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FULL RESEARCH PAPER

Management of resident plant growth-promoting rhizobacteria with the cropping system: a review of experience in the US Pacific Northwest

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Abstract In view of the inconsistent performance of single or mixtures of plant growth-promoting rhizobacteria (PGPR) strains formulated for commercial use, and the high cost of regulatory approval for either a proprietary strain intended for disease control or a crop plant transformed to express a disease-suppressive or other growth-promoting PGPR trait, management of resident PGPR with the cropping system remains the most practical and affordable strategy available for use of these beneficial rhizosphere microorganisms in agriculture. A cropping system is defined as the integration of management (agricultural) practices and plant genotypes (species and varieties) to produce crops for particular end-uses and environmental benefits. The build-up in response to monoculture cereals of specific genotypes of *Pseudomonas fluorescens* with ability to inhibit *Gaeumannomyces graminis* var. *tritici* by production of 2,4-diacetylphoroglucinol (DAPG), accounting for take-all decline in the US Pacific Northwest, illustrates what is possible but apparently not unique globally. Other crops or cropping systems enrich for populations of the same or other genotypes of DAPG-producing *P. fluorescens* or, possibly and logically, genotypes with ability to produce one or more of the five other antibiotic or antibiotic-like substances inhibitory to other soilborne plant pathogens. In the U.S Pacific Northwest, maintenance of threshold populations of resident PGPR inhibitory to *G. graminis* var. *tritici* is the centerpiece of an integrated system used by growers to augment take-all decline while also limiting damage caused by pythium and rhizoctonia root rot and fusarium root and crown rot in the direct-seed (no-till) cereal-intensive cropping systems while growing varieties of these cereals (winter and spring wheat, barley and triticale) fully susceptible to all four root diseases.

Keywords Take-all · Take-all decline · *Pseudomonas fluorescens* · Pythium root rot · Rhizoctonia root rot · Fusarium root and crown rot · Direct-seed · Crop rotation · Crop monoculture

Introduction

There are basically three strategies by which the biological control and other crop-production benefits of plant growth-promoting rhizobacteria (PGPR) can be exploited: (1) through mass production, formulation and timely introduction of select strains of PGPR, usually with the seeds or other planting material at the time of planting; (2) through transgenic expression in the crop plant itself of one or more specific traits identified with a biological control/growth promotion

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phenotype; and (3) management of their resident populations and beneficial activities with the cropping system. A *cropping system* is defined as the integration of management (agricultural) practices and plant genotypes (species and varieties) to produce crops for particular end-uses and environmental benefits (Cook 2006).

Initial optimism based on results of pot tests and small-scale field trials that the disease-suppression and other agronomic benefits of PGPR might be attained commercially through use of a single proprietary strain or defined mixture of strains (Cook and Baker 1983) has long since been countered by the realities of their notoriously inconsistent performance from site to site and year to year (Bakker 1989; Cook 1993; Weller 1988). To claim disease control for a proprietary strain intended for commercial use, most countries require that the strain as formulated be registered by the regulatory authority as a microbial pesticide. The cost for attaining and submitting the data necessary to register and label a strain cannot be justified if the performance is inconsistent, especially if, in addition, the strain has activity only against the pathogen or pathogen complex for which it was selected and on the host from which it was selected (Mathre et al. 1999). Activity of a given strain may be broadened through genetic transformation (Blouin Bankhead et al. 2004; Fenton et al. 1992) but this will only further complicate and extend the regulatory approval process.

The use of PGPR as a genetic resource has potential to serve as a source of resistance to soilborne plant pathogens, and should be pursued in view of the dearth of useful genes for resistance to these pathogens within the gene pools of crop plants. Several studies have shown the potential for the *EnCh42* gene from *Trichoderma harzianum* for production of endochitinase as a source of resistance to *Rhizoctonia solani* (Harman et al. 2004). However, unlike the use of *EnCh42*, or the *Bt* gene from *Bacillus thuringiensis* for resistance to certain insect pests, transgenic expression of a functional PGPR trait will likely require the considerably more difficult transfer of a complex multi-gene pathway (Bangera and Thomashow 1999; Mavrodi et al. 1998) and possibly quantitative trait, preferably combined with a tissue- (root-) specific promoter. Moreover, the same or even more comprehensive regulatory requirements must be met for use of a PGRP trait expressed transgenically in the host plant than required for use of the donor PGPR strain itself.

