ECOLOGY OF SOIL-BORNE PLANT PATHOGENS

Prelude to Biological Control

KENNETH F. BAKER and WILLIAM C SNYDER

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An International Symposium on
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Held at the University of California, Berkeley, April 7-13, 1963

Edited by
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Rhizoplane of mustard (*Brassica nigra*) root from garden soil; electron micrograph, × 32,000. Part of outer epidermal wall of nonpiliferous cell, showing microfibrillar network with clearly defined pits and bacteria in situ. The thin coating of mucilage and cutin has been removed during ultrasonic treatment. Bacteria may be attached in or near pits. (See F. M. Scott, pages 145, 152.)

Foreword

KENNETH F. BAKER AND WILLIAM C. SNYDER—*Department of Plant Pathology, University of California, Berkeley*

When plants emerged from warm primeval seas and invaded the land in the Devonian Period, about 300 million years ago, they were undoubtedly accompanied by fungi and bacteria which had been parasitizing them for millions of years. As roots evolved, they were invaded in turn. Certainly, fossil roots of the Carboniferous show extensive invasion by fungi (Fig. 1). Thus, parasitic fungi and bacteria have been part of the environment of roots for at least as long as the soil itself. It is, therefore, to be expected that the interactions between the parasite, root, and soil, and between parasitic and saprophytic microorganisms, have become extremely complex. Those organisms which did not adjust to this competitive state, by one means or another, did not survive. A state of fluctuating biological balance thus developed for each native habitat, and was self-adjusting for the relatively slow evolutionary and climatic changes.

When man began cultivating crops 8,000-9,000 years ago, the stage was set for frequent, rapid, and drastic ecological changes. With intensification of agriculture, losses from root diseases have increased as the buffering effect of biological controls diminished. When biological control is temporarily or permanently inhibited, severe outbreaks of root disease occur. A well-known example is the epidemic root disease that follows pathogen reintroduction into soil so treated by heat or chemicals as to destroy most of the microflora. It needs to be kept in mind, however, that root disease, like pathogenesis in general, is the exception rather than the rule. Indeed, biological control of root pathogens must be generally and effectively operative for there to be as little root disease as there is.

The study of soil microorganisms has developed rapidly in the last decade, in part due to man's need to understand this reservoir of disease organisms that attack both him and his crops. Although it is generally recognized that interactions of microorganisms constitute an important limiting factor to survival of disease organisms in soil, widespread utilization of such biological control awaits greater understanding of the processes involved. As clearly indicated in this symposium, effectiveness and dependability of biological control of root pathogens is enhanced when it is integrated with other control procedures, such as cultural manipulations, soil disinfestation, crop sequence, or

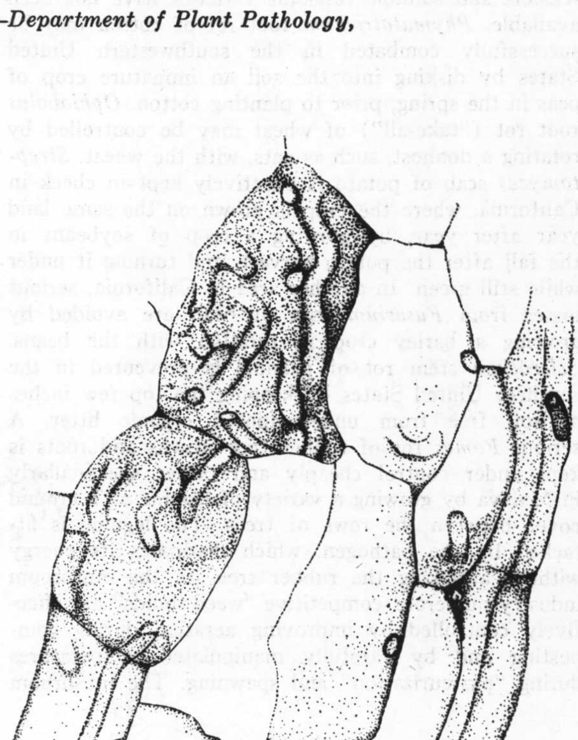

Fig. 1. Mycelia and vesicles of a fossil fungus in the cortex of rootlets of *Amyelon radicans* from English Coal Measures, Carboniferous Period of the Paleozoic, perhaps 230,000,000 years ago. (T. G. B. Osborn, Ann. Bot. 23: 603-661. 1909).

fertilizer practices. In this it resembles other plant-disease controls, for there are few successful single-shot methods in phytopathology.

