving individuals on "flax-sick" soil led to the production of several resistant varieties. But the resistance of the flax varieties proved to be unstable, and many investigations were initiated to pinpoint the underlying causes. Out of these studies came two well-established concepts: (1) the almost limitless abilities within the flax wilt organism to generate new races capable of attacking presumably resistant flax varieties; and (2) the dependence of the host on specific homozygous genotypes to combat specific strains of the wilt pathogen.

In order to obtain wilt resistant watermelons Orton had to resort to hybridization. The cultivated watermelon did not yield resistant individuals for progeny testing, but the citron melon, grown only for livestock, was remarkably resistant. The F_2 generation segregates produced resistant watermelon types, and subsequent selection and crossing to watermelon led to the introduction of the wilt resistant watermelon Conqueror. This is probably the first use of the back-cross method in breeding for disease resistance.

As early as 1901 Farrer in Australia reported on the breeding of wheat varieties resistant to bunt or stinking smut. Biffen, in England, crossed two wheat varieties, one resistant and one susceptible to stripe rust. Cognizant of Mendel's work, Biffen established that resistance was conditioned by a simple recessive factor and that resistance was inherited independently of other parental traits. His findings contributed to the reasoning that resistance could be combined with other characteristics desired in commercial varieties. Thus, a new dimension was added to the value of hybridization between different genotypes; a dimension that was to be used extensively in subsequent years.

The Present

If I have seen a little farther than others it is because I have stood on the shoulders of giants. . . .

Newton

It is likely that more than 75 per cent of the current agricultural acreage in the United States is planted with varieties resistant to one or more plant diseases. When Coons (1953) estimated a one-half to three-quarters of a billion dollars financial benefit to growers in the United States from using resistant varieties in 1953, he estimated that 50 per cent of all crop acreage utilized resistant varieties. Compounded the world over today, benefits accrued from the use of resistant varieties certainly would amount to many billions of dollars annually.

Another means of viewing the economic value of disease resistance was illustrated succinctly by Stakman and Harrar (1957) when they stated, "were potatoes resistant to the principal pathogens that attack them in certain areas of the northern United States, the cost of production could be reduced at least $50 an acre." Similarly, Reitz (1954) discussed the value of breeding for disease resistance in the United States and estimated that "the increased income from wheat alone at $2 per bushel would return four-fold the annual cost of all tax-supported agricultural research." Although the development of resistant varieties is not inexpensive, the benefits more than justify the costs. Furthermore, resistance is the only means of disease control that does not add directly to cost of production, although seed of newly released resistant varieties may command a premium price until ample stocks are available.

Resistance enables crop plants to defend *themselves* against their pathogens or against a level of disease deleterious to the crop. All other control measures dictate man's continued involvement in performing one or more of a variety of operations before, during, and/or after crop production. Frequently, the relative success of other control measures is determined by the preciseness of their use. The success of resistance is not so subject to such external variation.

The genetic control of plant diseases is isolated in this book in order to focus attention upon the impact of accomplishments that have occurred and upon the methods that have made this approach a viable and dynamic part of modern agriculture. And yet the threads of scientific pursuit are so interwoven that one principle of disease control is seldom employed exclusively. Combinations of principles creep unobtrusively into almost every facet of plant disease control. The integrated use of disease resistance with principles of exclusion, eradication, physical or chemical protection, avoidance, therapy, cross-protection, and biological control is commonplace in modern agriculture, and it further illustrates the importance of genetic control of diseases. Combinations of principles are used to combat the same or different diseases. The value and/or stability of resistance to a particular disease is enhanced by eliminating weed or alternate hosts from cultivated areas, for example virus infected *Sorghum halepense* from corn fields, and barberries and buckthorn from areas grown intensively to wheat and oats. Turf grasses with partial resistance to *Helminthosporium* leaf spot diseases commonly are sprayed with fungicides to control the same diseases.

Similarly, potato varieties exhibiting some degree of resistance to the late blight pathogen are protected further by fungicides. The net result in both instances is either more effective control or adequate control at a reduced cost. Disease resistance often is more effective when crop rotation or sanitation is utilized, since both of these cultural practices frequently tend to reduce the amount of initial inoculum available for disease onset. The stability of disease resistance is enhanced by quarantine restrictions regulating the introduction of germ plasm of hosts and pathogens from other geographic areas. The inadvertent introduction of a new race of a pathogen can be disastrous when current resistant varieties have not been evaluated for their response to the race. Plowing-under of green cover crops reduces the incidence of scab of potatoes, presumably by creating a soil environment more conducive to certain microorganisms that are antagonistic to *Streptomyces scabies*.

Combinations of control measures to combat different diseases are virtually standard practices. It is unlikely that a single variety of any crop species will be developed with resistance to all races of all its pathogens. Resistance to one disease would be meaningless should the crop succumb to another disease. Most crops are subject to attack by one or more pathogens from planting until harvest. Thus it is commonplace to treat seeds of blight resistant maize hybrids with fungicides to combat damping-off and seedling blights. Wilt resistant vegetables are often sprayed for foliar diseases. When several diseases are potentially common threats to a crop, resistance to some diseases may make fungicidal control of the remaining ones an easier and economically feasible task.

The crop often determines the method of disease control to be employed. Crops of high unit value, such as orchard fruits, vegetables, glasshouse crops, and ornamentals, are commonly protected from disease by fungicides. Their value justifies the cost. Crops of low unit value have been protected largely by hereditary control. Wheat, oats, barley, corn, flax, forages, and sugarcane are not normally protected from disease principally by fungicides. Their value does not justify the cost. However, application of fungicides on wheat at critical periods in the development of the crop has shown considerable value in protecting the crop against a significant increase in disease. The principle of using fungicides to reduce the rate at which disease develops, rather than as a protectant in the classical sense, is virtually unexplored and may provide a new dimension to disease control. This would certainly be the case should breeding for disease resistance shift primary goals toward accenting field resistance rather than race-specific resistance.