Studies of the ecology of PGPR populations would suggest that resident PGPR populations are likely to respond simply to the agricultural practice of growing crops, whether recognized or unrecognized by science, and may with more knowledge of these interactions be further enhanced by deliberate use of the cropping system with no requirement for regulatory oversight. Indeed, the evidence, albeit empirical, would suggest further that the modern-day success of intensive cropping, including some crop monocultures or near-monocultures, may well be the result of protection from root diseases afforded by naturally occurring PGPR (Cook 2006, 2007). Take-all of wheat caused by *Gaeumannomyces graminis* var. *tritici* and its decline as the soil becomes suppressive in response to continuous wheat or barley monoculture has become a model system for understanding the effects of crop plants and more particularly the cropping system on the populations and activity of PGPR strains of *Pseudomonas fluorescens* (Weller et al. 2002, 2007). Cook et al. (1995) suggested further that, since wheat and related grasses evolved as a monoculture or near-monoculture, natural suppression by PGPR responsible for take-all decline would have been redundant with and therefore could account for the lack of useful genes for resistance to the take-all pathogen. This paper briefly reviews the current state of knowledge of the role of PGPR in take-all decline, their possible role in the success of intensive cropping more generally, and their exploitation as a component of an integrated approach to management of root diseases of wheat and barley in cereal-intensive direct seed (no-till) cropping systems in the US Pacific Northwest.

Role of PGPR in take-all decline

The phenomenon whereby take-all caused by *G. graminis* var. *tritici* increases during the initial years of continuous wheat monoculture but then declines and grain yields increase as the soil becomes suppressive to the pathogen has been well documented since first demonstrated experimentally by Gerlach (1968) in The Netherlands. Research by Shipton et al. (1973) with monoculture wheat-field soils in the Washington State confirmed the findings of Gerlach (1968), including that the factor responsible for pathogen suppression is sensitive to 55°C moist-heat treatment of the soil for 30 min. This work showed further that a take-all suppressive agent present specifically in soil from a field in continuous wheat monoculture was transferable to another field by movement of the soil and that it could multiply (reviewed in Cook 2007). Cook and Rovira (1976) concluded that suppression of the pathogen occurred in the rhizosphere rather than in the bulk soil and suggested that fluorescent *Pseudomonas* species were somehow involved. After some 30 years of research on take-all decline, the evidence now points clearly to a major if not exclusive role of a select few genotypes of *P. fluorescens* with ability to produce the antibiotic 2,4-diacetylphlorglucinol (DAPG) inhibitory to *G. graminis* var. *tritici* (reviewed in Weller et al. 2002, 2007). The threshold population of DAPG-producing psuedomonads required for disease suppression is log 5 colony forming units (CFU)/g root. Raaijmakers et al. (1999) showed further that the amount of DAPG produced in the rhizosphere of wheat is a constant 0.62 ng/log 5 CFU when populations of a wheat-adapted DAPG-producing strain ranged between log 6 and log 7 CFU/g root.

Ability to produce DAPG is a highly conserved trait within the populations of *P. fluorescens* worldwide (Keel et al. 1996). However, based on polymorphisms in the *phlD* gene contained within the five-gene DAPG-biosynthesis operon (Mavrodi et al. 2001), together with DNA fingerprinting, it is possible to detect, quantify, and characterize distinct genotypes of DAPG-producing *P. fluorescens* (McSpadden Gardener et al. 2000, 2001) in the rhizosphere of economically important crops. To date, at least 22 distinct genotypes of DAPG-producing *P. fluorescens* have been identified among the thousands of isolates obtained from rhizospheres (Landa et al. 2005). Among these, the D genotype has been the dominant strain in take-all decline fields in Washington State (Weller et al. 2002, 2007), whereas genotypes F and M were dominant in take-all decline fields in The Netherlands (Souza et al. 2003). Ability to produce DAPG is only one aspect of the effectiveness of a PGPR strain in suppression of take-all. The other aspect is ability to colonize the roots of wheat and sustain a take-all-suppressive threshold population. Strain Q8r1-96, a D genotype, exemplifies both traits; in addition to its ability to produce DAPG, this strain is a highly aggressive colonist of the wheat rhizosphere and was shown to sustain a take-all-suppressive population in competition with other potential rhizosphere colonists in natural soil over successive cycles of growing wheat (Raaijmakers and Weller 2001).