Some of man's applications of biological control have proved successful or even spectacular, especially where chemical control has not been economically feasible and suitable resistant varieties have not been available. *Phymatotrichum* root rot of cotton may be successfully combated in the southwestern United States by disking into the soil an immature crop of peas in the spring, prior to planting cotton. *Ophiobolus* root rot ("take-all") of wheat may be controlled by rotating a nonhost, such as oats, with the wheat. *Streptomyces* scab of potato is effectively kept in check in California, where the crop is grown on the same land year after year, by growing a crop of soybeans in the fall after the potato harvest, and turning it under while still green. In another area in California, serious losses from *Fusarium* root of bean are avoided by growing a barley crop in rotation with the beans. *Sclerotium* stem rot of peanuts is prevented in the southern United States by keeping the top few inches of soil free from undecomposed organic litter. A serious *Fomes* rot of rubber tree crowns and roots is kept under control cheaply and rather spectacularly in Malaya by growing a variety of legume as a ground cover between the rows of trees. The legume is attacked by the pathogen, which dissipates its energy without attacking the rubber tree. In the mushroom industry numerous competitive "weed molds" are effectively controlled by improving aeration during composting and by carefully manipulated temperatures during "pasteurization" and spawning. The mushroom industry thus provides an outstanding example of effective biological manipulation of soil microflora for the benefit of a crop.

Soil microorganisms present one of the most complex, difficult, and rewarding present areas of exploration. Contact with this frontier has been established by the disciplines of plant pathology, microbiology, soil science, plant physiology, plant anatomy, biochemistry, bacteriology, nematology, mycology, virology, and zoology. Penetration in depth has, however, awaited the overcoming of this compartmentalization of the scattered, diffuse, isolated, and uncorrelated knowledge in these fields. It is increasingly clear that mastery of the soil microflora will come only when we understand the obscure complex of nonparasitic organisms, even though the pathogens have seemed the logical point of attack.

This was the first international symposium on the biological control of soil organisms. Since the field is new, emphasis was placed on background information drawn from many fields, as reflected in the title of these proceedings. To some this may be a disappointment, but most scientists will agree that this is a proper starting place. "It is no small part of the function of science to define the limits of knowledge. Unjustified optimism is as much the enemy of science as is unreasoning credulity." (C. Singer, *A History of Biology,* 1959.) Through these published proceedings, the whole symposium is now made available to interested scientists everywhere. Proceedings of subsequent symposia on this subject will chronicle the rapid rise of effective biological control of soil-borne plant pathogens.

Preface

The Agricultural Board of the Division of Biology and Agriculture of the National Academy of Sciences–National Research Council established in 1958 a Committee on Biological Control of Soil-Borne Plant Pathogens to stimulate work in that field. The Committee consisted of:

W. C. Snyder, Chairman (University of California)
K. F. Baker, Cochairman (University of California)
R. R. Baker (Colorado State University)
F. E. Clark (U. S. Department of Agriculture)
A. W. Dimock (Cornell University)
W. A. Kreutzer (Colorado State University)
J. D. Menzies (U. S. Department of Agriculture)
L. I. Miller (Virginia Polytechnic Institute)
Z. A. Patrick (Canada Department of Agriculture)

The Committee decided that its purpose would best be discharged by organizing an international symposium to: (1) stimulate research on the important problems in the biological control of soil microorganisms; (2) bring together active investigators of the world in this and related fields for discussions aimed at synthesizing and unifying the underlying concepts, and to consider needed future work; (3) assemble the scattered basic information on the biology of soil microorganisms, to evaluate, and to publish the papers and discussions in a reference volume that would constitute a basic work in this new field.

