

GARRETT MEMORIAL LECTURE

Problems and progress in the biological control of wheat take-all*

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It is truly a privilege and an honour to be invited to present this inaugural Garrett Lecture. It was also a privilege and an honour the first time I met Professor S. D. (Denis) Garrett, which was in October 1963, when I was a graduate student at the University of California, Berkeley, under the late W. C. Snyder. Professor Garrett was the invited keynote speaker (Garrett, 1965) at the First International Symposium on Ecology of Soil-borne Plant Pathogens (Baker & Snyder, 1965). Little did I know then that I would spend my career working on root and crown diseases of cereals, including take-all of wheat that had already, by then, been the subject of his own research for about 30 years.

The concepts developed by Professor Garrett and expressed in his extensive writings created the area of science that we know today as ecology of soil-borne plant pathogens. Contemporary microbial ecologists planning to investigate and develop models to predict the fate of new genotypes of microorganisms released into the environment would do well to examine the works and consider the concepts set forth by Professor Garrett during the 60 years of his career. All of us working on ecology and management of soil-borne plant pathogens would do well to read his writings again.

In preparation for this lecture, I took particular note of the paper that Professor Garrett presented at the Berkeley symposium, as this was his first to focus so completely on biological control. Reading this paper again was a humbling experience because I realized that most of the concepts established by the work I present below were stated already in Professor Garrett's chapter written over 30 years ago.

My research as an employee of the US Department of Agriculture, Agricultural Research Service, has focused on methods to manage the root diseases of wheat and barley in modern farming systems. I use the term 'modern' to cover several factors, including the use of short, or no, crop rotation, as opposed to more traditional long rotations, little or no tillage (i.e. direct drilling) to conserve water, soil, and fuel, in contrast to conventional clean tillage, and centre pivot irrigation in the arid and semi-arid (once-desert) parts of the Pacific Northwest.

An assignment to develop methods to manage root diseases of wheat and barley without using crop rotation, tillage, host-plant resistance (no useful genetic resistance to take-all has been found in wheat; Scott & Hollins, 1985), or soil fumigation may give the impression that biological control through the use of microorganisms was the last resort. On the contrary, the influence of Garrett's work, as well as the strong influences of K. F. Baker and W. C. Snyder, prepared me both philosophically and scientifically for development of a programme based first on ecological principles, of which biological control is a major application.

In this lecture, I focus on the problems and progress in the development of biological control for wheat take-all, caused by *Gaeumannomyces graminis* var. *tritici*. Take-all can serve as both a model system for biological control research and a practical disease problem of major significance waiting to be solved by use of biological control. It has become a model system in large part because of the excellent foundation set in place on the ecology of this fungus by the work of Garrett. It has become a disease problem of major practical significance because, among the arable crops, wheat occupies the most agricultural land world-wide, and take-all is the most important root disease of wheat. Indeed, there may well be more agricultural land infested with *G. g.* var. *tritici* world-wide than with any other specialized root pathogen.

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This lecture will focus further on the problems and progress in the development of biological control for wheat take-all in the US Pacific Northwest. This programme was begun in 1968, 3 years after I assumed my responsibilities with the USDA-ARS on wheat root diseases at Pullman, Washington (and the year of the First International Congress of Plant Pathology and the Second International Symposium on Ecology of Soil-borne Plant Pathogens in London).

In addition to the foundations laid by Dr Garrett, my work was inspired by the report of Gerlagh (1968) in The Netherlands on the appearance of take-all on wheat and its decline with monoculture of wheat in the 'new' polder fields. My work was also inspired by the report of Menzies (1959) of a decline in severity of common scab of potatoes (*Streptomyces scabies*) on the 'new' agricultural lands of the Yakima Valley and Columbia Basin of Washington State with continuous cropping to irrigated potatoes. Other fields in the Yakima Valley and Columbia Basin were, or potentially could be, cropped continuously to irrigated wheat, and while take-all was becoming important for wheat on these new lands with irrigation (Cook *et al.*, 1968), the findings of Gerlagh for the 'new' fields in The Netherlands gave reason for some optimism that take-all could be managed or that it might decline over time.