Possible role of PGPR in the success of intensive cropping more generally

Like any new area of science, the fundamental revelations and practical implications of research on take-all decline has been done in concert with and inspired by the discoveries made through research on other examples of plant growth promotion and pathogen suppression by fluorescent *Pseudomonas* species (Schippers et al. 1987). Of particular relevance is work in Switzerland led by G. Dèfago demonstrating a primary role of fluorescent pseudomonads in the suppression of black root rot of tobacco caused by *Thielaviopsis basicola* in a soil cropped 24 years to monoculture tobacco (Stutz et al. 1986). Initial findings with one particular strain isolated from the rhizosphere of tobacco grown in this soil, now the well-known model strain *P. fluorescens* strain CHAO, indicated that the suppression of black root rot with monoculture of the host crop involved a combination of iron starvation by production of siderophores and inhibition of the pathogen by both hydrogen cyanide and antibiotics (Ahl et al. 1986). Subsequent work showed that *P. fluorescens* strain CHAO produces DAPG (Keel et al. 1992), and that up to 23% of 1,100 pseudomonads isolated from the rhizosphere of tobacco grown in the 24-year tobacco-monoculture soil produced DAPG (Keel et al. 1996). *Pseudomonas fluorescens* CHAO is member of the A genotype of DAPG-producing *P. fluorescens.*

Another example is the finding in a plot on the Washington State University, Northwest Research and Extension Centre at Mount Vernon, Washington, that DAPG-producers exceeded log 5.0 CFU/g root in the rhizosphere where peas had been grown in monoculture for the past 30 years and the soil was suppressive to fusarium wilt caused by *Fusarium oxysporum* f. sp. *pisi* (Landa et al. 2002). Six distinct DAPG-producing genotypes were identified in the rhizosphere of pea growing in this soil, with the D and P genotypes being dominant. The D and P genotypes recovered from the pea rhizosphere were shown to colonized the rhizospheres of wheat and pea, respectively, better than the other four DAPG-producing genotypes, namely A, L, O, and Q, also isolated from this pea-monoculture plot.

Further evidence that the different DAPG-producing genotypes may be crop-specific was recently reported by Landa et al. (2005) following their analysis of genotypes present in plots on the campus of North Dakota State University, Fargo, North Dakota, where wheat and flax were grown as monocultures in side-by-side plots for more than 100 years. Populations of DAPG-producing pseudomonads exceeded log 5.0 CFU/g root in the rhizospheres of both wheat and flax grown in the soils. However, roughly 80% of the genotypes in the rhizosphere were of equal frequencies of genotypes F and J in soil where flax had been grown in monoculture, and 77% were genotype D in soil where wheat had been grown in monoculture. The genotype(s) in soil from the plot that had been in crop rotation (i.e. bean, corn, oat, soybean, sugar beet, sunflower etc, or left fallow) for over a century could not be assessed because the population of DAPG-producing PGPR were below the level of detection (10^4 CFU/g root) on roots in this soil.

McSpadden Gardner et al. (2005) found the D genotype in the rhizospheres of both maize and soybeans in Ohio State in all 15 counties sampled over a 3-year period, exceeding log 3.4 CFU/g root on 77, 84 and 81% of maize plants sampled in years 2001, 2002, and 2003, respectively, and 78, 67, and 52% of soybean plants sampled during those 3 years, respectively. Picard et al. (2000) similarly documented high populations of DAPG-producing genotypes of *P. fluoresens* in the rhizosphere of maize in Spain. About half of the 120 million hectares of crops planted each year in the USA are planted to maize and soybeans (about 32 million hectares each). The maize-soybean rotation is the dominant cropping system, but at least 2 million hectares of soybeans are grown in a wheat-soybean double crop system and an equally large area is planted each year to continuous maize. Plant breeding can account, in part, for the continued increases in average annual yield of both crops, including for resistance to the soybean cyst nematode and phytophthora root rot of soybean. However, other than selecting the highest yielding maize inbreds and hybrids under field conditions, there is no deliberate effort by the seed companies to breed for resistance to root diseases of maize. While it can only be speculative at this stage, the pathogen-suppressive benefits of DAGP-producing PGPR enriched, respectively, by the corn–soybean, corn–corn or soybean–wheat double cropping systems and possibly even the PGPR-enriching effects of the corn hybrids and soybean varieties themselves cannot be overlooked and deserve more study.