In the preparation of the program for the symposium the Committee sought the advice of a number of scientists in various parts of the world: T. C. Broyer, N. T. Flentje, S. D. Garrett, P. H. Gregory, H. Katznelson, A. Kerr, L. W. Koch, P. J. Kramer, A. Newsam, G. S. Pound, J. T. Presley, G. Stotzky, J. H. Warcup, and the faculty of the Department of Plant Pathology, Berkeley.

To facilitate discussion between active leaders in this and related fields, participation was by invitation. In addition, announcement of the symposium was published in *Nature*, *Science*, *Phytopathology*, and the *American Institute of Biological Sciences Bulletin*, so that any interested scientists could arrange for an invitation.

The 310 participants (listed on pages 525-535) from 24 countries represented most of the world laboratories active in this field. Of those attending, 20% were from 23 foreign countries, and 80% from 37 states of this country.

Invitations for authors, discussants, and chairmen were issued in May-July, 1962, and papers were due in March, 1963. Most authors revised their manuscripts following presentation and discussion of the papers at the symposium. The above Committee served as an Editorial Board, concerning itself primarily with subject matter. Mrs. Mary Rubo, formerly Agricultural Publications Editor, University of California, edited the papers for form and style, prepared the manuscript for the printer, and indexed the volume.

The symposium was held in the Student Union Building of the Berkeley campus of the University of California, April 7 to 13, 1963.

Abridgements of 41 published papers by 44 authors were presented orally, each followed by a general discussion. Of the 27 hours of sessions, 56% were spent in formal papers, and 44% in discussion. There were 287 questions or comments by 97 participants (31% of those attending), and the extent and enthusiasm of discussion participation was exceptional. Nearly all discussion periods were terminated because of time, and numerous questions or comments that could not be presented from the floor were submitted in writing for the proceedings. The presentation abridgements of the papers led to a few queries or comments which became unnecessary with the full text; these have been deleted here. More than 3200 references are cited.

Comments were written on a card by the questioner and the speaker immediately after presentation, and from these, supplemented in a few cases by a tape recording, concise summaries of the discussions were prepared (A. R. Weinhold and K. F. Baker, *Science*, 14: 1474, 1964).

The Style Manual for Biological Journals, published by the American Institute of Biological Sciences, was followed in preparing the book for publication. As recommended in the *Manual*, the *Chemical Abstracts* system of abbreviations for journal titles is used in citations.

WILLIAM C. SNYDER
KENNETH F. BAKER
Berkeley, California
April 6, 1964

Acknowledgments

As with all such large conferences, many agencies and interested people contributed in various ways to make possible the meeting and the published proceedings.

The Symposium was supported by grants from the National Science Foundation, the National Institutes of Health, and the Agricultural Research Service of the United States Department of Agriculture, and administered by the Agricultural Board of the National Academy of Sciences–National Research Council. Additional funds were made available by a number of universities and agricultural experiment stations in this country and abroad, and by the United States Department of Agriculture, to cover in whole or in part the expenses of speakers, discussants, or chairmen representing them. Mayor C. B. Hutchison, an international figure in scientific agriculture, welcomed participants to the City of Berkeley.

The University of California, the Department of Plant Pathology, and University Extension, Berkeley, contributed personnel and facilities to make the Symposium and preparation of the Proceedings possible.