Our efforts continue to include research on biological control of take-all of irrigated wheat in the arid and semi-arid regions of the Pacific Northwest. However, the disease has since become a major obstacle to adoption of no-till (direct drill) management systems in the rainfed semi-arid and subhumid agronomic zones of the Pacific Northwest. These zones include much of eastern Washington and adjacent northern Idaho and north-eastern Oregon. The effort has therefore been expanded to include rainfed as well as irrigated agroecosystems.

BIOLOGICAL CONTROL OF WHEAT ROOT DISEASES BY RESIDENT ANTAGONISTS

In his keynote paper in 1963, Professor Garrett stated that

'Biological control can be brought about by introduction or augmentation in numbers of one or more controlling organisms, a change in environmental conditions designed to favour the multiplication and activity of such organisms, or a combination of both procedures.'

An important point in this statement, that seems to have been left behind during the past decade or so, is that biological control can be brought about by cultural practices designed to take advantage of one or more controlling organisms already present in the soil or on the plants. There is great anticipation that biological control products can and will be forthcoming (Cook, 1993). However, biological control can also be achieved with a cultural practice. These alternatives — product or practice — match up with introduced and resident antagonists, respectively (Baker & Cook, 1974). In many cases, success will involve a combination of introduced and resident antagonists.

Crop rotation

Crop rotation allows time between susceptible crops for the resident mycoparasites, competitors, predators, and antibiotic-producing microorganisms to lower the inoculum potential (*sensu* Garrett) of soil-borne plant pathogens below some economic threshold. There is concern today for the loss of soil fumigants in the production of high-value crops. It is worth keeping in perspective, however, that adequate crop rotation as a means to take full advantage of controlling organisms already present in the soil has been replaced for many high-value crops, over many decades, by soil fumigation. It is also worth keeping in mind that root diseases not controlled by either crop rotation or soil fumigation, such as take-all of wheat in modern farming systems, can be devastating both as unrealized yield and as wasted investments. Wheat with root diseases not only yields poorly, it is less competitive with weeds and leaves nitrogen fertilizer unused in the soil (Cook, 1992a).

The problem of carry-over inoculum of soil-borne pathogens may well be exacerbated in the cooler, semi-arid areas such as northern Idaho, north-eastern Oregon and eastern Washington. When soils in these areas are wet enough for microbial activity needed for soil sanitation, they are commonly cold. When they are warm enough for microbial activity, they are commonly in equilibrium with relative humidities well below 90–95%, and the top 10–15 cm may be in equilibrium with relative humidities of 50% or lower. Indeed, the trashy tillage used in the semi-arid parts of the region (Cook, 1980) is

designed to accelerate the drying and preserve the residue as a mulch to limit wind erosion. Under these conditions, *G. g. var. tritici* can survive through a year of fallow. This matches Garrett's observations in Australia when he reported that take-all can be severe on wheat after a dry fallow (Garrett, 1940). In the US Pacific Northwest, this fallow extends from the harvest of one crop in August until sowing of the next crop in September of the following year.

Over some 15 years of using soil fumigation as a research tool in the Pacific Northwest, the average response of winter wheat in areas with 45–50 cm or more of precipitation, or precipitation plus irrigation, was 70, 22 and 7%, respectively, in fields cropped every year, every other year, and every third year to wheat (Cook, 1990). Take-all occurs as a mixture with rhizoctonia root rot caused mainly by *Rhizoctonia solani* AG8 (Ogoshi *et al.*, 1990; Smiley *et al.*, 1992), and pythium root rot caused by several *Pythium* species (Cook & Haglund, 1982; Chamswarng & Cook, 1985; Cook *et al.*, 1987). Most of the response to soil fumigation for wheat grown with no crop rotation and much of the response to wheat growth in 2 year rotations is probably due to control of take-all (Cook *et al.*, 1987).

