PRINCIPLES OF BIOLOGICAL CONTROL
OF SOIL-BORNE PLANT DISEASES

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Summary—Unexpected results derived from applications of chemicals to soils led to investigations of the soil biology, discovery of the rhizosphere and eventually to research on mechanisms of biological control. Decisively, chemicals have staved off major disasters in agriculture. In instances of successful monoculture, below ground pathogens appear to be suppressed by an injurious biology, in principle not unlike an injurious host-specific biology which increases with repeated cultivation of the same crop. Crop diversity, nevertheless, is basic to continued successful production agriculture. Decoy hosts which initiate germination of resisting structures may deplete pathogens of energy reserves, and serve to protect the major host. Endogone, which occupies root cortical tissue of most plants, in addition to the traditional mycorrhizal function, may afford protection against invasion by pathogens. Healthy Endogone may be essential to healthy crops.

INTRODUCTION

My objectives in this symposium will be to develop and illustrate a few principles which have broad, general application to the subject of biological control of soil-borne plant diseases. In a way I feel somewhat out of place because I have been regarded as a chemical control man; I have had the pleasure of observing increased effective chloropicrin—methyl bromide fumigation of strawberry and other field soil for the control of Verticillium wilt and weeds—a process, by the way, which leaves no harmful residues in the environment. Chemical and biological control, however, need not be mutually exclusive, and, as we shall see, the chemical may initiate a chain of biological events culminating in destruction of pathogen inoculum and disease control. Nevertheless, as typically regarded, the concept of biological control encompasses only the predicted interactions of the triple biological association of susceptible host, pathogen and general soil microflora and microfauna, which are set in motion by specific manipulation of the environment.

Biological control has become an attractive topic of the ecological sophist whose hypermania is cutting deeply into public and legislative concern for research in the serious problems of agricultural crop production. True, in the United States today, we produce food enough and to spare; we destroy fertile lands with shabby urban sprawl, limit acres planted and subsidize certain crops; but farms of healthy crops are basic to public health, and cities and homes with attractive gardens are the truly hopeful signs of a nation's progress.

CHEMICALS MAKE AGRICULTURAL HISTORY

Let me recall the past and remind you that it was agriculture that received a major portion of the attention of early chemists. Three-quarters of a century ago, for instance, when Sir William Crookes, an English chemist, delivered his presidential address to the British Association (1899), the world faced an impending food shortage from scarcity of wheat. The average world yield then was approximately 30 bushels per hectare. The wheat was produced
on land limited in supply, and Crookes warned that the land could not continue long to feed the expanding millions of the earth. Today we speak of billions. One way only was forecast out of the dilemma—namely through the laboratory of the chemist who in the future, Crookes stated with confidence, would transform atmospheric nitrogen into a form available to the plant. Crookes stressed further that the welfare and happiness of the civilized races of mankind depended on this discovery then still awaiting the ingenuity of chemists. About 1910 the welfare arrived through the researches of Fritz Haber, Walter Nernst and Georges Claude, leading to the synthesis of ammonia from the air. Only then did the more than 2000-year-old four-course rotation of turnips, barley, clover, wheat—biological diversity providing disease control—typical of cultivation in Europe, give way to wheat, and since then yields have steadily increased. Through Dr. James Cook I learned that wheat yields of 500 bushels per hectare are possible today in the United States and that experimentally he has already exceeded this figure.

Allow me another digression into history. In the 1860's and 70's, France was faced with an extensive Phylloxera calamity, in severity, because of the eminent role of viticulture in French economy, a national emergency. Impending economical disaster joined French scientists, engineers, nobility and vintners in one of the greatest series of research projects of all time. In the process, one experiment, that of Baron Paul Thenard in 1869, inaugurated a new concept in control of soil-borne plant pests and diseases. By injecting carbon disulfide into the soil Thenard achieved therapeutic or eradicant control of Phylloxera, depending on the dosage of the chemical (Tietz, 1970).

