Toward cropping systems that enhance productivity and sustainability

R. James Cook*

Washington State University, Pullman, WA 99164

The defining features of any cropping system are (*i*) the crop rotation and (*ii*) the kind or intensity of tillage. The trend worldwide starting in the late 20th century has been (*i*) to specialize competitively in the production of two, three, a single, or closely related crops such as different market classes of wheat and barley, and (*ii*) to use direct seeding, also known as no-till, to cut costs and save soil, time, and fuel. The availability of glyphosate- and insect-resistant varieties of soybeans, corn, cotton, and canola has helped greatly to address weed and insect pest pressures favored by direct seeding these crops. However, little has been done through genetics and breeding to address diseases caused by residue- and soil-inhabiting pathogens that remain major obstacles to wider adoption of these potentially more productive and sustainable systems. Instead, the gains have been due largely to innovations in management, including enhancement of root defense by antibiotic-producing rhizosphere-inhabiting bacteria inhibitory to root pathogens. Historically, new varieties have facilitated wider adoption of new management, and changes in management have facilitated wider adoption of new varieties. Although actual yields may be lower in direct-seed compared with conventional cropping systems, largely due to diseases, the yield potential is higher because of more available water and increases in soil organic matter. Achieving the full production potential of these more-sustainable cropping systems must now await the development of varieties adapted to or resistant to the hazards shown to account for the yield depressions associated with direct seeding.

Historically, the productivity and sustainability of any given cropping system have been thought to require, as a foundation, the use of a long (3-year cycle or longer) and diverse crop rotation. For purposes of this work, a cropping system is defined as the integration of management practices and plant genotypes (species and varieties) to produce crops for particular end uses and environmental benefits. Management involves making the growing environment and supply of resources (plant nutrients and water) more favorable for the crop. Plant genotype determines the ability of the crop to withstand any hazards (biotic and abiotic stresses) and to produce to the limits set by the environment and the supply of resources. Both management and plant genotype are local. As an example, at least 1,000 different varieties of wheat are planted in any given year to produce the U.S. wheat crop, each adapted to a particular locality and/or suited to a particular end use and management.

Although the benefits of crop rotation are beyond reproach, to remain competitive in today's global commodity markets, farm businesses have had to specialize in the production of typically two crops (more rarely three), and many specialize in a single crop or in closely related crops, such as different market classes of wheat and barley. The efficiencies gained by specializing, e.g., using the same planter, harvester, and marketing infrastructure for all crops, have increasingly outweighed the risks of putting "all eggs in one basket." Moreover, the more uses that are found for commodity crops such as corn and soybeans (e.g., biofuels), with the declining landbase available for agricultural uses, the more intensely these crops will be and can be grown in the same fields as continuous or near-continuous monocultures. Consider, for example, that of the ≈300 million acres of crops and ≈300 crops planted each year in the U.S., more than two-thirds (220 million) are planted with just three crops, corn, soybeans, and wheat. Double cropping, such as the wheat–soybean double-cropping system in the Southeast U.S. and Brazil and the rice–wheat double-cropping system in India and China, qualifies as "crop rotation" but still involves planting each crop every year in the same field.

Crop monocultures have been taboo largely for one reason, crop health, and hence yields typically decline, leading to more safe sites within the field for weeds to flourish. This practice also requires greater use of pesticides and usually also tillage (soil cultivation) to manage or at least stabilize yields at some economic level. Classic but unproven explanations for yield decline with crop monoculture have included the following: different crops remove different plant nutrients from the soil until one nutrient becomes limiting, but not if a different (unrelated) crop is then grown in that field; the crop is toxic to itself (allelopathy); as thought after the 19th and early 20th century yield declines of monoculture cotton in the U.S. Southeast, the soil becomes "worn out" and "needs a rest." With the exception of nitrogen-fixing legumes, any crop sequence where a product is hauled from the field will deplete the soil of its fertility, which must be replaced as an input (1). Furthermore, annual plants now domesticated as crop plants evolved under selection pressures that included the ability to survive, if not thrive, by reseeding themselves in the same sites year after year.