The goal of our research programme is to develop the products and practices needed to achieve yields of wheat in a 2-year rotation that are now only possible with wheat in a 3-year rotation, or with wheat in monoculture that are now only possible with wheat grown every other year in the same field. This must be accomplished while also permitting minimum or no tillage. It also requires attention to control of rhizoctonia and pythium root rots, because (a) wheat exposed to a mixture of root diseases will not yield to its full potential by controlling only one of the diseases, and (b) the risk that control of only take-all could lead to increased rhizoctonia root rot (Cook, 1988). Fortunately, rhizoctonia root rot of cereals can be controlled to an amazing degree simply by proper management of volunteer (self-sown) and grass weed hosts (Smiley *et al.*, 1992).

Early elimination of volunteer and grass weeds

It has been a common practice among growers who plant wheat or barley directly into wheat or barley stubble to apply glyphosate or other non-selective herbicides only 1–3 days before planting. Roget *et al.* (1987) showed in the south Australian wheat belt that rhizoctonia root rot of cereals direct drilled into pasture grasses was more severe if the grasses were sprayed with a non-selective herbicide immediately before planting than if sprayed two or more weeks before planting. Their report led to studies in Washington and Oregon (Smiley *et al.*, 1992) showing that wheat and barley were significantly less damaged by rhizoctonia root rot when direct-drilled into standing stubble if volunteer and grass weeds were sprayed 10–14 days or longer before drilling than if sprayed 1–3 days before drilling. The response to early elimination of volunteer and grass weeds has been especially striking for spring cereals planted directly into stubble of cereals harvested the previous fall.

Johal & Rahe (1984) and Lévesque & Rahe (1987) showed that treatment of plants with glyphosate is quickly followed by colonization of the roots of treated plants by *Pythium* and *Fusarium* species, which in turn contribute to the killing of plants treated with this herbicide (reviewed by Lévesque & Rahe, 1992). Based on these results, Smiley *et al.* (1992) proposed that *Rhizoctonia solani* AG8 might help kill these weedy plants, as proposed for *Fusarium* (Lévesque & Rahe, 1992) and *Pythium* (Johal & Rahe, 1984), but also that colonization of the roots and other tissues of these plants temporarily increases the inoculum potential of this pathogen. Conversely, because this substrate consists mainly of juvenile root tissues, in some cases roots of seedlings, this material should be both relatively short-lived as a foodbase for *R. solani* and overrun relatively quickly by successions of saprophytes. This could account for the increased amount of disease when volunteer and weeds are sprayed 1–3 days before drilling, and the decreased amount of disease (in some cases remarkably little disease) when volunteer and weeds are sprayed 2 weeks or, better yet, 2–3 months before drilling.

Professor Garrett would have enjoyed knowing about this—how such a simple change in management could have such profound effects on severity of a root disease, presumably achieved with the help of resident antagonists. The explanation by Smiley *et al.* (1992) fits with a statement in his 1963 keynote at Berkeley.

'Every soil microbiologist should keep constantly in mind the simple fact that the commonest cause of death in a microorganism, in whole or in part, is straight starvation ... other microorganisms accelerate this starvation, through their competition for a limited supply of nutrients.'

BIOLOGICAL CONTROL OF WHEAT ROOT DISEASES BY INTRODUCED ANTAGONISTS

In the autumn of 1969, Dr Peter Shipton and I set up a field experiment on the Washington State University experimental station at Puyallup, in western Washington, to test whether we could transfer a factor suppressive to take-all from a field suspected of take-all decline to a site not cropped to wheat for many years (there was no record of wheat ever having been grown on this site, although wheat production on the site earlier in this century cannot be ruled out). This study was concurrent with a more comprehensive project on the nature of suppression of take-all in certain wheat-field soils in the Pacific Northwest (Shipton *et al.*, 1973). We mixed soil from six eastern Washington sites; three of the sites had a long history of wheat and three corresponding sites were not under cultivation. The soils from the six sites were mixed by rotovation to a depth of 15 cm in replicated plots 1.7 m wide and 3.6 m long; the entire experimental site was then seeded uniformly with winter wheat mixed in the drill box with oat-grain inoculum of *G. g. var. tritici*.