Crop monoculture has also been shown to convert soil from suppressive to conducive through shifts in populations of rhizobacteria. In Washington State, soils not previously planted to apples are naturally suppressive to a fungal/oomycete complex of apple root pathogens responsible for the apple replant problem but become conducive to these pathogens after apples are grown in the soil (Mazzola 1998). Mazzola (1999) found that, concurrent with enrichment in the inoculum density of root pathogens in response to roots of apple growing in the soil, the populations of microorganisms antagonistic to these pathogens were replaced by pseudomonads not inhibitory to these pathogens, thereby helping to account for the poor growth of apples replanted in this same soil. However, by planting wheat in old apple-orchard soil prior to replanting apples, the population of rhizobacteria returned to predominantly inhibitory pseudomonads and the disease-suppressive state of the soil was restored (Mazzola and Gu 2000).

The diversity of genera, species, subspecies and genotypes of PGPR functioning as resident antagonists of pathogens in soil may well be an order of magnitude greater than the ‘tip of the iceberg’ revealed to date for the DAPG-producing genotypes of *P. fluorescens*. Even among the diversity of fluorescent pseudomonads, we might assume a similar hierarchy of subspecies and genotypes based on ability to produce one or more of the five other antimicrobial substances produced by strains of this diverse genus (Hass and Défago 2005) and no less conserved globally than ability to produce DAPG. In the same way that the different genotypes of DAPG-producers appear to be adapted to different crops, soils and possibly climates, and suppressive to specific diseases caused by soilborne plant pathogens, it is not a stretch to speculate that other antibiotic-producing genotypes contribute to the suppression of these same or different diseases in agricultural and natural environments. The door to study of the fluorescent pseudomonads was opened with the development by Sands and Rovira (1970) of a selective medium for their isolation and enumeration. The door to the study of other groups, including the unculturables, will depend on the newer methods of isolation and characterization of DNA recovered directly from soil and the rhizosphere of crop plants. This is an exciting yet complex area of rhizosphere microbiology, but one well worth pursuing if science is to more fully understand and exploit the pathogen-suppressive soils as a component of sustainable agriculture.

Exploitation of take-all suppression combined with agricultural practices to manage wheat and barley root diseases in cereal-intensive direct-seed cropping systems

The U.S intermountain Pacific Northwest represents nearly 5 million hectares of farmland in Idaho, Oregon and Washington. With its Mediterranean climate of cool wet winters and dry summers, the region is ideal for but also largely limited to production of cool-season crops, especially wheat and barley. Similar to northern Europe, the yield potential under rainfed conditions in the Palouse region of southeast Washington and adjacent northern Idaho with its deep loess soils is in the range of 8–10 t ha^{-1}, being limited primarily by annual precipitation (Cook and Veseth 1991). Travelling west from the Washington–Idaho border towards the Cascade mountains, annual precipitation drops approximately 1 cm every 10 km and the environments under which wheat and barley are grown change accordingly from subhumid to semi-arid and then arid-irrigated. Yields under irrigation have been documented as high as 14 t ha^{-1}.

Not surprisingly, the conditions ideal for cool-season cereals are also ideal for the diseases of these cereals. Stripe (yellow) rust, pseudocercosporella eyespot, cephalosporium stripe and a snow-mold complex caused by several soil- and crop-residue-borne pathogens have come under control over the past 40 years largely through the use of resistant or tolerant varieties and crop rotation. In contrast, and typical of root diseases more generally, progress towards control of cereal root diseases has depended almost entirely on refinements in agricultural practices, with little if any help from the breeding programmes. Adding to the challenge, decomposition of pathogen-infested roots and stem bases of the host in the top few centimeters of soil (where most concentrated) occurs relatively slowly; when wet enough for microbial breakdown, e.g. late fall to spring, soil temperatures are typically low and when warm enough, e.g., summer and early fall, the soils are dry. The result is that a 1-year break from wheat or barley is not sufficient to control these pathogens by crop rotation. Lengthening the rotation depends on planting cool-season broadleaf crops such as pulses and brassicas, all of which are minor crops that have limited markets, or the production economics is not competitive with production of the same crops in Canada. Adding further to the challenge, growers are moving towards wider adoption of direct seeding (no-till) to lower the cost of fuel, machinery, and time required to produce crops while reversing a 100-year trend of decline in soil organic matter (Rassmusen and Rhode 1989) and preventing soil erosion. The same agricultural practices intended to delay the breakdown of crop residue further increase the potential for crop damage from residue-borne pathogens such as *G. graminis* var. *tritici* (reviewed in Cook 2006). The result is that, while the yield potential for wheat and barley under rainfed conditions is typically higher with direct-seeding compared to the use of conventional tillage, owing to more water captured and kept in the soil, actual yields may be lower due to the increased pressure from root diseases.