These early explanations for the "crop-monoculture effect" remain amazingly engrained as part of conventional wisdom, despite their illogical nature. Overwhelming scientific evidence has shown that yields decline with crop monoculture because exposure of the soil microbiota to the roots of the same crop year after year steadily enriches for yield-debilitating populations of soil-borne pathogens of that crop. The resultant root infections also then limit the ability of the crop plants to compete with weeds and cause the plants to appear as if the soil is depleted of nutrients, when instead the plants are depleted of roots needed to absorb nutrients. Consider, for example, that one of the most successful crop monocultures historically and still today, paddy rice in Asia, with rice only and more commonly two or more rice crops grown in each field each year, involves the use of soil flooding to control weeds; flooding also has a significant soil-sanitizing effect on soil-borne plant pathogens (2).

Fig. 1. Seeder (drill) designed to simultaneously seed and fertilize corn, wheat, soybeans, canola, or other agronomic crop directly (no-till) into undisturbed soil and residue of the previous crop left lying on the soil surface. This drill, developed by Horsch Equipment Manufacturing (Schwandroft, Germany) and in use on the private farm of Agro Soyus in South Central Ukraine near Dnepropetrovsk, is 18 m wide and can plant at speeds up to 16 km/hr (nearly 30 hectares/hr), not including time required to refill the seed and fertilizer tanks. The tools (openers) used on this drill to place seed at one level, e.g., 3 cm deep, and fertilizer beneath the seed, e.g., 7–8 cm deep, are spaced 30–40 cm apart, depending on the crop and yield potential of the region; these tools were developed by Anderson Machine (Andover, SD).

Concurrent with the modern trend toward crop monocultures or near monocultures, farmers worldwide, for a combination of economic and environmental reasons, are reducing and even eliminating the use of tillage. This tillage had been used historically to bury the residue of the previous crop, control weeds, and prepare a seedbed for the next crop (3). Direct seeding, also known as "no-till farming," saves time, energy, and steel by allowing annual crops to be produced with a sprayer (for weed control), planter [that simultaneously and precisely places seed and fertilizer in the same seed furrow in a single pass over the field (Fig. 1)], and combine harvester, thereby eliminating the need for plows, cultivators, disks, and harrows to till the soil. As an example of economic benefits, growers in both Washington state and Ukraine report that it takes as little as one-fourth as much diesel fuel ($\approx$5 liters/tonne compared with 20 liters/tonne of grain) to produce wheat with direct seeding compared with wheat production using the standard and multiple tillage operations. More importantly than just the greater use of fuel, four times the amount of diesel must be visualized in terms of additional time and steel needed to use that much more diesel fuel.

In addition to the economic benefits, leaving all residue of the previous crop on the soil surface protects against evaporative loss of water needed to grow the next crop, essentially stops soil loss from wind and water erosion, and results in a buildup (sequestration) of soil carbon as organic matter. Addition-ally, the stubble with all weeds seeds left on the soil surface provides habitat and food for birds and other wildlife. Indeed, direct-seed cropping systems can provide the same ecosystem services expected of natural ecosystems, including mitigation of floods and droughts, purification of water and air, recycling of nutrients, and protection of biodiversity. North American agriculture has been moving slowly but steadily in this direction since the Dust Bowl of the 1930s.

Yield-Limiting Hazards of Direct Seeding

Many plant pathogens use the residue of their host crop as a food base and springboard to infect the next crop. This includes a diversity of necrotrophic leaf-, stem-, and inflorescence-attacking fungal pathogens that survive as reproductive and spore-dissemination structures formed within the dead tissues of their hosts. These structures are thereby ideally positioned on the soil surface and beneath the canopy of the next crop in direct-seed cropping systems. Likewise, many insect pests are harbored in the residue of their host plant and are then positioned to do greater damage when this residue is left on the soil surface compared with when it is buried. The obvious answer to these crop-production hazards is longer crop rotations; one should allow more time for the relatively specialized soil- and residue-borne pathogens and insect pests of any given crop to die out through starvation and natural attrition before again planting that crop. Even a 1-year break, i.e., a 2-year rotation cycle, can offer significant relief from these pest pressures.

However, pests can also adapt to crop rotation. The selection pressure of a 1-year break from corn provided by a corn–soybean rotation, formerly sufficient to control the corn root worm, has selected for a biotype of this pest with a life cycle timed to hatch every other year rather than every year; the pest is therefore able to remain dormant during the year of soybeans but become active in the year of corn (4).