Take-all was severe in 1970 throughout the experiment. However, when the experimental site was seeded again in the fall of 1970, with wheat only, i.e. no new source of inoculum of the pathogen, take-all was suppressed in 1971 exactly to the borders and within each of the four replicate plots that had received the previous year soil from one field near Quincy, Washington. The field was a silt loam in an arid, once-desert, currently irrigated area and had been cropped to wheat with irrigation for 12 consecutive years at the time we removed soil for incorporation at the Puyallup site some 200 miles away. Remarkably, the soil incorporated into the plots amounted to only about 0.5% w/w. The suppressive properties generated in response to this (a) 'starter soil', (b) one season of severe take-all, and (c) two consecutive crops of wheat were evident in April when the plants were at growth stage 4-5 on the Feeks scale or 24 on the Zadoks scale (Baker & Cook, 1974). The results of this one experiment convinced me that biological control of take-all with introduced microorganisms was possible if only we could introduce precisely the right microorganisms responsible for this suppressive effect. The results in the Puyallup experiment also supported a principle set only a few years earlier by Garrett in his keynote address at Berkeley.

'The flora and fauna of a habitat will be selected by the environmental conditions from amongst the species currently available. The balance of the flora and fauna can be upset only temporarily by augmenting artificially the population of a species already present.'

Take-all declined over the entire experimental site with the third crop of winter wheat (and two previous years of severe take-all). This decline regardless of treatment, including in the untreated checks, is best explained on the basis of microorganisms already available or present in the soil. However, the microbiota suppressive to take-all in the second year at the Puyallup site were transferred from among the species already present at the Quincy site where wheat had been grown for the previous 12 years. These results also confirmed the observations of Gerlagh (1968) for take-all development and its decline in the polder soils of The Netherlands by showing that take-all decline can develop relatively quickly at a site with no history of wheat culture, but showed further that a suppressive factor could be transferred from soil to soil and that it could multiply.

Cook & Rovira (1976) subsequently showed for two soils, one from the Quincy field and the other from a site at Horsham, Victoria, Australia where wheat had been grown for more than 50 consecutive years, that both were suppressive to take-all when diluted 1:100 with a common fumigated soil used as the rooting medium. Three other US and Australian soils from fields in crop rotations or not cropped showed no suppressive effect to take-all in the same experiment. This further supported the idea that effective antagonists occur at virtually any site, that their numbers can be increased by monoculture wheat, and also that a suppressive effect can be achieved by transfer of microorganisms into a conducive soil.

Indeed, more than 20 years of research and hundreds of experiments since the field experiment at Puyallup have taught us to take advantage of the principle stated by Garrett that 'most species of microorganisms that could thrive in a particular soil are there already'. Our experiments have shown further, however, that the development of effective populations of species suppressive to root disease can be assisted with introductions to augment the populations of these beneficial microorganisms. The Quincy field continues to provide us with some of our most interesting and effective strains for biological control of take-all.

Discovery and performance testing of antagonists

Taking our clues from take-all decline, we use regular and repeated exposures of the soil microbiota to wheat roots with take-all to enrich for microorganisms already present in the soil, adapted to roots and especially roots with take-all, and inhibitory to the wheat take-all fungus. The approach is no different than enriching for microorganisms with ability to break down chitin, cellulose, or some pesticide by adding these substrates repeatedly to the soil and then selecting or screening for the desired phenotypes. The 'discovery' phase (Cook, 1993) also includes isolation from the rhizosphere of wheat growing in local soils amended with inoculum of *G. g. var. tritici* and subjected to several cycles of planting wheat in the glasshouse.

Starting with this wide array of microbial germoplasm, we either screen *in vitro* for inhibitory activity against the *G. g. var. tritici*, from which candidate strains are selected for further testing on plants in the glasshouse (Weller *et al.*, 1985), or we go directly to testing on plants in the glasshouse. Strains that show activity in the glasshouse are then tested in small-scale field plots as seed treatments on wheat with introduced inoculum of the pathogen (to create uniform disease) on the Washington State University Plant Pathology Farm at Pullman, the WSU Northwestern Research and Extension Center at Mount Vernon, Washington (north of Seattle), or both locations. Strains that perform in one or both of these tests are then moved to replicated performance trials in naturally infested soils in cooperation with growers. The process is similar to breeding new cultivars of crop plants, where large numbers of new strains are always entering the programme; ineffective strains are eliminated by screening and performance testing, and the 'pipeline' is always full.

