# The Nature and Practice of Biological Control of plant pathogens

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# Preface

Our original intention in writing this book was to revise and update our *Biological Control of Plant Pathogens*. However, it was clear already from the first efforts that we were writing a completely new book and that the first volume would therefore still be useful to workers in this field. Furthermore, the quantity of new information on biocontrol was so large that to incorporate it into a second edition was almost impossible. Our decision to build on and extend the principles of the first book, rather than to revise it, was strengthened when the American Phytopathological Society (APS) suggested in early 1982 that they reprint our first book which had been out of print for two and a half years. This solved the problem of continued availability of the first book and led to our agreement that APS would also publish the second book as a companion volume.

This book differs from the first in several important respects. The broad subject of biological control of plant pathogens—whether of aerial or subterranean plant parts, whether viroids, viruses, prokaryotes, fungi, or nematodes—is treated in an integrated, unified framework of concepts and principles. Relevant information is included from soil physics on the water and gaseous environment of soil, and from soil microbiology on microbial biomass and biomass turnover in the soil. Mechanisms of biological control are emphasized and related to current concepts of plant physiology, soils, and microbiology. Although some of the aspects covered are outside our expertise (e.g., cross protection between viruses and the physiology of host-parasite interactions), we hope that our perspective as biocontrol specialists may provide useful insights to the experts of these subjects and motivate them to apply these phenomena in biological control. One of the principal themes of this book, only briefly discussed in our earlier work, is that slight changes in an environmental factor often produce striking effects in interactions among microorganisms, or between them and the crop plant, and provide an effective means of achieving biological control of plant pathogens. Pathogen-suppressive soils, which have been the focus of much new research since our first book, are discussed in the context of the soil ecosystem and in relation to the source fields.

The beginning of a roster of the diverse agents shown to be antagonistic to plant pathogens is presented to stimulate more study of the biology and ecology of the microbial agents of biocontrol as well as of the pathogen to be controlled. Biological control by introduced antagonists, now a promising frontier, was represented 20 years ago by only three examples, and 10 years ago by only six examples, only two of which were used commercially.

The subject is here developed around the broad definition of biological control introduced in the first book, because this broad definition has been widely accepted and has proved to be useful and workable. Principles are again set forth in boldface type, 30 in this book, 51 in the first book. Of the 1081 references in this volume, 60% are since 1974, and 87% were not cited in the first volume. This provides a bibliography of 1,557 references on biological control. Fifteen key examples of the successful application of biocontrol are highlighted as boxed summaries set apart from the text. These summaries give a "thumbnail sketch" of the pathogen and the disease caused as well as the method of biocontrol, and they reveal the variety of approaches now in use against these important diseases.

This book, *The Nature and Practice of Biological Control of Plant Pathogens*, explains how biocontrol works in soil, in crop residue, on the surface of the living plant, and inside the plant. Investigations of this subject should never be futile or sterile laboratory exercises, but should start in the field, "where the clues and the action are," and after a phase of detailed laboratory study, should return to the field for testing and application. This book shows how biological control can be achieved in practice and lists more than a dozen potential opportunities for application in the field that have not been exploited. Biological control is as applicable to the agriculture of developing countries as to the high-production, high-energy practices of the western world, and it provides answers to many problems in the ultimate development of a sustainable world agriculture.

The landmark studies in the development of biological control of plant pathogens are presented, and photographs of 36 contributors from nine countries to these landmark studies are included. Biological control as a research field is still young, perhaps just entering its exponential growth phase. However, in some ways it is a maturing, organized discipline with research contributions dating back 60 years. Certainly, it is today one of the most exciting and rapidly developing areas of plant pathology, drawing on basic information from many related disciplines and source fields. Although no single book can now hope to cover biological control completely, we hope that this volume will provide focus and guidance to this expanding subject, stimulate more and better research in the laboratory and the field, and lead to wider application of biocontrol in agriculture. Although plant pathologists are no longer skeptical about the feasibility of biological control, the task of applying it to field conditions is only beginning.

