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Timothy C. Paulitz

Plants can be attacked by a variety of parasitic microorganisms, primarily fungi, bacteria, nematodes, and viruses. From 2001 to 2003, an average of 7% to 15% of the major world crops (wheat, rice, potato, maize, and soybean) were lost due to fungi and bacteria (Oerke, 2005). Along with weeds and insects, plant pathogens are the major biotic limitation to crop health and yield. Many of these pathogens are foliar and attack aboveground parts of plants, with inoculum spread by wind and rain. Examples are rust, powdery mildew, and foliar leaf pathogens such as the fungus *Septoria.* However, some of the most severe, intractable, and difficult to control pathogens are soil-borne pathogens, which live in the soil for part or all of their life cycle and interact with the soil biota and the edaphic environment. These pathogens can survive in the soil and infect the root systems of plants. Fungi, fungus-like Stramenopiles (Oomycetes) and nematodes are probably the most important of the soil-borne pathogens. Fungi are eukaryotic organisms that form threadlike filamentous hyphae that can spread through the soil and form resistant structures such as oospores or sclerotia. These structures allow the fungus to survive in the absence of the host, or during unfavorable environments such as heat, cold, or dry soils. When these resting structures encounter a seed or root in the soil, they are stimulated to germinate, chemotactically grow toward the root, and infect the epidermal cells. Some fungi can also destroy seedlings before they emerge from the soil. Once the root is infected, fungi can spread inside the root, rotting the root by producing enzymes and toxins. Fungi also destroy lateral roots, feeder roots, and root hairs. As a result, the plant loses its ability to absorb water and nutrients. Above ground, plants are stunted and show nutrient deficiencies, and yields are reduced. Some pathogens can also move up the roots to the base of the plant, girdling the base or infecting the lower stem. Finally, another group of fungal pathogens can induce wilt by colonizing the xylem system, restricting the conduction of water to the leaves.

Nematodes are microscopic invertebrate wormlike organisms. They can feed on the root system using a stylet, a hollow needlelike feeding structure that can penetrate root cells. Some can move to foliar plant parts, but most feed on root systems. They spend most of their life in the soil, feeding on the outside of the root (ectoparasites), while others can feed and move inside the root system (endoparasites). Root knot and cyst nematodes become sedentary in the root and the females will set up a feeding site by modifying plant cells and lay eggs. But all plant parasitic nematodes spend significant parts of their life cycle in the soil.

Monetary losses due to soil-borne diseases in the United States are estimated to exceed $4 billion per year (Lumsden et al., 1995), and losses due to parasitic nematodes exceed $100

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billion per year worldwide (Bird and Kaloshian, 2003). Detailed studies on wheat crops in the Pacific Northwest (PNW) have documented losses of up to 36% due to the Oomycete *Pythium*, the fungi *Fusarium* and *Rhizoctonia*, and the nematode *Pratylenchus* (Cook et al., 1987, 2002; Smiley et al., 2005a,c). These genera, along with the Oomycete *Phytophthora*, are common in other major agronomic crops.

Another group of fungal pathogens spend part of their life in or on the soil, but infect the aboveground portions of the plant, and survive on crop residues resting on the soil surface. Examples would be apple scab [*Venturia inaequalis* (Cooke) G. Winter], Sclerotinia white rot of canola and beans [*Sclerotinia sclerotiorum* (Lib.) de Bary] and Fusarium head blight of wheat and barley [*Fusarium graminearum* Schwabe = *Gibberella zeae* (Schwein. : Fr.) Petch]. This latter disease has become epidemic in the upper Midwest since the mid 1990s, produces mycotoxins in the grain, and has caused billions of dollars of losses (McMullen et al., 1997). These pathogens can overwinter in the crop residue, and the following spring produce air-borne ascospores that can infect the wheat at flowering. Part of the reason for the increase in disease has been the move toward no-till. Under conventional tillage, the residue is plowed under and decomposes quickly, because of the action of saprophytic fungi and actinomycetes. This deprives the pathogen of a niche to survive. If the residue is left on the surface, the pathogen can overwinter and produce air-borne inoculum in the spring.

