In Defense of Crop Monoculture

R.J. Cook[1] and D.M. Weller[2]

[1] Interim Dean, College of Agricultural, Human, and Natural Resource Sciences, Washington State University, Pullman, WA 99164
[2] Research Leader, Root Disease and Biological Control Research Unit, Agricultural Research Service, U.S. Department of Agriculture, Washington State University, Pullman, WA 99164

Abstract
Because yields typically decline, crop monoculture is commonly considered as not sustainable. This yield decline is due largely to soilborne plant pathogens adapted to/specialized for the roots of the crop. For high-value fruit and vegetable crops, yields are maintained with monoculture using soil fumigation or soil solarization. Soils can also be sanitized by flooding, which may account for the success of paddy rice monocultures. Our work in the U.S. Pacific Northwest has focused on four root and crown diseases of wheat and barley, namely take-all caused by *Gaeumannomyces graminis* var. *tritici*, Fusarium crown rot caused by *Fusarium culmorum* and *Fusarium pseudograminearum*, Rhizoctonia root rot caused by *Rhizoctonia solani* AG8 and *R. oryzae*, and Pythium root rot caused by several *Pythium* species. Herein, we describe a remarkable and apparently wide-spread microbiological control (disease suppression) in the rhizosphere that is responsible for the well-documented decline of take-all and coordinate increase in crop yield following one or more outbreaks of the disease and continued monoculture of wheat or barley. Since this disease suppression is specific for take-all, other strategies are under development for control of the other three root and crown diseases with wheat-intensive cropping systems, including in direct-seed systems. The strategies include the development of transgenic resistance in barley to Rhizoctonia root rot using the *ThEn42* gene from *Trichoderma harzianum* for production of a 42-Kda endochitinase, selection of wheat cultivars for tolerance to Fusarium crown rot, and use of a systemic seed-treatment chemicals and current-year seed for seedling protection against Pythium root rot.

Introduction
Crop rotation, which we define as the practice of growing different crops in sequence in the same field, is nearly as old as agriculture itself and remains the centerpiece of most cropping systems worldwide. Crop monoculture, which we define as the practice of replanting the same crop species in the same field, with no break to a different crop, has an equally long but less successful history, except for some high-value fruit and vegetable crops grown with the aid of soil fumigation or soil solarization, and also possibly for paddy rice. "Crop monoculture" is also used to describe large areas planted to the same crop species, e.g. the vast area planted to wheat each year in the North American Great Plains. For purposes of our *defense of crop monoculture*, like crop rotation, we mean crop monoculture in the temporal and not the spatial sense.

Growers that practice crop monoculture generally do so for economic reasons. The selected crop is the most profitable and any profitability loss from yield declines are less than that which occurs from any rotational options available. In these situations, the ability to minimize the losses associated with monoculture can provide the best option to increase productivity and profitability.

Many names have been given to the phenomenon of yield decline with monoculture, including replant problem, autotoxicty, and monoculture injury. Even perennial crops such as alfalfa and grasses are prone to show yield (or stand) decline over time, typically starting in the third or fourth year following their establishment. Similarly with annual crops, yields typically decline starting in the third or fourth year of the monoculture, although some yield decline may occur already in the second year of monoculture (Cook and Baker, 1983). Because of these yield declines, crop monoculture is commonly considered as not sustainable.

Crop rotation, like tillage, is an invention of agriculture. Indeed, annual plants in the wild reseed themselves in more or less the same places year after year—and without tillage. The occurrence of wild plants in polycultures could provide a kind of rotational benefit in cases where the seeds of one species happen to fall on the site occupied the previous year by a different species. In the case of wheat, the

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natural domination of vast areas of the "Fertile Cresent" by *Triticum* and related grasses leads logically to the thesis that crop monocultures can be sustainable.

Obviously crop rotations provide many benefits to the farming business, including more than one kind of crop to sell, spreading the workload (e.g., planting and harvesting) over more of the growing season, and managing soil water supplies and harvest residues by rotating a shallow-rooted low-residue crop such as peas with a deep-rooted high-residue crop such as wheat, as examples. Crop monoculture also offers many advantages, including the economic advantages of specialization, flexibility to intensively grow a high-value cash crop ideally suited to local growing conditions, and the means to assure adequate supplies of a staple such as rice in Asia. Herein, we address the fundamental reasons for yield decline with crop monoculture and approaches to maintaining high yields as exemplified by monoculture wheat and barley.