The Committee on Local Arrangements consisted of the following: W. C. Snyder, K. F. Baker, R. V. Bega, C. M. Olsen, J. R. Parmeter, Jr., M. N. Schroth, T. A. Toussoun, A. R. Weinhold, and S. Wilhelm. They were ably assisted by Patricia Abramovitz, J. V. Alexander, J. A. Bourret, T. Bowman, Flora A. Coach, R. J. Cook, Patricia J. Cove, K. L. Downes, Bonnie J. Eidman, N. T. Flentje, Sara A. Ford, M. O. Garraway, C. C. Gill, W. D. Harris, Luise Healey, Katherine Isaeff, C. I. Kado, W. J. Kaiser, Ming-tan Lai, R. G. Linderman, Anne L. Maino, R. W. Meyer, P. R. Miller, R. Muñoz, S. M. Nash, Barbara O'Meara, R. E. Reichle, J. E. Sagen, S. H. Smith, Jane Suman, D. S. Teakle, J. P. Thompson, G. L. Vertrees, and T. Watanabe.

The National Science Foundation made possible the publication of this volume by a partial support grant. The University of California Press, and particularly Mr. Ernest Callenbach, have been most coöperative and helpful in bringing this whole project to fruition. Mrs. Mary Rubo provided thought, experience, judgment, and effort beyond the call of duty in preparing the manuscript for the publisher. Katharine C. Baker and C. M. Olsen prepared illustrations for the printer. R. E. Reichle and C. M. Olsen checked some of the references. Dr. Frank L. Campbell, Dr. Paul F. Sharp, and Mr. R. E. Krauss, as officers of the National Academy of Sciences–National Research Council, were most helpful in implementing the activities of the Committee before, during, and after the Symposium.

Authors, discussants, and summarizers are to be especially commended for promptness and thoroughness in the preparation of their manuscripts, and for their coöperation in conforming to suggested standards.

Chairmen of Symposium Sessions

MARTIN ALEXANDER, Department of Agronomy, Cornell University, Ithaca, New York (Wednesday morning, April 10)

KENNETH F. BAKER, Department of Plant Pathology, University of California, Berkeley, California (Monday morning, April 8)

A. W. DIMOCK, Department of Plant Pathology, Cornell University, Ithaca, New York (Thursday afternoon, April 11)

GEORGE H. HEPTING, Southeastern Forest Experiment Station, U. S. Department of Agriculture, Asheville, North Carolina (Friday afternoon, April 12)

ARTHUR KELMAN, Department of Plant Pathology, North Carolina State College, Raleigh, North Carolina (Friday morning, April 12)

A. G. NORMAN, Department of Botany, University of Michigan, Ann Arbor, Michigan (Tuesday morning, April 9)

DENNIS PARKINSON, Department of Botany, University of Liverpool, Liverpool, England (Thursday morning, April 11) (now: Department of Biology, University of Waterloo, Waterloo, Ontario, Canada)

WILLIAM C. SNYDER, Department of Plant Pathology, University of California, Berkeley, California (Monday morning, April 8)

ROY A. YOUNG, Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon (Monday afternoon, April 8)

GEORGE A. ZENTMYER, Department of Plant Pathology, University of California, Riverside, California (Tuesday afternoon, April 9)

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PART I

INTRODUCTION

A Landmark in Biology

VICTOR R. BOSWELL—*Crops Research Division, Research Station, United States Department of Agriculture, Beltsville, Maryland.*

One does not need to be either a plant pathologist or a soil microbiologist to appreciate the significance of this First International Symposium on Factors Determining the Behavior of Plant Pathogens in the Soil. It is evidence of the growing momentum of research in a vital field. Research in microecology as an approach to certain plant-disease problems is by no means new but it has been much too long neglected, almost ignored, except by a chosen few. Those few, by their vision and their scholarly accomplishments through the years, have kept before us the great potentials of using microscopic living things to help solve problems that involve other living things. An important by-product of this symposium should be an improved popular awareness of the work you biologists are doing, and of why much more such work needs to be done.

There probably is no more difficult, urgent, and profitable area of research in agricultural biology today than that of soil microecological phenomena in relation to plant disease. Probably also no area of research is less popular, less glamorous, among investigators and agencies that are impelled to try to produce spectacular results in a hurry. But we face problems of increasing urgency in this area. Why has the challenge of these soil-borne plant-disease problems been picked up by so few investigators and agencies?