Unlike foliar pathogens, soil-borne pathogens are difficult to diagnosis and control. Foliar pathogens can be controlled with systemic or protectant fungicides applied as sprays to the leaves. But there are few chemicals that can be applied to soil and effectively control soil-borne pathogens. Soil fungicides can be leached away, bound to soil particles, or broken down by microorganisms. A soil-applied chemical must protect a constantly growing and expanding root system, but no chemicals move in the phloem down into the roots system. In addition, a large volume of soil must be treated, since the root systems of most plants can extend down more than 1 m. There are some nematicides that can be applied to the soil, but only for high-value crops. Soil-applied fungicides and nematicides may also have environmental effects, destroying beneficial fungi and nematodes, or contaminating groundwater. Fumigation with compounds such as methyl bromide is effective, but is very expensive and is being phased out because this compound is destroying the ozone layer.

Genetic resistance has been the basis of sustainable management of many foliar pathogens. But there are few examples of genetic resistance to soil-borne root-rotting organisms, possibly because of the nature of these pathogens, which kill the host ahead of the advancing fungus and do not show a gene-for-gene coevolution like biotrophic pathogens. Because of the lack of chemical and genetic tools to manage these diseases, growers have relied on cultural methods to control soil-borne pathogens. Tillage is one cultural method that has the most profound effect on soil-borne pathogens. Tillage has been a part of agriculture since its inception almost 10,000 years ago. The domestication of cereals has selected for *r*-strategist plants, which can thrive in disturbed areas, grow quickly, and produce reproductive structures (seeds). Tillage has served several important purposes: preparation of the seed bed, reduction of compaction for soil aeration and better root growth, weed control, incorporation of fertilizer and organic amendments, and residue management (Gebhardt et al., 1985). But tillage has also been an important disease management tool for soil-borne pathogens.

Tillage can control pathogens by several mechanisms. Many pathogenic fungi (and beneficial fungi such as arbuscular mycorrhizal fungi) form networks of filamentous hyphae in the soil. Tillage can break apart these networks, which connect the fungi to food sources such as residues and plant roots (Deacon, 1996; Kabir, 2005). Tillage results in increases in microbial activity (Aon et al., 2001), as organic matter is exposed to microbial degradation, and the increase in microbial activity can suppress pathogen activity. Many pathogens produce inoculum and survive in infected crop residue. Tillage places this debris into a lower soil profile, which accelerates the decomposition of this material, depriving the pathogenic fungus of a niche. Pathogen inoculum is also reduced by the antagonistic action of soil microbes and microfauna. Examples are mycoparasites, organisms that degrade the cell walls of fungi, and fungal-feeding nematodes and invertebrates.

Conversely, some pathogens may be favored by tillage. Tillage reduces soil organic matter and microbial activity in the long term, which may reduce populations of antagonistic microbes. Tillage can produce compaction and tillage pans, decreasing soil infiltration and drainage. Root-rotting pathogens such as *Phytophthora* and *Pythium* require wet soils so motile spores (zoospores) can be formed and released, and swim to the root surface. Soils that are too wet can also become anaerobic, making the dying roots yet more susceptible to pathogens.

Tillage causes severe degradation of soil resources and soil erosion, as covered in other chapters of this book. One solution is reduced tillage or no-till (direct seeding). In direct seeding or no-till, the soil is left undisturbed from harvest to planting. The crop is seeded directly into the previous stubble, using a no-till drill. Planting is done in one operation, with no seedbed preparation, leaving most of the residue from the previous crop on the surface. No-till offers growers several economic and environmental advantages. With the residue of standing stubble covering the soil, soil loss from wind erosion is significantly reduced (Papendick, 2004). Soil particles less than 10 μm in diameter have been shown to have adverse effects on human health, and can contribute to pollution in downwind urban areas. Fuel, labor, and machine costs are reduced. In conventional tillage in eastern Washington with summer fallow, a grower may require seven or more tillage or cultivation operations in a single season, compared with a no-till grower who uses herbicides for primary weed control. The increasing cost of diesel fuel in the past few years has resulted in rising costs, and no-till can reduce diesel consumption by up to 80% (Baker et al., 1996). Organic matter increases with no-till (Dao, 1993; Douglas and Goss, 1982), improving soil structure and water infiltration. No-till can improve the soil water balance with crop residues that trap more snow, and by earthworm and root channels that allow water to penetrate without running off. Gradual reductions in tillage from 1982 to 1997 have reduced soil loss from farmland by an estimated 1 billion tons per year (NRCS, 2000).