We are happy to have participated in the growth of biological control as a subject during the "vintage years" of its development, and we look forward with confidence to the fruitful maturation of the subject and to its incorporation into world agriculture.

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*Kenneth F. Baker*

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# CONTENTS

# 1

# WHY BIOLOGICAL CONTROL?

*All things are connected. . . . Whatever befalls the Earth*
*befalls the sons of the Earth. . . . This we know—*
*the Earth does not belong to man, man belongs*
*to the Earth. . . . Man did not weave the web of life;*
*he is merely a strand in it. Whatever*
*he does to the web, he does to himself.*
—CHIEF SEATTLE, DWAMISH TRIBE, 1854

*We have not inherited the earth from our fathers,*
*we are borrowing it from our children.*
—LESTER A. BROWN, 1981

This, our second book on biological control of plant pathogens, appropriately begins with "Why Biological Control?," the question asked nearly 10 years ago in the concluding chapter of our first book (Baker and Cook, 1974). An attempt is made here to build on the foundation laid in that book, emphasizing progress of the last decade, particularly in the changing viewpoints and approaches. Our earlier work presented evidence to uncertain or skeptical plant pathologists for the existence of biological control; its reality now accepted, interest is shifting from "why" to "how."

The subtitle of the proceedings of the first international symposium on biological control (Baker and Snyder, 1965) phrased this uncertainty simply as *Prelude to Biological Control*. The editors sometimes jokingly were asked when the rest of the symphony could be expected. Perhaps our earlier book was the andante first movement of that symphony. This volume, we hope, may be the rondo second movement, complete with halftones and footnotes. If so, the final coda is for the future to compose.

In the first volume, we held that "a degree of biological control of diseases in crop plants is being achieved, even under present methods, and that by specific and judicious manipulation of environmental factors, perhaps without destroying the pathogen or even preventing it from infecting, satisfactory control of many additional diseases may be achieved." A thesis of the present volume is that biological control offers answers to many serious problems of modern agriculture and is an essential component in the development of a sustainable agriculture capable of continuing without interruption or diminution.

History bears witness that civilizations have rarely developed an enduring agriculture. Ancient Egypt apparently did so, because the land was replenished with silt in each annual flood; now that the Aswân High Dam is in place and the land is not replenished as before, the above statement is again true. The Sumerians in what is now Iraq, the Indians of the Indus Valley, the Mayans of Guatemala, the Aztecs of Mexico, the Incas of the Andes, the Anasazi of southwestern United States, the Singhalese of Ceylon, the Khmers of Cambodia, and others developed strong civilizations based on agriculture. When agriculture became nonproductive because of soil erosion, silting of irrigation systems, soil deterioration from slash-and-burn agriculture, soil salinity, or other causes, these civilizations declined and some vanished. Ancient China had devastating soil erosion problems, but developed a labor-intensive agriculture based on extensive use of organic manurial treatments that has made the People's Republic of China largely self-sufficient in food production, despite having the largest population of any country. The example of China offers hope that extensive adoption of biological control measures may help retard the environmental deterioration brought about by modern agriculture.

## BIOLOGICAL CONTROL ANSWERS MANY AGRICULTURAL PROBLEMS

Events of the past decade have reinforced our view that biological control holds the answers to many problems of today's agriculture.

### Increasing Crop Production Within Existing Resources

The success of modern agriculture in providing sufficient food for the increasing world population has come largely from the increased use of fossil-fuel energy and from increasing the area of cultivated land. Both of these factors have limits that have been reached or exceeded. The Organization of Petroleum-Exporting Countries (OPEC) has made us acutely aware of limitations on the energy supply, and the moment of truth on the amount of available land and on production ceilings is now recognizably at hand. The challenge facing agriculture today is to discover how to maintain, much less expand, production without making greater demands on limited nonrenewable resources.