The great importance of this discovery, however, was far surpassed by that of the incidental phenomenon observed as early as 1876 that “soil sickness”, which attended the long cultivation of land to single crops—grapes, cabbage, beets, alfalfa, clover or beans—was “cured” by exposure of the soil to carbon disulfide. Though the chemical contributed nothing directly to fertility, “sick soils” were restored to, or improved beyond, their original productivity, an effect that rich, heavy manuring could not achieve. These observations, clearly summarized by Oberlin (1894), initiated (1) the science of soil microbiology in relation to crop production; (2) a basis for understanding the natures and the control of soil-borne plant diseases; and (3) the knowledge that the foundation of biological control resided not so much in manure as in the understanding of the biological properties of an industrial chemical.

We know today that industrial chemicals have contributed immensely to the reduction of world food shortage; they have saved agriculture from the certainty of devasting biological events and have freed agriculture from the uncertainties of natural ameliorative processes. Biological nitrogen is insufficiently available to meet the needs of modern crops, but industrial nitrogen makes up the lack, and the plant uses one as readily as the other because both are chemically identical. Industrial chemicals, though stopping temporarily the biological process of nitrification, vastly improve fertility (Wilhelm, 1965).

**MONOCULTURE AND DISEASE-SUPPRESSIVE SOILS**

Biological control of soil-borne plant diseases belongs to the North American continent—to G. B. Sanford, W. A. Millard, C. B. Taylor, H. L. Bolley, W. N. Ezekiel, J. J. Taubenhaus, H. S. Fawcett, R. Weindling and to our moderator, W. C. Snyder. But American agriculture also evolved a monoculture system, and herein lies a dilemma—are biological control of soil-borne diseases and monoculture compatible? At first thought we are inclined to say no, because we believe, with some justification, that a system of rotating crops will always be necessary to good farming. I take pleasure in pointing out that the
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anonymous American who wrote the book entitled *American Husbandry* (1775) recommended a seven-phase crop sequence for the North Central Colonies that would never “exhaust” the land, namely, Indian corn—potatoes—Indian corn—peas or beans—barley—clover—wheat. How is it then that monoculture became such an important factor in American agriculture? The report of Stokes (1867), Acting Commissioner of Agriculture, gives an historical clue: namely, “As settlers moved west . . . reckless waste stripped the fairest fields of their wealth and fertility. Every new state added to the Union boasted of great crops of wheat, but within a few years spoke equally intensely of remarkable reductions in yields due to pests and diseases. The stigma upon American agriculture was the cheapness of western lands, the original price bearing no proportion to the intrinsic value, and owners deemed it cheaper to remove to new lands than to sustain the costs involved in improving the productive capacity of their occupied lands.” In short, they destroyed wealth to sow poverty.

Confidence in the stability of land resources was precursor to the poverty. When it does not crush, however, poverty is an effective spur. For American agriculture, the spur initiated research, government-supported research, through the Agricultural Experiment Stations of each state—under the maxim “cultivate fewer acres, cultivate them better”—resulting in the monoculture system of agriculture seen today. Without question, monoculture is the most efficient method of farming; it allows for food and fiber crops to be produced in regions of the country best suited in climate and soil, and today large, steady acreages of wheat, rice, corn, potatoes, beans, soybeans, citrus, sugar cane, pineapple, cotton and even strawberries dot our land.

Crops under monoculture generally are threatened far less by below-ground diseases than by above-ground diseases in a favorable environment, because below ground, in addition to host and pathogen, there is the modulating effect of a third biological factor absent in above-ground diseases, namely the resident soil microflora and microfauna. Manipulation of this third factor is the tool of biological control.