Soilborne plant pathogens—Common cause of the yield decline with crop monoculture

Historically, the explanations for the yield decline with crop monoculture have fallen into three groups: a) growing the same crop species in the same soil year after year leads selectively to a deficiency in one or more plant nutrients not limiting to other crop species; b) the crop plant builds up a toxicity to itself; and c) growing the same crop species in the same soil year after year enriches for soilborne pathogens of the roots of that crop. While logic might suggest that any combination of all three explanations could apply, depending on the crop, soil, and environment, the consistency of yield enhancement in response to crop rotation and yield decline with crop monoculture points to a common cause.

For example, there is no evidence that the variation in nutrient requirements of different crop species is sufficient to account for even a single case of yield decline offset by the common crop rotation effect. Indeed, Rovira (1976) and Cook (1992) both reported nitrogen left unused in the soil after harvest of wheat grown in monoculture, in stark contrast to its depletion in the soil profile where the crop remained healthy because root diseases were controlled by soil fumigation.

Similarly, there is no evidence that self-inhibition can account for the almost universal yield decline when crops are grown in monoculture, and, biologically, it makes no sense that the plants used as crop plants each would have evolved a mechanism to inhibit itself after the second or third generation at the same site.

Enrichment of populations of soilborne pathogens in response to the steady diet of roots of the same crop species is the one explanation that can account for the common yield decline with crop monoculture. First, there is ample variation in susceptibility of different crop species to the different species of root and stem infecting soilborne pathogens to predict that, biologically, each crop species will select for a population of pathogens uniquely adapted to its roots. Increases in the obvious vascular wilts, crown rots and plant blights such as caused by *Fusarium* species leave no doubt about this cause and effect cycle; less apparent, but equally important, is the gradual loss in root density due to destruction of the fine rootlets and associated nutrient-deficiency symptoms in the tops such as caused by species of *Pythium* and *Rhizoctonia* (Cook et al., 1987; Weller et al., 1986). Even *Pythium* species respond differentially to different crops species (Harvey et al., 2001). Second, yields can be maintained universally with monoculture if the soil is treated with a fumigant (Wilhelm and Paulus, 1980). There has been no unambiguous evidence to support the hypothesis that increased yields in response to soil fumigation is due to nutrients released from killed soil microbial biomass, and in the case of wheat in the Pacific Northwest, this explanation has been ruled out experimentally (Cook, 1992). Third, one need only compare the washed roots of crops grown in monoculture with roots of the same crops grown in rotation to see the obvious difference in health and density of the roots (Cook and Veseth, 1991).

Wheat monoculture in the U.S. Pacific Northwest

The semi-arid and sub-humid intermountain (Inland) Pacific Northwest of the USA, some five million hectares, is suited almost exclusively to cool-season crops—wheat, barley, canola, mustard, and cool-season pulses (peas, lentils, and chickpeas). However, because of competition from lower-cost regions such as Canada, Montana, and the Dakotas for the limited canola, lentil, pea and chick pea markets, Inland PNW growers are turning increasingly to intensive and even continuous wheat and barley. Fortunately, the region is equally suited to spring- and fall-sown varieties of these crops, which provides another means to diversify. For example, three year crop sequences such as winter wheat/spring

barley/pea or lentil (Cook, 1992) are being replaced with sequences such as winter wheat/spring wheat/spring barley.

Sequences that alternate winter- and spring-sown varieties of wheat and barley provide weed-control and market-diversity benefits, but in terms of potential enrichment of soilborne pathogens, they are crop monocultures. The pathogens responsible for yield declines with intensive wheat and barley include, *Gaeumannomyces graminis* var. *tritici*, cause of take-all, *Fusarium culmorum* and *Fusarium pseudograminearum*, causes of Fusarium crown rot, *Rhizoctonia solani* AG8 and *R. oryzae*, causes of Rhizoctonia root rot, and several *Pythium* species responsible for Pythium root rot (Cook, 2001; Paulitz et al., 2002).

In the lower precipitation zones (200-450 mm annual precipitation) of this region, Fusarium crown rot dominates on wheat when grown in the conventional two year winter wheat/fallow sequence with conventional tillage (Cook, 1980; Paulitz et al., 2002), and Rhizoctonia root rot dominates when the cropping system is intensified to include annual cereals with direct seeding (Cook et al., 2002; Paulitz et al., 2002). All four diseases occur in various mixtures in the higher-precipitation zones (450-600 mm annual precipitation), with take-all and Rhizoctonia root rot tending to be dominant on cereals grown with direct seeding (Moore and Cook, 1984; Weller et al., 1986; Paulitz et al., 2002). Pythium root rot is ubiquitous within the region in both direct-seed and conventional-tillage systems (Cook et al., 1987).