Cereal-intensive cropping systems in the Inland PNW include the use of different market classes of wheat (either high-grain-protein bread-type or low-grain-protein pastry type wheat of either a winter or spring growth habit), barley (malting and feed types, two-row and six-row, and either a winter or spring growth habit), and triticale (either winter or spring growth habit). Typical cereal-intensive direct-seed cropping systems vary within the region, depending on the annual precipitation and include: a 3-year winter wheat/spring wheat/spring barley, spring wheat, or chemical-fallow sequence; 2-year winter wheat/spring cereal or chemical-fallow sequence; and different combinations of continuous spring barley, spring wheat and/or spring triticale. Continuous direct-seeded winter cereals leads quickly to unmanageable winter annual grasses such as *Bromus tectorum* and is therefore avoided.

The important root diseases of cereals in these systems include, in addition to take-all, pythium root rot caused by several *Pythium* species; rhizoctonia root rot caused by *R. solani* AG8, *R. oryzae* and possibly one or more other *Rhizoctonia* species; and fusarium root and crown rot caused by *F. pseudograminearum* and *F. culmorum* (Paulitz et al. 2002). Recent findings by Smiley et al. (2004) reveal that plant parasitic nematodes, including *Heterodera avenae, Pratylenchus thornei,* and *P. neglectus,* are also part of the root-pathogen complex limiting yields of dryland winter and spring wheat in the semiarid PNW.

Take-all and pythium and rhizoctonia root rots are favoured by the cool moist soil conditions of late fall and early spring, especially soils covered with residue of the previous crop (typical of direct seed systems) compared to the bare-black soil surface achieved when the crop residue is buried or burned. Indeed, because soil covered with crop residue stays wet longer into the growing season, direct seeding has extended the area favourable to take-all well into the lower precipitation part of the region and beyond its normal range. The occurrence of fusarium root and crown rot requires a period of predisposing water stress on the crop during the reproductive stages of plant development and therefore historically has been most important in the semi-arid parts of the region (Cook 1980), although both take-all and fusarium root and crown rot caused by *F. pseudograminearum* can develop on different plants in the same field in direct-seeded spring wheat in the subhumid parts of the region.

Dependence on spontaneous take-all decline is fundamentally the most important component of the integrated system used to manage root diseases in the direct-seed cereal-intensive cropping systems used in the intermountain Pacific Northwest. Take-all left uncontrolled will dominate the root system, especially of winter wheat, making pythium and rhizoctonia root rots (but not fusarium root and crown rot) largely irrelevant. A 1-ha plot on the WSU Research Station near Lind, WA (in the semi-arid region) and cropped every year to either winter or spring wheat with supplemental sprinkler irrigation (simulating a higher precipitation area) showed maximum take-all by the 7th year and maximum take-all decline by the 15th year (Fig. 1). Thereafter, and through year 19, rhizoctonia root rot caused by *R. solani* AG 8 became increasingly more important, indicating that this otherwise highly destructive root disease was somehow suppressed during the years when take-all was the dominant root disease.

While experimental evidence is limited, the use of certain break crops to control take-all can also leave the soil conducive to the return of take-all with the resumption of wheat monoculture. In the 1-ha long-term wheat-monoculture plot, replicated subplots planted either to alfalfa (lucerne), soybeans, or oats for three consecutive years caused a complete loss of suppressiveness (equivalent to soil fumigation with methyl bromide), compared to replicated subplots of wheat in the same complete block design that maintained suppressiveness (Cook 1981). Two other treatments – replicated plots cropped, respectively, to a mixture of grasses and continuous potatoes – during the 3-years of the experiment were intermediate in maintaining suppressiveness of the soil to take-all when the entire site was again planted uniformly to wheat. Rothrock and Cunfer (1986) reported that take-all decline failed to develop in Georgia in fields double-cropped to wheat and soybeans, suggesting