Potatoes, for instance, face the scab disease caused by *Streptomyces scabies* in California and elsewhere in the United States, typically suffering most severely in “new” potato land. Scab declines in severity with the continued monoculture of potatoes to a point of unimportance, as if a scab-suppressive factor developed and intensified. Interrupt the cultivation of potatoes with another crop—barley, cotton, corn, cowpeas—and scab again becomes severe. Add old potato soil to young potato soil (i.e. scab-suppressive soil to scab-conducive soil) and scab is suppressed. Sterilize the old scab-suppressive soil with heat and the suppressing qualities are destroyed. Thus, a biotic principle—maybe a strain of *Bacillus subtilis*, maybe a virus effective against scab and favored by potatoes—effects control of scab (Menzies, 1959; Weinhold and Bowman, 1968). Isolate the principle, increase it in the laboratory, formulate and package it as a potato seed piece or soil dressing, and you are nearly back into the chemical business and in competition with soil sulphur, which probably would be a much cheaper soil treatment and in the final analysis may even work through the same or a closely related mechanism.

Inoculum of *Ophiobolus graminis*, cause of take-all disease of wheat, also tends to decrease the longer wheat is grown on the same land, and researchers are looking for a suppressive factor among fungal viruses, protozoa, bacteria and hyperparasitic fungi. The bare-patch syndrome of wheat in Australia likewise decreases in severity as monoculture increases; eventually it disappears. The bare-patch disease, severe in areas of newest wheat cultivation, has been attributed to *Rhizoctonia solani*, *Pythium ultimum* and other species of *Pythium*, *Fusarium* spp., and to root lesion nematodes, all of which may be acting individually or in consort. Roots on affected plants become brown and lack root hairs. Infest soil or
inoculate seed of wheat with select strains of *Bacillus subtilis* developed by K. F. Baker, such as strain A13, and the disease is controlled. Field tests have supported the unique position of *B. subtilis* in the salutary effects. A point of great interest is the high specificity of *B. subtilis*, for only a few isolates of this large, heterogenous species of bacterium effect control. In addition the *Bacillus* also induces earlier fruiting in the wheat by an average of 10 days, an important bonus, which suggests the bioproduction in soil and absorption by wheat roots of a growth-regulating substance. Soils recently planted to wheat probably contain a very low natural population of *B. subtilis*—the A13 strain—and consequently the crop is prone to bare-patch. Repeated cropping of the same soil to wheat undoubtedly favors increase of A13, which in turn causes bare-patch to decrease, an ideal example of what we mean by "balance in nature." I have greatly simplified the picture; we anticipate further results of research in this fascinating area and compliment R. D. Price and his colleagues of the Victorian Plant Disease Institute, and K. F. Baker, our own colleague, for these preliminary details (Price, Baker, Broadbent and Ridge, 1971; Broadbent, Baker and Waterworth, 1971).

**THE ELTON PRINCIPLE**

Generally, because of another principle, disease control by direct seed or soil treatment with disease-suppressive factors, such as organisms, infested soil or even viruses, is difficult to achieve, unless the suppressive factor is directly parasitic to the plant pathogen in question and has immediate access to it. However, large-scale bacterial treatment of planting seed of major crops as carried on in the Soviet Union effects many benefits (Cooper, 1959). From our point of view, successful agriculture in the presence of soil-borne pathogens depends upon the Elton principle observed by K. F. Baker, cited by Wilhelm (1965), that the greater the complexity of a microbiological community in terms of total number and kinds of organisms, the greater the stability of the community. This means that ordinarily no one organism in soil is in a position to increase at anywhere near its full potential; other members of the biological community keep it in check. Before an organism can be successfully introduced into a soil, the biological complexity of that soil usually must be simplified. Chemical treatment, heat pasteurization, and the application of amendments are the ways of achieving simplification and some such treatment probably will have to accompany future additions to soil of specific disease-suppressive factors.