In the case of three taxonomically different but ecologically similar root diseases of wheat, namely take-all caused by *Gaeumannomyces graminis* var. *tritici* (an ascomycete), *Pythium* root rot caused by several *Pythium* species (oomycetes), and *Rhizoctonia* root rot caused by *Rhizoctonia solani* AG 8 and *Rhizoctonia oryzae* (basidiomycetes), the potential for root infection is enhanced with direct seeding. This is because of the cooler, wetter, top few centimeters of soil (where these pathogens reside) that prevail when residue of the previous wheat crop is left on the soil surface, compared with when the residue is buried (5). Cold soil at the depth of seeding is itself stressful to young plants during seedling emergence, but in the case of wheat, the low-temperature stress predisposes the plants to greater pressure from root disease (6, 7). Fresh (unweathered) wheat straw also can serve as a source of readily available carbon and energy for *Pythium* species, but the straw itself is not toxic to young wheat plants, as was once thought (8). *Pythium* species are ubiquitous in agricultural soils, making it necessary to design experiments that separate the direct effects of crop residues and associated cold soil on the young plants from the predisposing and other effects of these variables on *Pythium* root rot.

Because of the wide host ranges of the pathogens, the use of crop rotation to manage *Pythium* and *Rhizoctonia* root rots must include a plant-free (clean fallow) break to be effective. This can also mean expense, but no income, from that field, depending on the duration of the break (5). Soil fumigation with methyl bromide has been used in Washington state as an experimental tool to reveal the high yields possible with continuous (monoculture) direct-seeded wheat and barley sequences (7, 8). However, fumigation is economical only for certain high-value horticultural crops, such as strawberries in California and tomatoes in Florida. Plant breeding has been highly effective against specialized pathogens, such as rust and mildew fungi, because of the availability of genes within the crop species and related species for resistance to these pathogens. It has been less effective

against the necrotrophic soil- and residue-borne leaf-, stem-, and influorescence-attacking pathogens and insect pests and ineffective against the nonspecialized root pathogens. Moreover, plant-breeding programs have not kept up or have even resisted the modern trends toward less or no tillage and shorter or no crop rotation by continuing to select new varieties in garden-type seed beds using 2- and 3-year crop rotations.

Whither Plant Biotechnology and Plant Genomics?

The development of crops resistant to glyphosate, namely the Round-up Ready varieties of soybeans, corn, canola, and cotton, use variations of the gene for production of 5-enolpyruvlshikimate-3-phosphate synthase, and they are resistant to European corn borer, corn root worm, and cotton boll worms using variations on the *Bt* gene from *Bacillus thuringiensis*. This development represents major advances using the new tools of biotechnology and plant genomics to address pest problems favored by intensive cropping and direct seeding. More than 60% of U.S. soybean farmers surveyed by the Purdue University-based Conservation Tillage Information Center (3) credited the availability of glyphosate-resistant varieties of soybeans for their decision to reduce or eliminate tillage on their farm. Although the insect pests of corn and cotton controlled by the *Bt* gene are problematic in both conventional and direct-seed cropping systems, pressures from these pests potentially become greater with the increased intensity of these crops within any given area. Like the rust fungi and many other specialized fungal pathogens of crops, these insect pests are now managed genetically through *Bt*-mediated host-plant resistance (9). The farm business thereby has the flexibility to manage according to market and environmental goals, without concern for crop damage caused by these insects and without having to invest in a more-expensive but less-effective pest-control technology, such as insecticides.

The new tools of biotechnology and genomics also facilitate the use of alien germplasm for resistance to plant pathogens. For example, the *RB* gene for resistance to the potato late-blight pathogen, *Phytophthora infestans*, was recently cloned from *Solanum bulbocastanum* and shown to confer resistance to all known races of *P. infestans* (10). The *RB* gene is structurally similar to the leucine-rich repeat nucleotide-binding site (LRR-NBS) family of plant genes for pathogen recognition and induction of the hypersensitive response that limits growth and reproduction of the pathogen. In addition, gene mapping and marker-assisted selection have become important tools in breeding for resistance to the residue-borne stem-, leaf-, and inflorescence-infecting fungal pathogens, typically involving genetically complex quantitative traits for resistance (more commonly partial resistance; see ref. 11). However, almost no work has been done to develop crop cultivars with genetic resistance to the unspecialized root-infecting pathogens such as *Pythium* and *Rhizoctonia* species that, because of the wide host ranges of these pathogens, will almost certainly depend on the use of transgenic resistance. Reports of transgenic resistance to *Rhizoctonia* root rot of several crops through expression of plant (12) and fungal (13) chitinases indicate some potential for genetic control of this widely distributed genus of plant pathogens. However, thus far the degree of control has been disappointingly small. Nevertheless, because of the enormous potential to increase both productivity and sustainability of food, fiber, and fuel crops globally, the concurrent trends toward more intensive cropping and less or no tillage must and will continue, with or without the help of plant biotechnology and plant genomics.