Breeding for host plant resistance has only provided useful tolerance for management of Fusarium crown rot (Cook, 1980) and no useful resistance or tolerance to take-all (Cook, 2003), Rhizoctonia root rot (Smith et al., 2002; Neate, 1989) and Pythium root rot (Vijian et al., 1998). Considering the fact that the progenitors of modern wheat evolved as a virtual monoculture, the lack of genes for resistance to root diseases implies that some other mechanism of defense exists to protect roots against these pathogens. Indeed, such protection develops against take-all with wheat monoculture—a natural biological control responsible for the well-documented phenomenon known as "take-all decline" (Gerlagh, 1968) and provided by specific genotypes of antibiotic-producing rhizobacteria inhibitory to *G. graminis* var. *tritici* in the rhizosphere (Raaijmakers and Weller, 1998, 2001; Raaijmakers et al., 1997).

Role of rhizobacteria in the natural defense of monoculture-wheat against take-all
Plant species have developed a defense strategy against soilborne pathogens that involves the selective stimulation and support of populations of antagonistic rhizosphere microorganisms (Cook et al., 1995). Natural disease-suppressive soils are the best examples in which the indigenous microflora protect plants against soilborne pathogens (Weller et al., 2002). Suppressive soils are divided into the categories of "long-standing suppression" and "induced suppression." Long-standing suppression is a biological condition naturally associated with the soil, its origin is not known, and it persists in the absence of plants. In contrast, induced suppression is initiated and sustained by crop monoculture (Hornby, 1983, 1998). Induced suppression is typically due to individual or select groups of microorganisms, is transferable to conducive soil by addition of 0.1% to 10% or less (w/w) of the suppressive soil, and is eliminated by pasteurizing (60°C, 30 min.) or fumigating (methyl bromide) the soil (Weller et al., (2002).

Take-all decline (TAD), the best example of induced suppression, is defined as the spontaneous decrease in the incidence and severity of take-all that occurs with monoculture of wheat after one or more severe outbreaks of the disease. TAD requires three components to develop: monoculture of a susceptible host, the presence of *G. g.* var. *tritici,* and one or more severe disease outbreaks (Cook and Weller, 1987; Hornby, 1998, Weller et al., 2002). TAD is a field phenomenon that occurs worldwide (Gerlagh, 1968; Hornby, 1998; Simon and Sivasithamparam 1989; Smiley, 1979; Weller et al., 2002). The development of TAD follows a consistent pattern everywhere and environmental factors and previous cropping history only modulate the speed of its development. Often four to six consecutive crops of wheat or barley are required before the onset of TAD, but the exact number can vary.

The suppressiveness associated with TAD is transferable to nontreated conducive, fumigated or pasteurized soil (Cook and Rovira, 1976; Gerlagh, 1968; Raaijmakers and Weller, 1998), eliminated by soil pasteurization or fumigation (Cook and Rovira, 1976; Raaijmakers and Weller, 1998) and reduced or eliminated by breaking monoculture with a crop that is not susceptible to take-all (Cook, 1981). A field

with a long history of TAD generally will regain suppressiveness with resumption of wheat or barley monoculture following a non-host break crop (Weller et al., 2002).

Microbiological changes in the bulk soil and/or rhizosphere environment resulting in antagonism of *G. g.* var. *tritici* are the mechanisms most commonly reported to be responsible for TAD (Cook and Weller, 1987; Hornby, 1998; Weller et al., 2002). Microorganisms suppressive to take-all are from many different taxonomic groups, and the pathogen is sensitive to different forms of antagonism, including destruction of hyphae (Dewan and Sivasithamparam, 1989), cross protection (Deacon, 1976), and antibiosis by *Pseudomonas* spp. (Weller et al., 1988), actinomycetes (Weller et al., 2002), *Trichoderma* spp. (Simon and Sivasithamparam, 1989), and *Bacillus* spp. (Kim et al., 1997). Therefore, most researchers have thought that different microbial antagonists are responsible for TAD worldwide.