But reduced tillage can increase disease severity of many soil-borne pathogens. The lack of tillage increased Rhizoctonia diseases in Australia and U.S. (MacNish, 1985; Rovira, 1986; Pumphrey et al., 1987). Recent work in the PNW has shown that *R. solani* J.G. Kühn becomes a major problem during the third and fourth year of the transition from conventional tillage to no-till (Schroeder and Paulitz, 2006). Tillage may break up hyphal networks or induce microbes that are antagonistic to *Rhizoctonia*. Standing stubble on the soil will trap more snow than bare soil will, resulting in higher soil moisture levels in the spring. Residues also reflect solar radiation, so soils do not warm as quickly in the spring as black soil, which absorbs solar radiation. Reduced temperatures delay planting and slow plant growth, but increase the activity of pathogens that have low temperature optima. For example, *Rhizoctonia solani* AG-8 is highly pathogenic at 10°C (Ogoshi et al., 1990). *Pythium ultimum* Trow is active at 10°C, and *P. irregulare* Buisman is active at 5°C (Ingram and Cook, 1990). Residue can also act as a mulch, reducing evaporation from the soil surface, so soil remains wetter in the spring. As previously mentioned, pathogens such as *Pythium* are favored by wet soils

No-till can also influence soil nutrients and pH. Because the soil is not turned over, nutrients from fertilizers can accumulate in the top layer. For example, in the PNW, anhydrous ammonium is widely used, which results in acidification of soil over long use. Take-all, caused by *Gaeumannomyces graminis* (Sacc.) von Arx & Olivier var. *tritici* Walker, is reduced by lower pH (MacNish, 1988), but other pathogens, such as Fusarium wilts, clubroot of crucifers, and Cephalosporium stripe of wheat, are increased at lower pH (Myers and Campbell, 1985; Hoper and Alabouvette, 1996, Murray and Walter, 1991).

Residue can act as a mulch to reduce the freezing and thawing cycles in the soil. Standing stubble reduces the wind velocity at the surface. Freezing and thawing may reduce the survival of some pathogens, but others may be increased. For example, Cephalosporium stripe, a vascular pathogen of wheat, infects fall-planted wheat through wounds in the roots and crowns caused by freezing and frost heaving (Specht and Murray, 1990).

Probably the most profound effect of reduced tillage is the increased amount of crop residue left on the soil surface, which decomposes slower than if the residue were covered by soil. Classic examples of diseases in wheat in the Great Plains of the United States that are favored by no-till residue are Fusarium head blight, tan spot caused by *Pyrenophora tritici-repentis* (Died.) Drechsler, *Septoria tritici* Roberge (cause of leaf blotch) and *Stagonospora nodorum* (Berk.) Castell. & E.G. Germano (cause of Nodorum leaf and glume blotch). These produce fruiting bodies on the residue in the spring, and ascospores or conidia can be ejected into the air or splash up on the foliage by rain or irrigation. In the PNW, it is too dry for foliar pathogens, since there is little rainfall in the summer. But Fusarium crown rot, caused by *F. pseudograminearum* O'Donnell & T. Aoki and *F. culmorum* (Wm.G. Sm.) Sacc. survives in the crop residue, and can be more severe under no-till conditions (Bailey et al., 2001)

This rest of this chapter will focus on this dilemma—how do growers preserve and enhance soil structure and health using no-till without exacerbating root diseases? How do growers manage soil-borne pathogens without resorting to extensive tillage?