Preoccupation with the nonliving components of the environments of organisms has too often tended to becloud our awareness of the living components and their importance. Indeed, it seems that for a long time the living components of the soil were largely forgotten by practitioners and researchers alike, as possible means of controlling certain plant diseases caused by soil-borne pathogens. Biological control through the development of resistant hosts quite properly has been given a great deal of attention, and with many notable successes. But if the search for disease resistance is not successful, and no industrial chemical or physical treatment is available for economically controlling a soil-borne pathogen, the disease generally goes uncontrolled. The problem is laid aside as unfinished business. Why is the microecological approach so rarely tried on a substantial basis? Is it too slow, too expensive, or just too hard? In view of the stakes to be won, and of some of man's efforts today, none of those terms seems to be applicable.

There is nothing wrong with man's desire to study "space" and to search for life beyond the earth. But his fascination for outer space and possible forms of extraterrestrial life should not be allowed to eclipse the greater importance of studying ***extensively*** the life that lies within those few inches of earth immediately beneath his feet. Can there be any doubt that what man can learn about subsurface terrestrial life is far more necessary to his welfare in the foreseeable future than what he may learn of extraterrestrial life? Is it well that man should reach for the moon before he has really tried very hard to understand the goings-on of the myriad life in the soil on which he stands? Wisely or not, he may reach the moon before he understands very much about the microlife of the soil, because he will have made a much greater effort to reach the moon.

When substantial intellectual and material resources are devoted to these microecological problems on a continuing basis, valuable results are produced. The work is slow, difficult, and expensive, but no more so than much other work of basic and practical importance that is far better supported. We who participate in this symposium and the agencies we represent have no greater responsibility than to promote popular understanding and appreciation of this problem area, to stimulate the interest of students in it, and to foster the expansion of sound research in it.

May this symposium be recognized as a landmark in a great renaissance of interest and research in microecological balance in relation to soil-borne plant disease, and in the development of more enduringly profitable and wiser farming practices.

Toward Biological Control of Soil-Borne Plant Pathogens

S. D. GARRETT—*Botany School, University of Cambridge, England.*

By the term biological control, we clearly imply control of a disease through some biological agency; by the term biological agency, we are bound to mean a living microorganism or macroorganism other than the diseased or damaged plant acting as host and the pathogen or pest causing the disease or damage. This interpretation of the term is supported both by its general usage by entomologists, who first introduced it, and by its more recent employment by plant pathologists. A more formal definition can therefore be proposed to comprehend both naturally occurring and artificially contrived biological control, as follows. Biological control of plant disease may be defined as any condition under which, or practice whereby, survival or activity of a pathogen is reduced through the agency of any other living organism (except man himself), with the result that there is a reduction in incidence of the disease caused by the pathogen. Biological control can be brought about either by introduction or by augmentation in numbers of one or more species of controlling organisms, or by a change in environmental conditions designed to favour the multiplication and activity of such organisms, or by a combination of both procedures.

Next we should consider the genesis of the idea of biological control of soil-borne plant diseases, and the early history of its development. I had nothing to do with the origin of this idea and indeed it took some years to reach me and then to sink in, but I joined in the general excitement of these new developments and attempted to take part in them—an attempt that I have been making, on and off, ever since. The job of the historian is to pinpoint, so far as he can, significant events that have determined important trends and developments, and this applies equally well to the history of science. Credit for discovery has almost always gone, and perhaps rightly, not to the man who first suggested an idea without adequate supporting evidence, but to the one who was able to convince his contemporaries of its rightness and importance.