**NITROGEN, PATHOGEN VIRULENCE AND INOCULUM POTENTIAL**

It has always been a good thing for man that he could accomplish so many valuable results in farming without altogether understanding the processes he has set in motion; and "the best method of circumventing a varmint," wrote E. P. Roe (1881), "is to learn its ways. There is a period in the life history when weakness [Roe wrote, stupidity] predominates over the damage that the varmint [or pathogen] can inflict." For soil-borne pathogens the weak phase is the period between germination and infection because the organism has then changed from a form inactive and resistant to a vulnerable active state (Cook and Snyder, 1965; Cook, 1969). This activity of pathogens may be triggered by exudations of amino acids and sugars from germinating seed, and seedlings, or from more host specific substances (Coley-Smith, King, Dickinson and Hall, 1967). In bean, for instance, amino acids and sugars exuded from underground parts are sufficient to stimulate germination of chlamydospores of *Fusarium solani f. phaseoli*, and to support mycelial growth (Schroth, Toussoun and Snyder, 1963). In the presence of dry barley straw resident
from a rotation, and the consequent low available nitrogen, the \textit{Fusarium}, though it may germinate and grow, cannot infect beans; it may, however, form more chlamydospores and survive (Snyder, 1963). Pathogen virulence, thus, is influenced by the nutrition encountered in the rhizosphere. Here, I believe, we are dealing with the principle that soil conditions which favor the opposite of nitrogen tend to control the soil-borne diseases (Burke, 1969). Manipulation of the soil environment to reduce nitrogen availability to pathogens provides a great area for exploration in the field of biological control.

If the seedling be corn or a related grass, and the pathogen \textit{Phymatotrichum}, a selectively stimulated rhizosphere and rhizoplane microflora provide immediate and lasting protection. This effect may reflect the capacity of corn to support unusually high populations of rhizosphere microorganisms which in turn reduce nitrogen availability to the pathogen. In the experimental absence of a rhizosphere microflora, corn readily succumbs to \textit{Phymatotrichum}, and similarly, as shown by Winter and Rümker (1949), peas in gnotobiotic culture become infected by strains of \textit{Fusarium roseum} which in nature are pathogenic only to wheat. Cotton also may escape \textit{Verticillium} wilt in the presence of certain rhizosphere bacteria (Klingner, Hildebrand and Wilhelm, 1971). Thus, host specificity as generally viewed for below-ground pathogens may involve interactions between rhizosphere microorganisms and pathogens, and the concept of host must include the plant and its dependent epiphytic rhizoplane microflora.

Root diseases of trees present a more complex problem. With a capacity of surviving in old tree roots for half a century or longer, \textit{Armillaria mellea}, pathogen of many fruit trees, has resisted efforts to achieve biological control. Weakened by a soil fumigant such as carbon disulfide, \textit{Armillaria}, resident in host root pieces no larger in diameter than a man's thumb, succumbs, and the ubiquitous \textit{Trichoderma viride} is thought to play a parasitic role in this. Thus, simplification of the soil biology by fumigation, attendant build-up of \textit{Trichoderma}, and no doubt some direct chemical injury to \textit{Armillaria}, tip the balance against \textit{Armillaria}.

With a fuller understanding of the \textit{Armillaria} pathogen, however, biological control may be possible, and great strides have been made in this direction. Rhizomorph formation in nature is the key to both pathogenicity and spread of \textit{Armillaria} through the soil. Foil this mechanism in the presence of hosts, or enhance it during host-free periods, and control may be achieved. Rhizomorph initiation can be stimulated by water-soluble, heat-stable extracts from a number of different kinds of woods, as if the woods contained selective growth-promoting and growth-differentiating substances (Raabe, 1962). Recently at Berkeley it was also shown that ethyl alcohol stimulated rhizomorphs (Weinhold and Garraway, 1966). Thermostable toxic substances produced by two species of the African Savanna grass (genus \textit{Hyparrhenia}, tribe \textit{Andropogoneae}) have been shown to suppress \textit{Armillaria} rhizomorph formation (Boughey, Munro, Meikeljohn, Strang and Swift, 1964). Thus, two choices leading to control of \textit{Armillaria} are open: suppress formation of rhizomorphs in the presence of a host—possibly by planting a specific, studied grass undercover in an orchard—or activate them in the absence of a host. For good measure, however, keep a barrel of carbon disulfide around.