Antagonistic *Pseudomonas* spp. have been widely implicated in TAD soils (Cook and Rovira, 1976; Raaijmakers and Weller, 1998; Smiley, 1979; Weller, et al., 1988). Efforts in Washington State to understand the role of pseudomonads in TAD have focused on suppressive soils from irrigated fields near Lind, Moses Lake, and Quincy, and non-irrigated fields near Pullman and Almota, WA. These soils were compared to conducive (non-suppressive) virgin (covered by native vegetation) soils, and to soils from fields in crop rotations but located near the TAD fields (Weller et al., 2002). Population densities of fluorescent *Pseudomonas* spp. inhibitory to *G. g.* var. *tritici* in vitro were significantly greater on roots from TAD soils than from conducive soils (Weller et al., 1988). Furthermore, when applied to wheat seeds at planting, pseudomonads from the TAD soils provided significantly better protection against take-all than pseudomonads from conducive soils (Weller et al., 1988; Weller et al., 1985).

Weller et al., (2002) hypothesized that enrichment of producers of either 2,4-diacetylphloroglucinol (DAPG) or phenazine-1-carboxylic acid (PCA) during wheat monoculture was a major contributor to suppressiveness in some Washington TAD soils. This hypothesis was prompted by earlier findings that a) antibiotic-producing fluorescent *Pseudomonas* spp. increased on wheat roots with TAD (Weller et al., 1988), b) some of the most effective *Pseudomonas* biocontrol strains isolated from TAD soils produced either DAPG (Harrison et al., 1993; Pierson and Weller, 1994; Vincent et al., 1991) or PCA (Thomashow and Weller, 1988; Pierson III, and Thomashow, 1992), c) pseudomonads synthesize these antibiotics in the rhizosphere environment (Bonsall et al., 1997; Thomashow et al., 1990), d) *G. g.* var. *tritici* is highly sensitive to these antibiotics, and e) they are responsible for the biocontrol activity of the strains producing them (Pierson and Thomashow, 1992; Thomashow and Weller, 1988; Vincent et al., 1991). The availability of cloned and sequenced biosynthetic genes (Bangera and Thomashow, 1999; Mavrodi et al., 1998) allowed the development of specific primers and hybridization probes to detect and quantify rhizosphere populations of fluorescent *Pseudomonas* spp. that produced either PCA or DAPG (Raaijmakers et al., 1997).

Comparisons of the frequency of DAPG- and PCA-producing pseudomonads on roots of wheat grown under controlled conditions in TAD and conducive soils suggested that DAPG producers, but not PCA producers, were involved in TAD (Raaijmakers et al., 1997). Several lines of evidence confirmed this initial observation and clearly indicated a key role for DAPG producing fluorescent *Pseudomonas* spp. in TAD: a) DAPG producers were present on roots from TAD soils at densities above the threshold level (10^5 CFU g^{-1} root) (Raaijmakers and Weller, 1998) required for take-all control, but were below the threshold or not detected on roots from conducive soils (Raaijmakers et al., 1997); b) successive plantings of wheat in a TAD soil (Quincy, WA) and its corresponding virgin soil demonstrated an inverse relationship between the population size of indigenous DAPG-producers and the severity of take-all (Raaijmakers and Weller, 1998); c) suppressiveness of the Quincy TAD soil was lost when DAPG-producers were eliminated by soil pasteurization (Raaijmakers and Weller, 1998); d) adding TAD soil to conducive soil established population densities of DAPG producers in the conducive soils above the threshold level required for disease control, and conferred suppressiveness (Raaijmakers and Weller, 1998); e) planting of a TAD soil to oats, (non-host crop), reduced the population density of DAPG-producers below the threshold required for take-all control; f) introduction of the DAPG producer *P. fluorescens* Q8r1-96 (from Quincy TAD soil) into conducive soils controlled take-all to a level similar to that of a TAD soil (Raaijmakers and Weller, 1998); and g) DAPG was detected on roots of wheat grown in Quincy TAD soil, but not on roots from Quincy virgin soil (Raaijmakers et al., 1999). These results were confirmed by findings from the field that DAPG-producing fluorescent *Pseudomonas* spp. were

abundant on roots of wheat collected from Pullman and Almota TAD fields, respectively, but were absent from roots collected only 50 meters from the Pullman TAD soil (Raaijmakers and Weller, 1998).