Fig. 1 Views of the same area within a 1-ha experimental plot cropped to continuous monoculture wheat starting in 1967/68 crop year. *Left*, 1974, the 7th year of monoculture facing north, showing the response to chloropicrin fumigation. *Right*, 1982, the 15th year of monoculture wheat, facing south but otherwise the same area within the 1-ha plot, with the man standing on the border separating a subplot fumigated from an adjacent subplot not fumigated. Yield of wheat in the non-fumigated plots was roughly 50% of the yield in fumigated plots in the 7th year of monoculture and 95% of the yield in fumigated plots in the 15th year of monoculture

that a single crop of soybeans alternated each 12-month period with wheat somehow prevents or limits ability of wheat to enrich and/or maintain a population of PGPR genotypes needed to suppress take-all. The results of Landa et al. (2002) showing that DAPG-producers exceeded log 5.0 CFU/g root of peas grown in monoculture, and that the D and P genotypes were dominant, would suggest that, unlike soybeans, alfalfa and oats in the 1-ha Lind plot, the occasional break to dry peas in the otherwise cereal-intensive cropping systems used in the higher precipitation region of the Inland Northwest may not interfere with the maintenance of take-all suppression.

A large portion of fields in the PNW intermountain region receiving 400 mm or more precipitation annually has produced at least 12 cereal crops in the past 20 years, about half have produced 15–18 and a few fields have produced 20 crops in 20 years. When not planted to a cereal, fields in the higher precipitation areas are typically planted to peas or lentils, and those in the lower precipitation areas are in a 12–14 month fallow alternated with winter wheat. A survey (Ramsey 2001; Cook 2003) of approximately 100 wheat fields in Idaho, Oregon and Washington in each of 1998, 1999, and 2000 using the 0–100 rating system of Shoeny and Lucas (1999) showed that take-all was no more severe in fields cropped every year to wheat (13.3 average rating for 108 fields) or wheat/barley (15.1 average rating for 16 fields) than wheat alternated with a broadleaf (mainly pea or lentil) crop (11.7 average rating for 41 fields). Interestingly, there was no difference in take-all severity between fields direct-seeded (3-year average rating of 13.2) and fields managed with conventional tillage (3-year average rating of 13.5). Raaijmakers and Weller (2001) showed that the population of DAPG-producing pseudomonads in the rhizosphere of wheat in a 1-ha experimental plot near Pullman cropped to wheat or barley for 14 of the previous 16 years was at or above the threshold log 5 CFU/g required for suppression of take-all.

More than conventional systems, the equipment for direct seeding is designed to place nitrogen, phosphorus, and sulphur 3–5 cm beneath or beneath but no farther than 3–5 cm to the side of the seed at the time of planting, thereby placing these nutrients within easy access of the seedling roots. Some growers use a two-pass system, where the bulk of nitrogen is applied through shanks about 10 cm deep prior to sowing and the phosphorus, sulphur and additional nitrogen as a 'starter' mixture is applied with or below the seed at sowing. The practice of applying all nitrogen before or at sowing is in contrast to fertilization practices west of the Cascade Mountains, e.g., in the Willamette Valley of Oregon, and much of Europe, where most or all nitrogen is applied after sowing to avoid leaching. Precision placement of the relatively immobile phosphorous with or below the seed is especially important for crops under pressure from root diseases, to facilitate its access to roots reduced in capacity to explore the soil for this nutrient. Proper placement of phosphorus is also thought to augment the benefits of PGPR in limiting damage from take-all, well known to be more severe on crops starved for phosphorus. The disks or points used to place fertilizer and seed within the same row, by also clearing the residue and creating a narrow zone of tillage within the seed row, is thought to also limit the severity of take-all and pythium and rhizoctonia root rots because of more warming and drying within this zone of disturbed soil. Rhizoctonia root rot caused by *R. solani* AG 8 is particularly sensitive to soil disturbance such as provided by the tools for seed and fertilizer placement (Roget et al. 1996). Paired-row spacing, i.e., positioning two rows 15–20 cm apart with 35–40 cm between the pairs, rather than a uniform 20–30 cm apart, can also help offset the yield-depressing effects of root diseases, by keeping the canopy open longer and adding further to the opportunity for warming and drying of the top few centimeters of soil where the pathogens are most active (Cook et al. 2000).