Take-All Decline: An Isolated Phenomenon or Source of Clues to the Success of Crop Monocultures?

Take-all, so named by early Australian farmers because of its ability "take all" the crop, is a root disease of wheat caused by the soil-borne ascomycete *Gaeumannomyces graminis* var. *tritici*. Unlike the wide host ranges of *Pythium* and *Rhizoctonia* species, the host range of *G. graminis* var. *tritici* is limited to wheat, barley, and closely related cool-season grasses, which is still a wide host range compared with pathogens that specialize not just in plant species but also in plant genotype within the species. Nevertheless, because of its relative inability to survive for long periods in soil without a host, almost any 2- or even 1-year break to a nonhost crop, such as a broadleaf crop or oats, can effectively control this disease (14). Yet take-all remains unquestionably among the most destructive root diseases of wheat worldwide (15), for the simple reason that markets for the rotation crops (other than corn and soybeans) are relatively small and quickly saturated compared with the global market for wheat. The result is in areas limited to cool-season rotation crops (peas, lentils, and canola), such as the U.S. Pacific Northwest, wheat or barley is commonly planted in the same fields in 2 of every 3 years or more frequently.

Some of the earliest successful high-yielding wheat monocultures were carried out in northern Europe in the late 1940s and 1950s. Take-all, being favored by the cool, moist soils of northern Europe, attracted a great deal of attention, and much effort was aimed at its control. However, observations and experimentation in both The Netherlands (16) and the United Kingdom (17) revealed, surprisingly, that take-all increased in severity at first, e.g., for the first three, four, or five consecutive crops of wheat, but then declined in severity with continued wheat (or wheat/barley) monoculture. Yields recovered, although not fully to the level achieved with crop rotation. Gerlach (16) followed disease development in reclaimed polder soils, showing that pathogen [apparently introduced into these previously noncropped (virgin) soils from nearby grasses, e.g., older established pastures] became increasingly destructive with successive wheat crops but then less destructive as the soil became microbiologically and specifically suppressive to the disease.

The development of a soil microbiotia suppressive to take-all in response to monoculture wheat in Dutch polder soils was confirmed in the U.S. Pacific Northwest for virgin desert soils brought into wheat production with irrigation, as part of the U.S. Department of Interior Columbia Basin Land Reclamation Project (18, 19). To test the hypothesis that the suppressiveness was transferable (19), soil from a field cropped each of the previous 12 years to irrigated wheat (with no evidence of take-all, although the disease was common in other fields within the area) from near Quincy, WA, in the irrigated Columbia Basin. This soil and a similar soil from an adjacent site still under its natural sage-brush vegetation were transferred to a site on a Washington State University research farm near Puyallup, WA, and mixed 15 cm deep into replicate plots ≈1.3 × 3 m in size. Wheat was then planted together with an inoculum source of the pathogen introduced into the seed furrows with the wheat seed at planting. Two other pairs of soils, representing fields in crop rotations and their corresponding uncropped sites, were included in this experiment, which was set up as a randomized complete block design with no added soil as a check.

As in the United Kingdom and The Netherlands, the soils and environment of western Washington are highly conducive to take-all, and, not surprisingly, the disease (in response to the introduced inoculum of the pathogen) was severe already in year 1 (1969/1970 crop

Fig. 2. Representative wheat plants from a field experiment in the second year of wheat monoculture showing severe take-all (left and center) or no apparent disease because of disease suppression (right) in response to the transfer of soil (0.5% wt/wt, rotovated to 15 cm depth) 2 years earlier from a wheat-monoculture field (12th year consecutive year of wheat monoculture) near Quincy, WA, in the irrigated Columbia Basin (far right). Plants with severe take-all were from plots amended with the same amount of soil from a noncropped (virgin) site adjacent to the wheat monoculture field (center) or no soil (check; far left). Take-all was uniformly severe in the first wheat crop, and take-all decline occurred uniformly throughout the experimental site in the third wheat crop, regardless of the one-time initial soil amendment (18).

year), regardless of the soil treatment. This site was then replanted in year 2 (1970/1971) with wheat only (but no additional inoculum of the pathogen), depending entirely on infected tissues of the previous wheat crop as the source of inoculum in the second year. Showing that suppressiveness to take-all is transferable, the roots were nearly disease-free, and the wheat matured normally exclusively within the four replicate plots treated with soil from the 12-year wheat monoculture field near Quincy (Fig. 2). The soil added to these plots amounted to only ≈0.5% (wt/wt). The site was replanted for the third time (1971/1972 crop year) with no further treatment; by then, take-all decline had occurred throughout the experimental site regardless of the treatment 3 years earlier.