A demonstration that the activity of a plant pathogen could be inhibited by an accumulation of its own metabolic products was furnished as early as 1908 by Potter (1908). Neither he nor anyone else, however, then followed up the implications of this discovery. I have already attempted (Garrett, 1956) to suggest a possible reason for this earlier neglect by plant pathologists of the microbiological factor in the environment of plant pathogens, but it will suffice here to say that their awakening seemed to be triggered off by a paper from Sanford (1926), in which he suggested that the control of potato scab by green manuring was a *biological control*, due to an increase in the populations of certain saprophytic bacteria that multiplied upon the organic material. It is important to note, however, that Sanford was not merely reiterating at a more opportune time the suggestions of earlier workers such as Hartley (1921); these suggestions had not gone beyond a general idea of inoculating either soil or plants with selected, "antagonistic" saprophytes. Sanford had, in fact, proposed not one but two concepts, the second of which was original at least in this particular context, and had integrated them into a concise hypothesis of biological control, as follows: (1) saprophytic microorganisms can control the activity of plant pathogens; (2) the microbiological balance of the soil can be changed by altering soil conditions; in particular, the addition of fresh organic material will promote the activity and multiplication of saprophytes, which both by their competition for nutrients and for oxygen, and by their excretion, will depress the activity and multiplication of the pathogens. Sanford's hypothesis had the three merits of being easy to understand, of explaining and collating earlier observations, and of being open to experimental test.

The results of such a test were not long in coming; in the following year, Millard and Taylor (1927) reported control of scab, in potatoes grown in sterilized soil and inoculated with *Streptomyces scabies*, through simultaneous inoculation of the soil with *S. praecox*, a vigorous saprophytic species. Sanford and Broadfoot (1931) then provided experimental evidence for Sanford's original hypothesis, by showing that infection of wheat seedlings by *Ophiobolus graminis* in sterilized soil could be completely suppressed by the antagonistic action of various individually coinoculated species of fungi and bacteria (Fig. 1). The impact of Sanford and Broadfoot's paper was soon reinforced by an extremely original and elegant demonstration from another Canadian worker, Henry (1932), that the influence of soil temperature upon the development of the take-all disease in glasshouse trials could be strongly affected by interactions between the pathogen and other soil microorganisms (Figs. 2, 3). I still think, as I thought then, that this work of Henry's has been one of the greatest single feats of intellectual and