\textbf{DECOY HOSTS}

It has also been demonstrated that virulence of a pathogen is linked to energy—young mycelium of \textit{Rhizoctonia} being more virulent than old, for instance (Kamal and Weinhold, 1967)—and the idea of energy has been incorporated into the concept of inoculum potential (Baker, 1969). It belongs there, to be sure, and even though I don't know whether
we can measure energy levels meaningfully, the lack of an accurate yardstick should not deter building with the new idea. It is a principle, however, that biological activity of inhibitors—antagonists, competitors or exploiters—is greatest when energy sources for growth of the pathogen are least. Pathogens whose resting structures can be induced to germinate by decoy methods in the absence of the host—often simply of the major host—die through autolysis of germ tubes, starvation or lysis, unless they are able to form new resting structures. *Verticillium albo-astrum, Fusarium solani f. phaseoli* and no doubt other *Fusarium* species can form the second resting structure if upon germination in soil they fail to infect a host. Pathogenic *Helminthosporium* species in general apparently cannot; they succumb (Chinn and Ledingham, 1957). Since microorganisms may favor or induce formation of resting structures in fungal plant pathogens (Ford, Gold and Snyder, 1970), it is an intriguing possibility that they may also initiate their germination. Survival of a plant pathogen in nature then not only means inactivity but also must embody the requirement of activation from dormancy, and germination; and pathogens appear to be less selective about the stimuli that initiate germination from a resting structure than about the hosts they attack.

Another example involving energy depletion of the pathogen is shown in the researches of R. A. Fox (1961) of the Rubber Research Institute of Malaya. White root rot caused by *Fomes lignosus* is the most important root disease of the rubber tree, *Hevea brasiliensis*; yet the mycelium of *Fomes* can neither survive long in soil nor cause infection of rubber trees if separated from its food base, namely infected rubber wood. When a legume is used as an undercover in rubber plantations, the root rot is controlled. The *Fomes* attacks the legume and dissipates its energy reserves to the point where its weakened rhizomorphs are subject to attack by other microorganisms. As Fox put it, “a large piece of infested wood, potentially dangerous to the rubber tree, may exhaust the inoculum potential below that required to infect rubber by infecting a large number of small roots of cover crop plants.”

The serious *Phymatotrichum* root rot of cotton is controlled in Arizona in much the same way. The Papago pea, a very hardy, vigorous, cold-tolerant pea, is sown in the fall, grown through the winter, plowed under while green in the spring together with supplemental nitrogen. The cover crop and nitrogen shift the energy relations in favor of organisms which are able to attack and kill dormant sclerotia of *Phymatotrichum*.

**ENDOPHYTIC MYCORRHIZAE MAY PROVIDE COMMON PROTECTION**

Another principle applicable for biological control is that involving territorial occupation of living root tissues. For parasitic fungi, particularly those that can be cultured on dead materials, any harmful effects of their excreted products on the green plant will ordinarily benefit the pathogen. Tissues thus killed or disoriented become readily invaded by secondary organisms saprophytes which compound the injury. *Phytophthora* root rot of pepper (*P. capsici*), red stele of strawberry (*P. fragariae*), and pink root of onion (*Pyrenochaeta terrestris*) are well-known examples where secondary invasion favored by tissue destruction augments the disease. Conversely, and enlarging the principle, those organisms that do not readily grow in culture and which do not cause host tissue disintegration are deterred by the harmful effect of their excreted products on the green plant. The typical resistance reaction in these is commonly referred to as hypersensitivity. The successful obligate or near-obligate parasites to which the host is not hypersensitive may act as a “territorial claimant,” and the tissues infected by them may tend to be inhospitable to invasion by other fungi. I believe, but can speak only from evidence of observations of roots, that a great deal of biological control is achieved in this way, and we know very little about it.
For example, the ubiquitous mycorrhizal root parasite *Endogone*, which invades the root cortex, occupies more host tissue than all of the other fungus parasites put together (Gerdemann, 1968). Most plants have true roots only when they are young; later they have endophytic mycorrhizae, at least in part. This raises some fundamental questions. For instance, does the juvenile susceptibility of some plants to root diseases reflect the fact that *Endogone* has not yet invaded all of the roots and established a protection role? Also, does the fact that pathogens of the genera *Verticillium*, *Fusarium*, *Phytophthora*, especially *Phytophthora cinnamomi*, which cause root diseases in old plants and invade near the root tips, reflect the fact that root tips typically are not occupied by *Endogone*?