After nearly 35 years of research since the field study at Puyallup, evidence now points clearly to a primary, if not exclusive, role of rhizosphere-inhabiting bacteria (rhizobacteria) of the taxon *Pseudomonas fluorescens* with the ability to produce the antibiotic 2-4,di-acetylphloroglucinol (DAPG) as the agent(s) responsible for take-all decline (20). The threshold populations of DAPG-producing strains of *P. fluorescens* required for take-all suppression, shown to occur naturally in the rhizosphere of wheat growing in soils that had undergone take-all decline, was log 5 cfu per g of root (21, 22). Raaijmakers *et al.* (23) showed further that the

amount of DAPG produced in the rhizosphere of wheat as a constant 0.62 ng per 10^5 cfu when populations of the DAPG-producing strain ranged between log 6 and 7.

The biosynthetic pathway for DAPG involves a highly conserved five-gene cluster (24). Based on polymorphisms for the *PhlD* gene within this cluster (25), an international effort over the past 5 years has revealed, at last count, 22 distinct genotypes of DAPG-producing *P. fluorescens* (26).

Of particular interest is evidence that the genotype(s) dominating the population of DAPG producers in any give rhizosphere is modulated, in part, by crop, length of monoculture, and geographic location of the field (27–29). McSpadden Gardner *et al.* (28) found the D genotype in the rhizosphere of corn, soybeans, or both in all 15 counties sampled in Ohio; it represented the most abundant of seven genotypes identified. On average, the D genotype was detected at populations exceeding log 3.4 cfu per g of root on 77%, 84%, and 81% of corn plants, representing 3 successive years, respectively; and 78%, 67%, and 52% of soybean plants sampled during those same 3 years, respectively.

Among the DAPG-producing genotypes associated with continuous wheat monoculture and take-all decline, the D genotype has been the dominant strain in Washington fields where take-all has declined, whereas in Dutch fields, geno-

types F and M were dominant (20). Strain Q8r1-96 is of the D genotype and, like all genotype D isolates, is a highly aggressive colonist of the wheat rhizosphere (30), which no doubt contributes to its ability to efficiently suppress take-all in fields under continuous wheat monoculture.

On the campus of North Dakota State University (Fargo, ND) where wheat and flax have been grown as monocultures in side-by-side plots for >100 years, populations of DAPG-producing pseudomonads exceeded the threshold log 5.0 cfu per g of root in the rhizospheres of both wheat and flax grown in the soils. However, 80% were approximately equal frequencies of the F and J genotypes in soil where flax had been grown in monoculture, whereas 77% were the D genotype in soil where wheat had been grown in monoculture. DAGP producers were below the level of detection (10^4 cfu per g of root) on roots grown in soil from a third adjacent plot that had been in diverse crop rotation for more than a century (27).

DAPG is one of at least six well characterized antibiotics or families of antibiotics produced by fluorescent *Pseudomonas* species worldwide (31). The other five are pyrolueteorin, pyrrolnitrin, phenazines, hydrogen cyanide, and viscosinamide. Based on the diversity of apparently crop- and location-specific strains of DAPG-producing *P. fluorescens*, it seems reasonable to infer that each of these antibiotic-producing populations of fluorescent *Pseudomonas* strains similarly includes a diversity of genetically distinct subpopulations associated with biological control of different soil-borne pathogens on different crops and/or in different geographic regions. These rhizobacteria also contribute to root defense through iron starvation of the pathogen by production of siderophores such as pyoverdin (32). Even more interestingly, rhizobacteria have been shown to suppress disease development through induction of systemic resistance (ISR) to plant pathogens (31), which overlaps biochemically with but is distinct from the pathogen-induced systemic acquired resistance. ISR depends on the jasmonic acid signaling pathway and has been described as enhanced basal resistance in plants, typically to their necrotrophic pathogens (31).