Evidence is now accumulating that DAPG producers contribute to TAD outside of Washington State. Weller et al., (2002) quantified DAPG producers in paired soil samples collected from fields across the U.S. that had or had not undergone wheat monoculture. DAPG producers were abundant in many of these monoculture wheat field soils. For example, roots from wheat grown in the greenhouse in soils from Fargo, ND (116 years of continuous wheat) and Hallock, Minnesota (10 years) (McSpadden Gardener et al., 2000; Weller et al., 2002) supported population densities of DAPG producers greater than 10^5 CFU g^{-1} root. In contrast, populations of DAPG producers on wheat grown in soils from adjacent fields without a history of wheat monoculture were at or below the limit of detection (10^4 CFU g^{-1} root). Recently, de Souza (2002) demonstrated a key role for DAPG-producing fluorescent *Pseudomonas* spp. in two Dutch TAD fields (14 and 27 years of continuous wheat) located in Woensdrecht, The Netherlands. DAPG producers also play a key role in the suppressiveness of other soils to diseases caused by soilborne pathogens (Keel et al., 1996; Landa et al., 2002; Weller et al., 2002).

DAPG-producing fluorescent *Pseudomonas* spp. appear to occur globally in agricultural soils, and strains have been divided into 17 different genotypes (designated A-Q) on the basis of genomic fingerprinting by whole-cell repetitive sequence-based (rep)-PCR with the BOXA1R primer (BOX-PCR) and RFLP analysis of *phlD*, a key gene in the DAPG biosynthetic locus (Keel et al., 1996; Landa et al., 2002; Mavrodi et al., 2001; McSpadden Gardener et al., 2001; McSpadden Gardener, 2000; Raaijmakers and Weller, 2001). The genotypes differ significantly in ability to colonize the rhizosphere of wheat and other crop species (Landa et al., 2002; Landa et al., 2003; Raaijmakers and Weller, 2001). Strains of genotype D are exceptional colonist of wheat roots, and this is no doubt one reason why they are the genotype primarily responsible for the suppressiveness of TAD soils in Washington State studied to date. A question of considerable interest is the mechanism by which DAPG producers, naturally present in the soil at low populations, are enriched during wheat monoculture and after an outbreak of take-all.

Prospects for management of Rhizoctonia root rot with transgenic resistance

Rhizoctonia root rot of wheat and barley in the Inland PNW is caused by two species, namely *R. oryzae* and *R. solani* AG8, and therefore any source of genetic resistance must be effective against both and not just one of these species. Thus far, all screening for resistance to Rhizoctonia root rot of cereals has focused on *R. solani* AG8 (Smith et al., 2002; Neate, 1989), and even this level of effort has revealed no useful resistance in any of the primary and secondary cereal gene pools. Equally or more significantly, the host ranges of both pathogens include all cool-season broadleaf crops available for use in rotations with wheat and barley in the Inland PNW (Cook et al., 2002; Paulitz et al., 2002), making it unlikely that resistance exists possibly in the plant kingdom and negating the potential benefit of crop rotation between cereals and broadleaf crops as a means of control.

Reports from South Australia (Roget et al., 1996), eastern Oregon (Smiley et al., 1996), and Washington (Paulitz, unpublished) have documented or suggested a decline in Rhizoctonia root rot with long-term monoculture of wheat or wheat/barley sequences. Moreover, replicated field trials in eastern Washington with select strains of antibiotic-producing rhizobacteria combined with the commercially available deficonozole and metalaxyl as seed treatments resulted in 5-8% higher yields (significant at $P < 0.05$) of continuous direct-seeded spring and winter wheat compared to yields in the same trials in response to either biological or chemical seed treatments alone (Cook et al., 2002). However, even these yields were 15-20% below the potential for the sites as reveal by soil fumigation with methyl bromide.

Lorito et al., (1998) showed that expression of the *ThEn42*gene from *Trichoderma harzianum* for production of a 42-Kda endochitinase provided significant resistance in both tobacco and potato to the *Rhizoctonia* pathogens of these plant species. Using this same gene, but codon-optimized so as to increase the GC makeup to 65.1% (from the natural 56.3%), as needed to optimize expression in barley (Jensen et al., 1996), Wu (2003) showed that the *ThEn42* is effective as a transgene against both *R. solani* AG8 and *R. oryzae* as pathogens of barley. Western and Southern blots, PCR tests, and polyclonal antibodies raised to the ThEn42 protein confirmed the presence and expression of the *ThEn42* gene in plants putatively transformed based on the *bar* gene used as the selectable marker. In vitro tests with the

purified ThEn42 enzyme added to potato dextrose agar showed inhibition of both species in the range of 50-100 ug/ml and complete inhibition of both pathogens at 400 ug/ml.