I will use examples from our research on management of root diseases of cereals in the PNW to address this question. Soil erosion, both wind and water, is a major problem in eastern Washington State because of the hilly topography with steep slopes. Despite the advantages of no-till, the adoption rates by cereal growers in the US are fairly low compared with other countries or cropping systems. In the United States, 54.7% of field crops, mainly soybean and corn, were produced using conservation tillage and 31.5% using no-till (CTIC, 2006). Canada, Argentina, Brazil, and Australia have high rates of adoption in cereal production. But in the PNW of the United States, less than 15% of cereal growers use no-till (Smiley et al., 2005b), and in Whitman County, the most productive wheat county in Washington, adoption is less than 10% (H. Kok, personal communication, 2008). One of the reasons for this reluctance to adopt no-till is the increased threat of root diseases.

Methods for Reducing the Impact of Pathogens in No-Till Systems

Genetic Resistance

The most economically and environmentally sustainable method of controlling plant diseases is genetic resistance. The grower does not need to change cultural practices or use fungicides. However, for many of the major soil-borne pathogens of cereals, such as *Rhizoctonia, Pythium* and *Gaeumannomyces graminis* var. *tritici*, genetic resistance has not been found (Smith et al., 2002a,b; Higginbotham et al., 2004; Tineline et al., 1989). But effective resistance has been found for Fusarium crown rot in Australian lines (Wildermuth and McNamara, 1994; Wallwork et al., 2004; Wildermuth and Morgan, 2004) and is being incorporated into PNW varieties. Single gene resistance to the cereal cyst nematode has been deployed in wheat in Australia and other countries (Cook and Noel, 2002). Several other pathogens are now minor problems in the PNW, because of resistant or tolerant cultivars, including Cephalosporium stripe (Bruehl et al. 1986), eyespot or strawbreaker foot rot (Allan and Roberts, 1991), and snow mold (Gaudet, 1994). For most soil-borne pathogens, resistance is fairly stable and durable, unlike with foliar pathogens such as rusts that have a race structure and mutate to overcome resistance genes.

Chemical Control

Because of the low economic value of cereal crops, the only fungicides that are economically feasible are seed treatments. Some of these seed treatments are systemic and control seed-borne and foliar pathogens such as bunts and smuts. These include tebuconazole, triticonazole, difenoconazole, and other demethylation inhibitors. Some chemicals only protect the seed and do not move into the seedling (e.g., metalaxyl, which protects against Pythium damping-off). Seed treatments can improve seedling health but rarely give yield increases, and no chemical moves systemically to protect the growing root system throughout the life of the plant.

Suppressive Soils

Many soils have the ability to suppress the growth and activity of soil-borne pathogens. Some of this is a general background or nonspecific suppression, caused by the total microbial biomass in the soil, sometimes referred to as biological buffering. This type of suppression can be increased by the addition of organic matter, compost, or green manure (Bonamomi et al., 2007; Zinati, 2005; Noble and Coventry, 2005; Bailey and Lazarovits, 2003). If the microbes are removed by pasteurization or chemical treatment, more disease will result from a given amount of inoculum. However, there is a more specific suppression in some soils, due to a specific group of microbes active against a specific pathogen. Cook and Baker (1983) define suppressive soils as "soils in which the pathogen does not establish or persist, establishes but causes little or no damage, or establishes and causes disease for a while but thereafter the disease is less important, although the pathogen may persist in the soil." The opposite of this would be a conducive soil. Specific suppressiveness can be eliminated by heating the soil to 60°C, and can be transferred to a conducive soil, indicating a biological basis. Specific suppression has been identified for a number of soil-borne fungi including *Fusarium oxysporum* Schltdl. : Fr., *Rhizoctonia solani*, actinomycetes such as *Streptomyces scabies* (Thaxt.) Waksman & Henrici, and nematodes such as *Heterodera schachtii* Schmidt (Alabouvette, 1999; Roget, 1995; Liu et al., 1996; Menzies, 1959; Westphal and Becker, 1999). A classic example is take-all decline in wheat, first discovered almost 60 yr ago. This phenomenon has been reported worldwide, and may result from a number of mechanisms (Weller et al., 2002). Monocropping of wheat will produce increasing take-all disease over the first few years, often peaking in years 3 to 4, but then the disease will start to decline with continued monoculture, reaching a low, economically unimportant level. In the PNW, take-all decline results from the buildup of *Pseudomonas fluorescens* that produce the antibiotic 2,4-diacetylphloroglucinol (Raaijmakers and Weller, 1998). These bacteria colonize the rhizosphere of plants infected with the take-all pathogen, *Gaeumannomyces graminis* var. *tritici*, especially the lesions caused by the pathogen. 2,4-diacetylphloroglucinol is produced in the rhizosphere (Raaijmakers et al., 1999) and the pathogen is sensitive to the antibiotic (Mazzola et al., 1995).