Our strategy has been temporarily to increase the populations of locally adapted strains of microorganisms in the rhizosphere in advance of infection by *G. g. var. tritici*, by introducing the bacteria as a live seed treatment at the time of planting. During some 14 years of performance testing, we have achieved an average of 10–15% greater yield (Cook & Weller, 1987; Cook *et al.*, 1988; R. J. C. & D. M. Weller, unpublished data) in commercial fields naturally infested with the take-all fungus. One strain in 1993, namely *Pseudomonas aureofaciens* strain Qc69, (the Q indicates from Quincy field) produced a 33% yield increase (from 5 t/ha in the check to 6.7 t/ha) in replicated plots on a rainfed site drilled directly and where wheat had been grown each of the previous 9 years (R. J. C., D. M. Weller & L. B. Iten, unpublished data). Similar encouraging tests have been carried out on wheat to control take-all in Australia (A. D. Rovira, personal communication) and China (Peng & Ellingboe, 1991).

The role of antibiotics in biological control

Dr Linda S. Thomashow joined Dr Weller and me in 1985 to develop a programme on molecular and biochemical mechanisms of biological control. This basic research has added to the total knowledge base available for biological control research and has contributed directly to advances towards our mission of biological control of wheat take-all. For example, *Pseudomonas fluorescens* 2-79 and *P. aureofaciens* 30-84 were shown to protect roots of wheat against take-all, mainly by production of phenazine antibiotics (Thomashow & Weller, 1988; Pierson & Thomashow, 1992). This has helped answer a question of long standing, whether antibiotic production is important to the ecology of soil microorganisms. Strains made phenazine-negative by Tn5 mutagenesis exhibited only about 20% of the activity of the wild-type parents, whereas mutant strains restored for phenazine-producing ability by genetic complementation exhibited 100% of the activity of the wild-type parents. In addition, phenazine was detected by HPLC in extracts made of rhizosphere soil, including those from the rhizosphere of plants growing in a field plot, but only detected in the rhizosphere of plants grown from seed treated with a wild-type or phenazine-restored mutant. Knowledge of the importance of this or other similar traits to biocontrol activity has been very useful to our screening programme.

The amount of phenazine produced on wheat at the 3-leaf stage in the field was estimated at 80–100 mg/ha (Thomashow *et al.*, 1990). This has helped to assure that the risk of significant non-target effects of enhanced antibiotic production in the rhizosphere is minimal or non-existent. However, in considering these results, another statement by Garrett from his 1963 keynote at Berkeley seems relevant.

'Gross analysis of soil . . . for antibiotic concentrations reveal merely the mean values; individual values at particular sites or microhabitats may depart from the mean value by factors of a high order.'

As pointed out above, several of our most interesting strains have come from the field near Quincy, Washington, and many of these are active because of their ability to produce the antibiotic phloroglucinol (Vincent *et al.*, 1991). Phloroglucinol-producing fluorescent *Pseudomonas* strains have also been associated with suppression of black root rot of tobacco in Switzerland (Défago *et al.*, 1991), pythium root rot of sugar beet in Ireland (Shanahan *et al.*, 1992), and rhizoctonia sheath blight of rice in the Philippines (A. M. Rosales & L. S. Thomashow, unpublished data, 1992). This raises the possibility that, while the strains of pseudomonads adapted to local soils and crops may be different, the traits by which they protect these crops may not be different. Mazzola *et al.* (1992) showed for both 2-79 and 30-84 (phenazine producers) that antibiotic-producing ability can be important to survival of these strains in competition with the native rhizosphere-colonizing strains of microorganisms. The repeat occurrence of traits such as phloroglucinol- (or phenazine-) producing ability among strains associated with disease suppression in the rhizosphere raises the possibility that plants also select for microorganisms with these traits for their own survival.