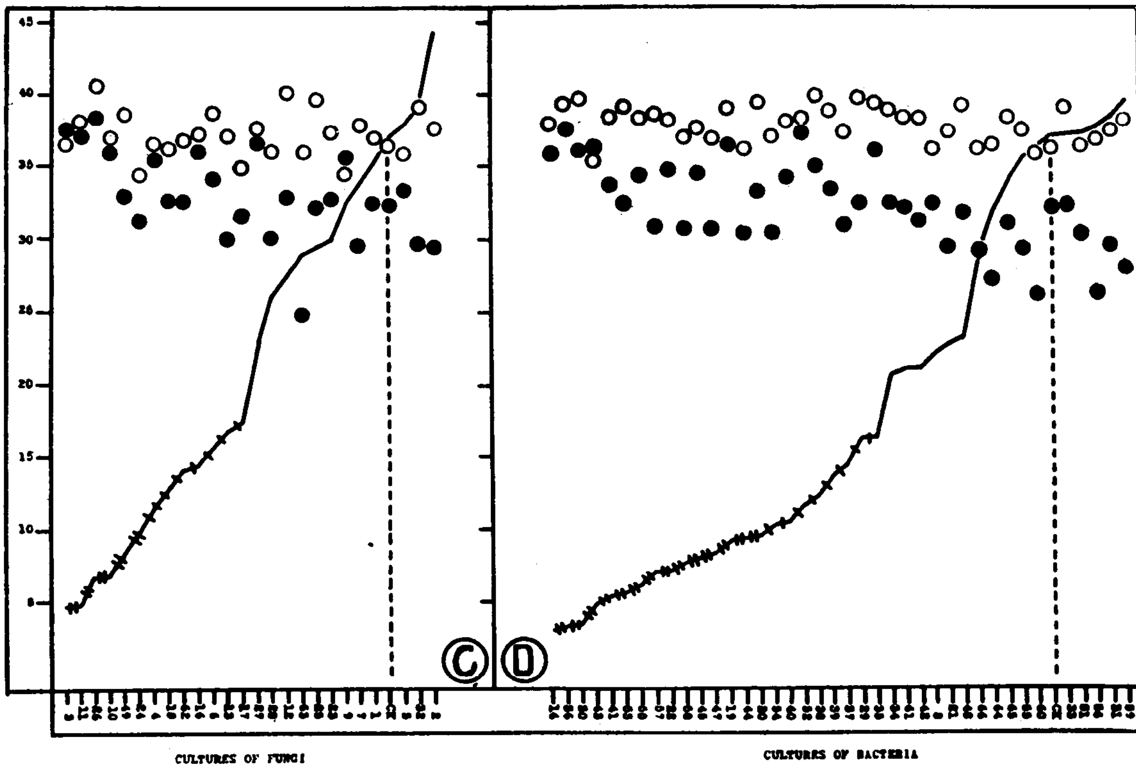

Fig. 1. The effect of 66 cultures of bacteria and fungi on the pathogenicity of *Ophiobolus graminis* on Marquis wheat seedlings. (C) Cultures of fungi. (D) Cultures of bacteria. Solid and barred line indicates the infection rating; double-barred part indicates control; single-barred-part, intermediate control; solid part, no control. Black dot = average height of plants, culture plus *O. graminis;* black circle = average height of plants, culture alone. (G. B. Sanford and W. C. Broadfoot. Sci. Agr. 11: 512-528. 1931.)

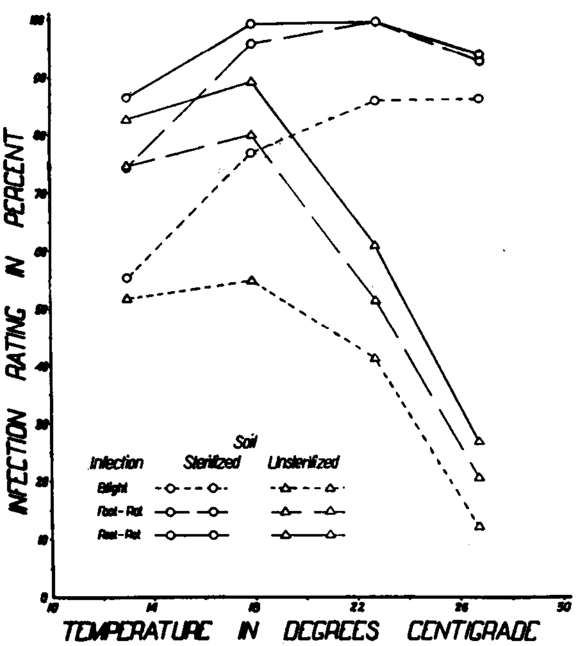

Fig. 2. Relation of Marquis wheat seedlings to *Ophiobolus graminis* at different soil temperatures in sterilized and unsterilized soil. (A. W. Henry. Can. J. Res. 7: 198-203. 1932.)

experimental analysis yet to have been performed in the field of root-disease investigation. My own earliest tribute to Henry's work (Garrett, 1934*b,c*) can be justly described as "the sincerest form of flattery" of which any young man is capable.

Last but not least, California played a prominent part in the early history of this new venture, the development of which belonged so largely to the North American continent. In 1930, Fawcett (1931) lent to this fresh departure both his personal prestige as an eminent plant pathologist, and that of his official position as President of the American Phytopathological Society, by devoting his presidential address to the subject "The importance of investigations on the effects of known mixtures of organisms." Shortly after this, one of Fawcett's research students, R. Weindling, published the first of a brilliant series of papers on the parasitism by *Trichoderma viride* of other soil fungi (Weindling, 1932, 1934, 1937, 1941; Weindling and Emerson, 1936; Weindling and Fawcett, 1936). This series of papers is now too well known to require further comment from me, except to say that I have never known which to admire the more—Weindling's original discovery of this phenomenon, or the pertinacious way in which he followed it up until he had thoroughly elucidated it. His achievement stimulated a great volume of further work on the