The expansion of agriculture into arid and semiarid land by use of irrigation, besides being limited by available suitable land and by a finite supply of water, much of it from ancient, slowly replenishing aquifers, is dependent on expensive energy for pumping. In addition, salts that accumulate in irrigated land can be managed only by increased use of water; the more saline the soil or water, the more water required to leach the salts from the root zone. This involves pyramiding expense for the energy necessary to supply the water.

Increasing cultivable land through deforestation also has limits. The perennial drought problem of once-productive areas of northern Africa is a tragic reminder of the dangers of expanding farmland by deforestation.

High-production western-type agriculture is high-energy agriculture. The cereal crops of the Green Revolution achieve their increased yield potential by increased use of fertilizers and water, made possible because the new cultivars with their short stiff stems are less prone to lodge than standard-height cultivars when heavily fertilized. The day of abundant natural gas or oil for manufacturing cheap nitrogen fertilizer is past, and energy costs can only increase. This imposes an economic limit to achieving the full yield potential of the dwarf cereals.

Meanwhile, much productive land is disappearing beneath cities and pavements, and soil is being lost through erosion. An estimated two billion tons of topsoil is lost from U.S. cropland annually. Although resources are declining, the human population is increasing, necessitating increased crop production.

Ways must be found to increase or at least maintain the level of food production per unit area of land, while protecting and preserving declining and nonrenewable resources. Agriculture must become more productive but must also be sustainable. Toward this end, even more effort must be directed at improving the health and hence the productivity of green plants. Control of plant diseases is among the most significant ways still remaining to increase crop production, and biological control achieves this goal in a way that is economical and, most important, sustainable.

Browning (*in* Kommedahl and Williams, 1983) describes the present and future as the "Age of Plants." Humans have experienced many ages, including the recent Atomic Age and Space Age. According to Browning, recognition of the Age of Plants arrived in the 1970s with the oil embargoes and resultant energy crises. The total dependence of civilizations on the production of green plants is now abundantly clear. We can no longer take plants, and especially plant health, for granted. Plant health is of more than academic interest.

Plant diseases also play an important direct role in the diminution of natural resources for agriculture. Farming with reduced tillage or no tillage conserves energy and decreases soil erosion but is unacceptable in many areas for many crops because yield is less. Winter wheat in the Pacific Northwest commonly yields 25% less when direct drilled (sown no-till) than with conventional intensive tillage systems. Significantly, yields are the same or better with no-till if the soil is freed of pathogens by soil fumigation

(Cook, *in* Bezdicek and Power, 1983). Therefore, the problems of poor wheat yield with no-till in the Pacific Northwest are biological, not physical. Specifically, the lower yields are caused by poor root health. The shift to less tillage provides ecological niches previously unavailable to certain soilborne pathogens and to soil- and residue-inhabiting pests. Through understanding the biological stresses responsible for lower yields and the reasons why these stresses become more acute with reduced tillage, we can make adjustments to again close these niches for the betterment of plant health.

Crops could use fertilizer much more efficiently if the problem of poor root health caused by soilborne pathogens could be eliminated. *Pythium* spp., nematodes, and many other pathogens responsible for root pruning on most major food crops of the United States greatly reduce nutrient absorption by roots (Cook, *in* Bezdicek and Power, 1983). Growers often try to compensate for poor root health of their crops by applying more fertilizer. The well-known increased-growth response (IGR) of crop plants to soil fumigation (Wilhelm and Nelson, *in* Toussoun et al, 1970) results largely from decrease or elimination of these "root nibblers" and other plant pathogens (Cook, *in* Bezdicek and Power, 1983). The IGR resembles a fertilizer response because the healthier roots are more absorptive and also more effective in manufacturing growth factors for transfer to the plant tops. Soil fumigation and the IGR reveal the yield potential for a crop, but fumigation is not an economical or sustainable practice for most food crops. Genetic modification of crop cultivars, combined with management of microbial populations to obtain biological protection of the roots, offers an acceptable and sustainable alternative.