Strain Qc69 has performed most consistently, yet to date no antibiotic activity has been detected with this strain *in vitro*. However, this strain produces HCN (L. S. Thomashow & D. M. Weller, unpublished data), and derivatives of Qc69 with ability to produce either phenazine or phloroglucinol, made possible by gene transfer from phenazine- and phloroglucinol-producing strains, respectively, have exhibited enhanced biocontrol activity against take-all under controlled conditions (H. Hara & L. S. Thomashow, unpublished data). This strain may be our most valuable strain isolated thus far, because of its apparently wide adaptation and the potential to enhance its activity even more by gene transfer.

Challenges ahead for scale-up and commercial use

Success in biological control of root diseases with introduced microorganisms depends on overcoming a long succession of technical but not insurmountable difficulties including, in addition to the discovery and performance-testing phases, finding the best methods for mass production, formulation and delivery and the best methods for use by farmers. We have spared no amount of labour to ensure quality control up to the day of planting, including the existence of a suitably high population of live cells on the seeds at the time of planting; thereafter, the strains are on their own. Several strains have produced remarkable results under field conditions, given these advantages. The challenge as we move towards commercialization is how to maintain technically and economically the same high standards and quality control on a large scale.

There is also the matter of registration of these agents with the US Environmental Protection Agency. It is US policy that microorganisms intended for pest control must be registered as microbial pesticides. It may be that each strain or combination of strains selected for the different soils or management systems will require separate registration. This raises a serious dilemma: it will be exceedingly difficult because of the cost of registration to follow the ecologically and biologically sound approach of using different strains to control take-all in different soils or under different management systems; it is unlikely that take-all can be controlled biologically over the wide range of environments with a single strain.

Drs John Rishbeth and Allen Kerr each made their biocontrol agents available to users as a public service, at least initially. Similarly, most invertebrate natural enemies of arthropod pests and weeds are released as a public service, as have most new crop cultivars until the past 10-20 years when seed companies have increasingly assumed this role. Accordingly, it seems logical, if not essential, that the public service also play a major role not only in the research needed to permit scale-up, but also in the delivery of these agents into commercial use.

In 1989, Dr Patricia Slininger joined this effort at the ARS National Center for Agricultural Utilization Research in Peoria, Illinois, by developing a programme on fermentation technology aimed mainly at candidate strains for biological control. Phenazine production by strain 2-79 was enhanced by zinc in the fermentation medium (Slininger & Jackson, 1992). Independent research by Ownley *et al.* (1992) at Pullman identified a significant positive correlation between take-all suppression by phenazine-producing derivatives of 2-79 and zinc content of the soil. Moreover, when a soil naturally low in zinc and relatively conducive to take-all on wheat treated with these phenazine-producing strains was amended with zinc, biological control was significantly enhanced. Based on these results, the

addition of zinc to the fermentation medium, formulation, or both, may serve to enhance the biocontrol activity of phenazine-producing strains.

Our performance trials now include a range of fermentation treatments where the strains are grown and the seed is treated in Peoria and planted in eastern Washington. In addition, a research effort is now underway at Pullman on development of formulation and delivery technology, including tests completed, underway or planned on the use of liquid, dry, or encapsulated product applied on or with the seed or in the seed furrow at the time of planting, mostly in cooperation with commercial growers.

INTEGRATION OF BIOLOGICAL CONTROL WITH CROP HUSBANDRY

It became apparent early in our field-testing programme that biological control had much to contribute but could not, by itself, provide the level of control possible with soil fumigation, a long crop rotation, or other standard. For example, in a field test in cooperation with a grower near Mount Vernon, Washington, the average yield was 3.3 t ha^{-1} in the check and 4.4 t ha^{-1} in response to three strains applied as a mixture on the seed. This 30% increase in yield was remarkable, considering that the experiment was done with the grower's equipment and with natural inoculum of *G. g.* var. *tritici*. However, based on yields in the area in response to crop rotation, the best yields in our test were still only 50–60% of the potential.