Cropping systems can be manipulated to favor and build up this specific suppressiveness. This suppressiveness, like genetic resistance, does not require any input from growers, and takes advantage of the natural microbial suppression.

Crop Rotation

One of the oldest and most effective methods of controlling disease is crop rotation. Some soil-borne pathogens have narrow host ranges, only attacking certain species of plants. If a resistant crop is planted, the inoculum in the soil cannot infect, and must remain dormant for a season, without a food source. Over the season without the host, inoculum can be reduced by the action of antagonistic soil microflora and microfauna, which feed on the inoculum. When a susceptible crop is planted the next year, inoculum is reduced below the economic threshold. For example, crop rotation with a broadleaf crop every third year effectively controls take-all caused by *Gaeumannomyces graminis* var. *tritici* (Hornby, 1998). However, many soil-borne pathogens such as *Rhizoctonia* and *Pythium*, have wide host ranges, and can attack the rotation crop, so crop rotation may not be as effective. In addition, pathogens that can survive in the soil for long periods of time cannot be controlled by rotation. For example, *F. culmorum*, cause of Fusarium crown rot, can survive for many years in the soil as chlamydospores (Inglis and Cook, 1986), and rotation is not effective.

Green Bridge Management

Many soil-borne pathogens can infect and survive in the roots of grassy weeds and crop volunteers. When these weeds are killed by herbicides before planting, the necrotrophic pathogens can colonize the dying plants and form more inoculum. Another reason is that herbicides such as glyphosate inhibit the biochemical pathway needed for plant defenses, and make the plant more susceptible to pathogens. This concept is known as "glyphosate synergy" (Lévesque and Rahe, 1992). If the crop is planted into these dying weeds, severe disease can result from this green bridge, where the pathogen moves from the dying plant to the young seedling (Smiley et al., 1992). On the other hand, the longer the inoculum is in the soil before planting the crop, the more inoculum activity can be reduced by antagonistic activity of soil microflora and microfauna. It is recommended that growers kill the green bridge at least 3 wk before planting to reduce this pathogen carryover (Fig. 17|1). Green bridge control has been shown to be effective against *Pythium*, *Gaeumannomyces graminis* var. *tritici* and *Rhizoctonia.*

Residue Management

Excessive residue can be removed by burning, but this has many environmental problems (smoke, health hazards, loss of organic matter from the soil, loss of nutrients from the straw). Growers can use harrows, light cultivators, or mowers to break up residue to allow for faster decomposition. Chaff spreaders can be used behind the combine to spread the straw and prevent it from being dumped in a row. Sickle bars in front of the combine reel can allow for the straw to be cut short. Straw can be baled and removed. However, for pathogens that survive in the root system and not in the crowns or straw, such as *Pythium* and *Rhizoctonia*, residue management may not be effective in reducing inoculum (Paulitz et al., 2010).

Fallow

Fallow is agriculture land that is left unseeded during the growing season, a soil without a crop. Growers in low-rainfall areas of the PNW practice summer fallow, and only plant winter wheat every

Fig. 17|1. Effect of timing of herbicide application on greenbridge carryover of *Rhizoctonia*. All plots of spring barley (cv. Baronesse) were planted at the same time, but glyphosate was applied 2 d, 1 wk, or 8 wk before planting. These plots had high levels of *Rhizoctonia solani* and *R. oryzae* in the soil, and crop volunteer (wheat) was allowed to overwinter on the plots before being killed out by glyphosate. Plots were 8 rows wide × 7.3 m long, planted at the USDA-ARS Palouse Conservation Farm, Pullman, WA.