Barley seedlings grown from seed representing the T-1 progeny of primary transformants showed segregation expected of a single gene. Seedlings confirmed as transgenic for the gene and resistant to Rhizoctonia root rot in a greenhouse seedling test have been selected for production of seed representing the T-2 generation and for use as parents in the barley breeding programs at Washington State University. While the gene is also needed in wheat, barley with resistance to this disease could provide a cultivar potentially more useful than current cultivars as a rotation crop with wheat, depending on the level of resistance achieved with this transgene. The *ThEn42* gene confers significant resistance but not immunity to the two species responsible for Rhizoctonia root rot, but will still provide a highly useful addition to the system already in use by growers to manage this disease.

Achieving the full yield potential of monoculture cereals with direct seeding

Monoculture of agronomic crops such as wheat and barley is not sustainable in most rainfed wheat- and barley-growing areas of the world if its success depends on continued conventional tillage (Shillinger et al., 1999). Soil organic matter contents in the Inland PNW have dropped to less than 50% of their original (virgin soil) contents during only slightly more than 100 years of farming (Rasmussen and Rhode, 1989). In addition, soil losses exceeding 10-12 mt/ha/year have been documented in the higher-rainfall Palouse region because of water erosion, and particulate-matter <10 microns in diameter (PM10) as dust caused by tillage has become a public health issue. Equally or more importantly, fuel usage and operator time required to produce crops can be reduced by 50% and greater with direct seeding compared to conventional farming. Not surprisingly, growers throughout the world and especially in North and South America, Australia, and South Africa are converting their farming operations to direct-seed systems. This trend must continue but clearly adds new challenges for control of root and crown diseases, especially for the root and crown diseases of wheat and barley.

Rhizoctonia root rot has become especially important in the Inland PNW (Weller et al., 1986) and in southern Australia (Roget et al., 1996) as a direct consequence of the shift in these areas to direct-seed cropping systems. Indeed, the controlling effects of tillage on this disease were not recognized until growers and researchers began to use direct seeding. Part of this response was subsequently shown to result from delayed or inadequate control of volunteer (self-sown) cereals (Roget et al., 1987; Smiley et al., 1992). The greater disease with direct seeding undoubtedly also relates to disease-favoring effects of the more persistent cool, moist soil conditions associated with crop residues left on the soil surface compared to soil made bare-black by tillage. Low disturbance drilling has also been shown to exacerbate this disease (Roget et al., 1996) and conversely, deep soil disturbance has been shown to reduce disease severity (Gill et al., 2001).

Take-all has been reported to be more severe with direct seeding (Moore and Cook, 1984; Roget et al., 1996), more severe with conventional tillage (Rothrock, 1987), or similar whether the crop is grown with direct seeding or conventional tillage (Ramsey et al., 2000). Limited originally to wheat and barley in the high-precipitation areas (>500 mm/year) and crops grown under irrigation in the PNW, the favorable effect of wet soil on take-all (Cook, 2003) have been extended because of direct seeding to rainfed areas of this region with only 350-500 mm annual precipitation. Fortunately take-all decline does not appear to depend on the use of tillage (Rajiimakers and Weller, 1998).

Like Rhizoctonia root rot and take-all, Pythium root rot is favored by the cool wet soil conditions associated with surface residues (Paulitz et al., 2002). Possibly, the gradual disappearance of the tillage pan and associated improved drainage of the top 10-15 cm of soil could offset the favorable effect of surface residues on the epidemiology of Pythium root rot, since tillage pans and associated puddling of the top soil during periods of rain and snow melt can be highly favorable to Pythium root rot (Allmaras et al., 1988). While not effective against root infections, use of current year seed (Hering et al., 1987) and seed treatments with either metalaxyl or mefenoxam (Cook et al., 2002) provides considerable protection against *Pythium* infections of emerging seeds and young seedling.