These kinds of results led us to evaluate the total management system for wheat grown without benefit of either adequate rotation or tillage. The result was development of a 'one-pass' method for planting with the following features or options for management of root diseases (Cook, 1992b).

Placement of fertilizer, either liquid or dry NPS, as a band 4–6 cm directly beneath the seed

Wheat yields were increased significantly by this practice compared with the standard preplant fertilization or placement of the fertilizer band 10–15 cm to one side of the seed furrow. With root diseases controlled by soil fumigation, yields were uniformly high whether the fertilizer band was directly beneath the seed or below but up to 15 cm to one side of the seeds. These results are best explained by the simple fact that healthy roots can reach further to obtain nutrients (especially phosphorus), while plants with diseased roots respond to placement of fertilizer directly beneath the seed (reviewed by Cook, 1992a).

Loosen the soil in each seed row using the fertilizer shank as a tillage tool

This aspect of our one-pass method of planting follows a report of Rovira (1986) that soil disturbance in the seed row helps control rhizoctonia root rot. In eastern Washington, soil disturbance in the seed furrow by the fertilizer shank, including 6–8 cm below the seed, resulted in significantly fewer roots infected with either take-all or rhizoctonia root rot (R. J. C. unpublished data, 1992) whether or not fertilizer was applied with these shanks.

Plant the rows in pairs, in contrast to the usual uniform spacing

Wheat yields are the same under rainfed conditions in eastern Washington and adjacent Idaho and Oregon whether rows are spaced 15 or 30 cm apart. Most growers use narrower spacing for weed control. Take-all development was the same on seminal roots of young plants, regardless of whether rows were paired 17.5 cm apart, with 42.5 cm between pairs, or spaced uniformly at 30 cm apart. However, take-all occurred on fewer crown roots when rows were paired than when spaced uniformly. This limitation to development of take-all on crown roots with rows paired, but not when rows were spaced uniformly, coincided with closure of the canopy with uniform (but not with paired) rows. In three different experiments, yields in fields with severe take-all were increased by pairing the rows but not if root diseases were controlled by soil fumigation. The most straightforward explanation is that the more open canopy created by pairing the rows allows for greater drying and more rapid or frequent warming of the top few centimetres of soil where the take-all fungus is active and where infection of crown roots occurs. Take-all development is highly sensitive to soil drying.

These three modifications in method of planting have helped enormously in elevating yields of wheat (and barley) planted directly into their own or each other's stubble. The fertilizer-placement effect has been especially evident with spring cereals direct-drilled into cereal stubble. The combination of one-pass method of planting and early elimination of volunteer and grass weed hosts (discussed above) has given new hope for the success of direct drilling in the region and has set the stage for biological control with microorganisms introduced into the rhizosphere.

Treatments such as fumigation and solarization are not options on the roughly 80 million acres (35 million hectares) of wheat grown in the United States. The use of wheat no more than every third or fourth year in the same field, likewise, is not an option for the vast semi-arid and subhumid areas of North America and other similar regions of the world so ideally suited to a cereal-based agriculture. The rotations must be extended as much as possible, but increasingly, and for social, political, and economic reasons, areas adapted to cereals will continue to be cropped to cereals without adequate rotation. All too often, these same regions are typified by fragile soils already low in organic matter and prone to erosion. The best protection for these soils is to reduce or eliminate tillage which, when combined with little or no crop rotation, is ideal for root diseases. Crops with diseased roots not only yield less, they leave nitrogen fertilizer unused in the soil profile and do not take full advantage of even the limited supplies of available water.

Our approach has evolved in response to new basic information on ecology of wheat, ecology and epidemiology of wheat root diseases, and now ecology and molecular biology of the root-associated microorganisms with potential to inhibit the root pathogens of wheat. Garrett reminded us in his 1963 keynote address that 'there are no short-cuts to biological control'. He also pointed out in that keynote:

'Biological control cannot be separated from the whole subject of disease control, which involves eventually a complete knowledge of the biology and epidemiology of a disease, and of the ecology of the crop plant.'

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