other year. This allows the moisture to be stored in the soil for the following year. Growers can also use fallow for weed control, and weeds can be suppressed with chemical herbicides or mechanical cultivation. Since there is no plant present, soil-borne pathogens do not have a host to infect. During this time, inoculum will decline due to depletion of energy in resting structures and degradation by microflora and microfauna, similar to when a nonhost crop is grown. Can fallow reduce soil-borne pathogens? A period of 3 to 6 wk of fallow reduced *Rhizoctonia* in direct-seeded wheat in Australia (Roget et al., 1987). In a series of trials conducted in annual cropping areas in the PNW, chemical fallow was not effective in reducing *R. solani* or *R. oryzae* Ryker & Gooch, possibly because of the intact root systems that serve as a protected niche for the pathogen. But in a low-rainfall area, mechanical fallow with inverted sweeps and chemical fallow reduced the activity of *R. solani*, but not *R. oryzae*. The latter organism forms microsclerotia, which can probably survive 1 yr in the absence of a host. Fallow can also reduce take-all disease. Wheat after fallow had significantly less take-all disease in long-term trials in the southeastern US (Cunfer et al., 2006). Many species of *Pythium* were reduced to below detectable levels in fallow fields, when quantified with real-time PCR (Schroeder and Paulitz, unpublished data, 2008). However, two species, *P. abappressorium* Paulitz & M. Mazzola and *P. irregulare* Group IV, were not affected by fallow, so this effect may be species-dependent.

Application of Starter Fertilizer in the Seed Row

Because of the rotting and reduction in the root systems, feeder roots and root hairs of young seedlings infected by root pathogens, nutrient deficiencies may result, especially relatively immobile nutrients such as phosphorus. No-till growers can apply starter fertilizer below or to the side of the seed in the seed furrow. This fertilizer will be readily available to the young seedling, and may allow the plant to compensate for root loss. Nutrients do not directly affect plant resistance, but enhance seedling vigor to compensate for pathogen damage (Patterson et al., 1998). Under Zn-deficient conditions, application of Zn decreased disease severity and patch area caused by *R. solani* AG-8 (Thongbai et al., 1993a,b; MacNish and Neate, 1996). However, additional Zn applications in patches in an experiment in the PNW did not provide a benefit (Cook et al., 2002). Application of starter fertilizer can be as effective as seed treatments in increasing yield of barley under high *Rhizoctonia* pressure (Paulitz and Reinertsen, 2005).

Altered Planting Date

Since disease can be increased by conditions that are more favorable for the pathogen or less favorable for the host, planting dates can be adjusted to avoid these periods. For pathogens such as *Rhizoctonia* and *Pythium* that are favored by wet, cool soil conditions, planting can be delayed in the spring until the soils warm and dry. However, this is often not possible with the short growing season of the PNW. Delays in planting past a certain date will severely reduce yield. With fall-planted wheat, early planting can increase Fusarium disease, since this disease is triggered by drought stress, and early-planted wheat would run out of water early in the spring.

Seed Quality

Although soil-borne pathogens are not generally seed-borne, use of quality seed that emerges quickly can reduce the impact of soil-borne pathogens such as *Pythium* spp. Older seed takes longer to germinate and emerge, increasing the time that the embryo and emerging seedling are susceptible to the pathogen (Hering et al., 1987). Deterioration of the seed coat in older seed also results in the release of more exudates that attract *Pythium*. Older seeds also produce more volatiles such as ethanol when germinating, especially under anoxic conditions (Rutzke et al., 2008), and ethanol is stimulatory to the growth of *Pythium* (Paulitz, 1991).

Conclusions

Soil-borne pathogens that cause root diseases spend most of their life cycle in or on the soil. Soil management decisions will influence the survival and growth of these pathogens, and the severity of disease. Many of the cultural methods that growers have relied on in the past to reduce the impact of these pathogens, such as tillage, can have negative effects on soil health and sustainability. But conversely, no-till practices, designed to improve sustainability, can exacerbate some diseases. Thus, growers must balance crop health vs. soil health in making management decisions. Innovative technologies, such as resistant cultivars and inducing and maintaining microbial suppressive soils, may solve this dilemma in the future.

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