Control of *Pythium* species starts and ends with the use of fresh high-quality seed (Hering et al. 1987) treated with a chemical protectant (Cook et al. 2002; Smiley et al. 1996). This is especially important for stand establishment in cool wet soils, typical for cereals seeded directly into cereal stubble; emergence of a winter cereal in this system must await the fall rains and emergence of a spring cereal is slow because soil covered with residue of the previous cereal remains cold and wet (Smiley et al. 1996). In addition, fresh wheat straw fragments are highly stimulatory to *Pythium* activity in soil (Cook et al. 1990), resulting in chlorotic and stunted seedings, symptoms that formerly but incorrectly were attributed to phytotoxic substances released from the residue (Cook and Haglund 1991). Metalaxyl (Apron®) is the dominant product used for control of *Pythium* on germinating seeds, used in combination with either difenoconozole

(Dividend®) or tebuconazole (Raxel®) for control of smuts (Smiley et al. 1996). No work has been done in the Pacific Northwest with the seed treatment product fluquinoconazole, shown in Europe to have some benefit against take-all (Bateman et al. 2004), but results from seed-treatment trails conducted with silthiofam, registered in Europe as Latitude® (Beale et al. 1998) and shown to provide some level of take-all control used as seed treatment (Bailey et al. 2005), has shown no benefit in the Pacific Northwest beyond the combination of agricultural practices described above (Cook, unpublished). In contrast, treatment of seeds with metalaxyl combined with either difenoconozole or tebuconazole produced average yield increases of 4–5% in continuous direct-seeded winter and spring wheat using the best agricultural practices described above (Cook et al. 2002).

The ability within the region to grow winter and spring varieties of cereals equally well offers mainly the means to manage weeds but also provides some opportunity to manage rhizoctonia root rot. In spite of the putative reputation of members of this form-genus as soil saprophytes, the rhizoctonias responsible for root rot of cereals depend for their survival primarily on roots of live hosts. Even a relatively short period of no-plants – as short as a few weeks of chemical fallow that includes use of an herbicide to eliminate the volunteer (self-sown) cereals – can result in significantly less pressure from rhizoctonia root rot in the next cereal crop (Roget et al. 1987; Smiley et al. 1992). This discovery has proven particularly important for the management of rhizoctonia root rot of spring-planted cereals where the volunteer cereals and grass weeds are treated with a burn-down herbicide late in the previous fall. Where the volunteer develops too late for fall treatment, spraying as early as possible in the spring and waiting at least 2 weeks and preferably 1 month before planting can also greatly limit the severity of this disease.

Management of fusarium root and crown rot, especially crown rot caused by *F. pseudograminearum*, remains a major challenge in cereal-intensive direct seed systems. Research done in the 1970s on root and crown rot caused by *F. culmorum* showed that the predisposing plant water stress was more likely to develop in crops supplied with excessive nitrogen fertilizer and led to the practice of more carefully matching nitrogen applications to yield goals as set by the amount of water available to finish the crop (Cook 1980). Reducing the amount of nitrogen provided for the crop remains the best if not only practice available to manage this disease. However, this practice has limits for wheat varieties managed for high grain protein, because of the additional nitrogen needed to achieve grain-protein goals.

Conclusions

It is significant that yields within 80–85% of the potential demonstrated in fumigated plots (Cook et al. 2002) can be achieved in cereal-intensive direct-seed cropping systems in spite of the more or less uniform susceptibility of the local cereal cultivars to the four root diseases widely present in these fields. The evidence is clear that DAPG-producing PGPR enriched by intensive cereals and suppressive to take-all is central to the success of these cropping systems. Different cropping systems offer the flexibility to integrate different sequences of spring and winter wheat, barley, and triticale with specific planting and other agricultural practices adapted to local conditions. Fundamental to the success of these systems is the recognition that take-all is only one of at least four different root diseases favoured by direct seeding with intensive cereals, and that dependence exclusively on take-all decline is rarely sufficient under the conditions discussed. Indeed, among take-all and pythium and rhizoctonia root rots, each likely to begin on the seminal roots, and each favoured by the cool moist soil conditions that prevail in direct-seed systems, there is evidence that control of only one can increase the potential for damage caused by one or both of the other two. While this experience shows what can be accomplished through management of resident PGPR as one component of a package approach to design of the cropping system, it does not preclude the potential to augment benefits of resident PGPR through introduction of specific genotypes that might then also be managed for greater performance by use of the cropping system. Even with these gains or potential for gains, the package will not be complete without some progress in breeding for varietal resistance. That may ultimately be the best if not only sustainable solution for control of fusarium root and crown rot.

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