Also, consider the recent announcement (Ko, 1971) that *Phytophthora* root rot of papaya, *Carica papaya*, caused by *P. palmivora*, can be controlled simply by planting the papaya seed in virgin soil, i.e. soil in which papaya has never grown. The soil, a shovel full or two, is placed in holes made in broken lava rock, typical of Hilo, Hawaii. Young seedlings grow disease-free in the virgin soil, and when 6–8-weeks-old, pass the point of susceptibility to *Phytophthora*; yet they continue to form new rootlets. Perhaps *Endogone* is responsible for the resistance, but I am speculating. From my own observations, *Endogone* colonizes the roots of papaya to an extent greater than I have seen on any other plant, and the *Endogone*-papaya mycorrhizal tissue is certainly both structurally and physiologically different from papaya root tissue alone.

At one time I thought that *Endogone* was injurious to strawberries, because in some fumigation trials conducted years ago it colonized roots so abundantly in the second year after fumigation that rootlets were ruptured by it and subsequently died (Wilhelm, 1959). No doubt too much of any good thing can be bad, but in this vast soil-borne, root-inhabiting fungus genus *Endogone* lies one of the most challenging areas for the plant pathologist interested in biological control.

**PERENNIAL ROOT SYSTEMS—SPECIAL PROBLEMS**

One additional view in closing. Biological control of root diseases of perennial plants—orchard trees and strawberries—presents a problem often vastly different from that of annual crops. An extensive fibrous root system of strawberries, for instance, occupies a limited volume of soil for a long time, through summer and winter environments. Within this soil volume rootlets develop, mature, die, and in the precise location of one that has died a new one develops to re-search the soil of nutrients, and so on and on in succession the process is repeated. Rootlet death and replacement occurs from non-pathological as well as from pathological causes (Wilhelm and Nelson, 1970). A parasite here, as exemplified by the *Ceratobasidium* pathogen of strawberry rootlets, has a tremendous advantage: contiguity with susceptible host tissues, protection during saprogenesis by encasement in sloughed, melanized host cells, and a favorable probability that during a cycle of 1 yr an environment will favor active pathogenesis (Wilhelm et al., 1972).

For orchards the Elton principle, viz. biological complexity insures stability, offers hope. Olives in California grown with a sod or grass undercover develop less *Verticillium* wilt and sustain a less severe reaction in affected trees than if cultivated clean. Clean cultivation, maintained by discing or oils, favors infestation of soils by *Verticillium* and a severe wilt reaction in affected trees (Ashworth and Wilhelm, 1971). What makes the difference? Under clean cultivation the roots and root secretions are those of olive, and thus the only food available to *Verticillium* is host tissue. Conversely, sod culture provides a diversity of root secretions, energy sources for diverse kinds of microorganisms, and even though *Verticillium* may form microsclerotia occasionally on or within non-host grass roots (Lacey
and Horner, 1966), the energy available to such microsclerotia may be too scant for infection of olive. Whatever the explanation: sod cover gives control, whereas clean cultivation is hazardous. Research on uncover crops for orchards may open up valuable methods of biological control and it is distressful how little has been done in this field since McBeth and Taylor (1944) showed that Crotalaria spectabilis controlled root knot nematodes in peaches.

In brief I have touched upon a few principles of biological control, synthesized by long association with interested colleagues. The principles integrate general biological knowledge and have prediction value.

REFERENCES