Although crops probably have a maximum yield that cannot be significantly exceeded by intensified management, the yield potential for a given area and agroecosystem is rarely attained. Perhaps the nearest approach to that level is attained in glasshouses with controlled environment and freedom from root nibblers. The record yields for corn, soybeans, potatoes, and most other food crops for a given area, soil, and climate are commonly double the average for that crop and area. The world record wheat yield of 209 bu/A (182 hl/ha) established 20 years ago under irrigation in the Columbia Basin in Washington still is unbroken. Indeed, the average yield in the same county is only about 100 bu/A (87 hl/ha), despite application of 75–100 cm of irrigation water and 150–200 kg of nitrogen per hectare annually. The yield of a given crop in a given area and season can be considered the product of an equilibrium between the genetic potential of the crop, the climate, and the availability of water and nutrients on the one hand, and the external biological stresses on that crop on the other (Chapter 11). Yields cannot even be maintained without adequate attention to plant health.

Biological control offers a powerful means to increase yield by suppression or destruction of pathogen inoculum, protect plants against infection, or increase the ability of plants to resist pathogens. The recent demonstration (Burr et al, 1978; Kloepper et al, 1980) of yield increases for potatoes following inoculation of seedpieces with *beneficial microorganisms* ("plant growth-promoting rhizobacteria") exemplifies the kind of crop response possible when nonpathogenic microorganisms are used to exclude or displace pathogens on roots (Figure 1.1). Biological control with beneficial microorganisms is in its infancy and has a promising future. It provides a way to increase production of crops without increased energy or land demands and without environmental pollution.

The alleviation or prevention of abiotic stresses on crop plants is another important means of increasing production. However, abiotic stresses rarely act alone when they affect plant productivity. The direct effect of abiotic stresses probably is significantly less important than their role in causing plants to become more susceptible to weak parasites. Winter barley and wheat are markedly more hardy and hence more able to survive severe winters in eastern Washington if they are protected by a fungicide from *Typhula incarnata*, a weak parasite but a potentially destructive pathogen of these crops (G. W. Bruehl, unpublished). In this same area, desiccation of wheat crowns caused by severe freezing for a few days early in the spring of 1982, when the plants had no snow cover, subsequently favored widespread damage from fusarium foot rot. The most winterhardy wheats had the least fusarium foot rot (R. J. Cook, unpublished). Also, in 1982, in plots of winter wheat near Pullman, Washington, plants were stressed by winter injury, growth was slow to resume in the spring, and the average yield was only 63.7 bu/A (55.6 hl/ha). However, in adjacent plots where soil had been fumigated with methyl bromide just before sowing the previous fall, plants were not damaged by the winter, grew vigorously early in the spring, and gave an average yield of 100.8 bu/A (87.8 hl/ha) (R. J. Cook, unpublished). Stress from winter injury predisposes wheat to some pathogens, whereas other pathogens apparently predispose wheat to greater winter injury. Soil fumigation as a research tool can reveal the greater yield that is possible in spite of abiotic stresses, if pathogens favored by the stresses can be controlled (Chapter 11). Adequate crop rotation allows time for biological control of the pathogens in soil, and the crop growth response can resemble that from soil fumigation (Cook, *in* Bezdicek and Power, 1983).

Even the milder frost damage that occurs on sensitive plants at temperatures only slightly below freezing is now known to involve microorganisms. Lindow et al (1975a, 1975b) showed that the bacterium *Pseudomonas syringae* on leaves of frost-sensitive plants provides nuclei for ice crystallization, which prevents water from supercooling below −2 to −5°C and increases frost damage. Plants having this bacterium or some strains of *Erwinia herbicola* on the foliage sustain frost injury, but plants lack-