Vijayan *et al.* (33) showed that mutants of *Arabidopsis* plants either unable to accumulate jasmonic acid or insensitive to jasmonic acid were coordinately hypersusceptible to *Pythium* root rot compared with wild-type plants with their functional jasmonic acid signaling

system. *Pythium* species are among the most common soil-borne pathogens of plants worldwide. Although best known for their ability to indiscriminately cause seed decay and damping off of seedlings, these oomycetes are equally or more important for their ability to destroy the plant's fine rootlets so critical for uptake of relatively immobile mineral nutrients such as phosphorus. *Pythium* species are also easily eliminated from soil by fumigation with chloropicrin or methyl bromide, which can account for the well known increased growth response of plants to fumigation of the soil (6). So-called plant growth promotion by rhizobacteria (31) could well be a plant response to less damage from *Pythium* root rot because of antagonistic effects.

Cook *et al.* (34) suggested the absence of useful genes in wheat and wheat relatives for resistance to take-all could be due to the protection afforded by the DAPG-producing rhizobacteria enriched by wheat monoculture, thereby relieving selection pressure on the host for evolution of resistance such as has occurred with foliar pathogens. Although rhizobacteria responsible for suppression of root diseases represent another genetic resource for use in breeding crop plants for enhanced resistance to pathogens, their management through the cropping system, e.g., crop monoculture, or their introduction with seeds or other the planting material (35) currently represents the best options for maximizing their benefits.

Interdependency of Management and Breeding to Gains in Crop Productivity and Sustainability

The remarkable gains in crop productivity (but not necessarily sustainability) in the 20th century are the outcome not just of ever-higher-yielding crop varieties developed by plant breeding but also of improved management practices needed to achieve the ever-higher yield potentials of the new varieties (1). A change in management, such as an earlier or later planting date or more intensive tillage, can reduce the risk of a pest or disease until a resistant variety can be developed. Conversely, a change in management intended to increase crop productivity, e.g., addition of nitrogen, can also introduce a new hazard, e.g., lodging, so that achieving the full benefit of the changes must await the development of new varieties with the ability to withstand or avoid the hazard(s) and produce at the higher level set by that management. Similarly, achieving the full yield potential of a new variety often must await the development of new management. Although seemingly hand-in-glove, evolution of these two fundamental derivers of the gains in crop productively and sustainability locally has been more upwardly stair-step than uniform and seamless. Further, the lack of yield increases locally over years and even decades can usually be attributable to the continued use of the same old management, e.g., the same planting rate and date, crop rotation, and amount of fertilizer added to the soil, and not to the lack of new varieties. Indeed, a yield plateau can become declining yields without new varieties needed to assure resistance to the ever-evolving pathogen populations.

The use of nitrogen fertilizer, irrigation, and herbicides for cereal grains increased dramatically after World War II, but achieving the high yield potential set by these management inputs had to await the adoption or availability of hybrid corn and short-stature (dwarf) varieties of wheat and rice, with their stiffer straw. The inbred varieties of corn and tall-stature varieties of wheat and rice were incapable of producing to the potential set by these management changes. Yields were then elevated to amazing new levels but still fell short of the full yield potential set by these cropping systems. Instead, the world-record yields documented with this new combination of management and genetics starting in the 1960s were rarely or never achieved in commercial practice, largely because of new combinations of disease, pest pressures, and abiotic stresses (36). Overcoming these hazards then required further changes in management, such as the development of crop-protection chemicals, changes in crop rotations and planting dates, and, more recently, varieties with genetic resistance to the disease and pest pressures.

The great majority of evidence indicates that the yield potential of direct-seed cropping systems is even higher than that of cropping systems that use conventional tillage, because of more water available for the crop, more soil organic matter and associated nutrient cycling, and better crumb structure and associated improvements in soil aeration. Indeed, the full yield potential of direct-seed cropping systems is still largely unknown or rarely achieved because of new hazards of biotic and abiotic stresses. In the U.S. Pacific Northwest, overcoming these hazards in wheat-based direct-seed cropping systems has involved still more changes in management (37), including early and effective elimination of volunteer cereals (hosts of the root pathogens) formerly allowed to grow between the harvest of one crop and planting of the next, placement of plant nutrients and especially the relatively immobile phosphorus within easy access of diseased roots, and some soil disturbance within the seed row. However, optimization of the full package of these management practices takes experience and the right equipment, and even then, yields for wheat average only ≈80% of the potential revealed in fumigated soil (35). Achieving the full yield potential of these more-productive and -sustainable cropping systems will depend ultimately on further changes in varieties, including greater use of transgenic varieties.

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