Fusarium crown rot has long been important on winter wheat in rainfall areas with <350-400 mm precipitation annually, where wheat is seeded early into conventional fallow in a two year winter

wheat/fallow rotation (Cook, 1980). Papendick and Cook (1974) showed that the disease on winter wheat caused by *F. culmorum* is favored by plant water stress during the heading stage and can be managed by use of a combination of a) water stress-tolerant or -avoiding varieties and b) use of later fall seeding and less nitrogen—practices that helped avert the onset of plant water stress as the plants reached adult-plant stages of development (Cook, 1980). Since this work, Fusarium crown rot caused by *F. psuedograminearum* has become more important in the region (Smiley et al., 1996), including in the higher precipitation regions (> 400-450 mm annual precipitation) and on spring wheat grown in direct-seed systems and managed for high-grain protein (Paulitz et al., 2002). The PNW grows spring wheats for low- (8-10%) or high- grain protein (11-15%). Experimental trials have consistently shown that genotypes bred for high-grain protein are intrinsically more susceptible to Fusarium crown rot than genotypes bred for low-grain protein (T. Paulitz, Kim Kidwell, and R. J. Cook, unpublished). The greater amounts of infested crop residue left on and near the soil surface with direct seeding (Burgess et al., 1993), the greater susceptibility of high-grain protein genotypes, and the tendency for early onset of plant water stress caused by the nitrogen applied to achieve high-grain protein (Papendick and Cook, 1974) probably accounts for the increasing importance of Fusarium crown rot in spring wheats that are managed both with direct seeding and for high grain protein. It may be necessary in this region to grow the *Fusarium*-tolerant low-grain protein varieties managed for low grain protein until such time as tolerance or resistance to this disease can be added to the high-grain protein cultivars.

With or without varieties of wheat and barley genetically resistant or tolerant to all four root and crown diseases, several management practices are critical to achieving the full yield potential of cereals grown in monoculture and without tillage. Most importantly, as discussed above, early and timely management of volunteer cereals provides a host-free period of at least two weeks and preferably one or two months before planting the next cereal (Roget et al., 1996; Smiley et al., 1992). This practice is especially important for management of Rhizoctonia root rot and probably also Pythium root rot and take-all. The second most important practice is fertilizer placement directly beneath the seed at the time of planting, so as to make the nutrients and especially the relatively immobile phosphorus more accessible to diseased roots (Cook and Veseth, 1991; Cook et al., 2000). Widening the use of paired-rows so as to keep the crop canopy open longer into the growing season has also proved beneficial to the crop, thought to result from greater warming and drying the top few centimeters of soil where the pathogens responsible for Pythium and Rhizoctonia root rots and take-all are most actively (Cook et al., 2000).

Conclusions

Yields can be maintained with crop monoculture provided that the soilborne pathogens are controlled. The most common soilborne plant pathogens include plant parasitic nematodes, root infecting fungi such as *Rhizoctonia* and *Pythium* species responsible for destruction of fine roots and root hairs, and the pathogens responsible for the more conspicuous blights, wilts, and stem and crown rots such as *Fusarium* species. For high value crops such as many fruits and vegetables, these pathogens are controlled and yields maintained worldwide using soil fumigation or heating the soil by solarization. For field crops such as wheat and barley, control of soilborne pathogens depends on integrated methods that make use of natural microbiological control, host plant resistance, plant nutrients made conveniently available to diseased roots through precision placement under the seed, widening the space between rows to favor the crop, and timely elimination of volunteers (self sown) and weed hosts so as to maximize the host-free period between harvest and planting. Wheat and barley evolved in the equivalent of monocultures, where plants reseed themselves in essentially the same sites each season without the benefit of tillage, yet natural selection has produced a wide diversity of genes for resistance to leaf pathogens of these crops but little if any useful resistance to the root pathogens of these crops. A study of the widespread phenomenon known as “take-all decline” as a model system for understanding crop monoculture effects of the soil microbiota indicates that wheat roots infected by the take-all pathogen, *G. graminis* var. *tritici,* select for specific genotypes of rhizobacteria (*Psuedomonas fluorescens*) that inhibit the take all pathogen through production of the antibiotic 2,4-diacetylphloroglucinol. The result of this remarkable microbiological change is that the disease declines and yields recover with continued wheat or barley monoculture. Ability to produce this antibiotic is highly conserved within a great diversity of genotypes of *P. fluorescens* and related *Pseudomonas* species. Successful crop monocultures are often accompanied by the unexplained absence of root diseases in spite of the presence of pathogens in the soil. Further studies are needed to investigate the potential for natural disease suppression by antibiotic producing rhizobacteria as another tool for maintaining yields with crop monoculture.

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