

Meeting the challenge of disease management in perennial grain cropping systems

C.M. Cox^{1,*}, K.A. Garrett², and W.W. Bockus²

¹The Land Institute, 2440 E Water Well Road, Salina, KS 67401, USA.

²Department of Plant Pathology, 4024 Throckmorton Plant Sciences Center, Kansas State University, Manhattan, KS 66506, USA.

*Corresponding author: cmcox@landinstitute.org

Accepted 29 November 2004

Review Article

Abstract

Perennial grain production will likely present unique challenges for managing diseases that affect the productivity and longevity of crops being considered. Typical cultural practices effective at reducing soil- and residue-borne pathogens, such as annual crop rotations, delayed fall planting, and tillage, are not feasible in perennial systems. Consequently, soil- and residue-borne pathogens, and pathogens such as root colonizers and viruses that survive in live tissue, may increase in importance in a perennial grain crop. Resistance genes will undeniably be important defenses against disease. However, it is seldom, if ever, possible to incorporate within a single cultivar resistance to all existing and future important diseases. Furthermore, genes vulnerable to 'boom and bust' cycles are generally short-lived when deployed in monocultures. For these reasons, the use of mixtures of crop cultivars or species that vary in resistance functions will likely be an important strategy for managing diseases and pests of perennial grains. Burning of plant residue, a natural phenomenon in native perennial grass systems, may also be an effective disease management strategy. The successful implementation of these management tools may reduce or eliminate the risk that perennial grain crops will become pathogen refugia that affect neighboring annual plantings and the productivity of perennial plants.

Key words: perennial wheat, host diversity, mixtures, blends, polyculture, resistance, burning

Introduction: A Perennial Problem

One of the most critical issues facing the growing global human population is the maintenance of agricultural productivity¹. Cereal grains provide more than 50% of human caloric needs, but problems associated with annual grain crops, such as soil erosion and degradation of water resources, indicate that reliance on annual grain production is a fundamental problem of current agricultural practice². Successful production of perennial grains could profoundly reduce the adverse effects of agriculture^{3,4}.

Management strategies for a perennial grain cropping system may depend more on ecological principles governing natural ecosystems, hay meadows, and rangeland than those governing an annual grain crop. It will be important both to understand ecological principles and to understand the process of breeding and selecting high-yielding perennial lines. Plant pathogens will likely play an important role in the production and persistence of

perennial crops. This paper reviews current knowledge relevant to management of diseases in a perennial grain cropping system, with emphasis on genetic resistance, host diversity, and burning. Included is a discussion of the potential challenges faced and perspectives from ecology. We highlight perennial wheat (*Triticum* spp.) and related cereals, although several other perennial crops are being considered in breeding programs, such as sorghum (*Sorghum* spp.), Illinois bundle flower (*Desmanthus illinoensis*) and sunflower (*Helianthus* spp.)⁵. Many of the concepts discussed here also apply to these other perennials, since the profile of pathogens infecting them is similar.

Perennial grain production will likely give rise to new disease management challenges. Cultural practices effective at reducing disease inoculum in annual systems, such as crop rotation, delayed fall planting, and tillage, are not feasible in perennial systems. In a no-tillage system, crop residue persists at the surface and subsurface soil layers,

providing a refuge for survival of pathogens between seasons. Similarly, live roots and crowns persisting in soil can harbor pathogens that require live tissue for survival, such as viruses and root-colonizing pathogens. Observations in Kansas, USA, of perennial progenitors, such as intermediate wheatgrass (*Thinopyrum intermedium*) and sorghum, show that these plants are emerging and assimilating carbon well before their annual counterparts (see DeHaan *et al.*, this issue). This lengthening of the growing season provides more opportunities for pathogenic relationships and greater potential for affecting other nearby crops. Meeting the challenge of managing diseases and pathogen populations in a perennial grain crop is, therefore, important for grain production and stand longevity.

Conversion from Annual to Perennial: Potential Impacts on Disease

A consideration of disease epidemics likely to arise in perennial wheat production provides a useful starting point for addressing potential problems in other perennial crops. In annual wheat (*Triticum aestivum*) production, many diseases are managed in part by cultural practices that disrupt the disease cycle (e.g., tillage, rotation and delayed seeding). Such diseases may pose significant problems for perennial wheat, characterized by low disturbance and stand persistence over multiple growing seasons. Disease problems of continuous, no-tillage annual wheat, in particular, provide insight into disease challenges likely to be faced by perennial wheat. As in the case of no-till annual wheat production, soil- and residue-borne pathogens may thrive under perennial wheat production, as well as pathogens, such as root colonizers and viruses, that survive in live tissue. In addition, the ability of the pathogen to compete in the soil or on plant residue as a saprophyte must also be considered. Various pathogen characteristics, therefore, can be used as predictors for increased disease problems under perennial wheat production in the Great Plains: survivability between crops in host residue, soil, or live tissue; high saprophytic competitiveness on colonized crop residue; the ability to infect older roots; and whether or not the disease is typically managed in part through delayed planting and tillage. The presence of any of these characteristics may indicate increased disease potential (Table 1), assuming limited resistance, although one characteristic may prove to be more important than another.

Before making assumptions about disease potential, the differences in root systems between a perennial plant and an annual plant must be understood. Annual wheat roots (Fig. 1) live for a fraction of the year, with 62%⁶ to 90%⁷ of the total root mass located in the upper 0.3 m of soil. Roots of perennial relatives (Fig. 1) extend much deeper into the soil profile, have greater biomass^{8,9}, and are present throughout the year. Additionally, more complex crowns may act as a barrier to soil-borne pathogens, even in the absence of resistance genes (i.e., receptors). For example,

Mathre and Johnston¹⁰ demonstrated that movement of *Cephalosporium gramineum* was slower through roots and crown tissues of *Thinopyrum elongatum* and *T. intermedium* than those of wheat lines, and therefore, suggested that a more complex crown structure contributed to *Cephalosporium* stripe resistance in these perennial species.

Thick, healthy perennial grass stands, like those established on Conservation Reserve Program land, reduce soil erosion¹¹, restore soil nutrient levels and organic matter¹², increase soil quality¹³, and increase soil microbial activity¹³ and diversity¹⁴. The ability of soils to generally suppress soil-borne diseases is often enhanced by the addition of organic matter, the build-up of soil fertility, and certain agronomic practices such as no-till^{15,16}, all of which potentially increase soil microbial diversity and activity. Consequently, competition shifts between pathogenic, beneficial, and saprophytic organisms may compromise the dominance or fitness of those pathogenic on the host. For example, differences were found in the diversity of several microbial groups between permanent grassland and arable cropland under rotation, and the evenness of ecophysiological differing bacterial types was higher in grassland¹⁷. Further, growth of the root rot fungus *Rhizoctonia solani* AG3 was suppressed more in grassland than in arable soils. Earthworms, often more abundant in undisturbed soils¹⁴, also decrease the effects of some soil-borne diseases, including take-all (caused by *Gaeumannomyces graminis* var. *tritici*)¹⁸. Indeed, it has been suggested that indicators for soil health may be indicators of a soil's ability to suppress disease caused by root pathogens¹⁹.

Disease-suppressive soils, in which indigenous microflora effectively protect plants against soil-borne pathogens, have been described for many soil-borne pathogens. This phenomenon depends on plant species, the disease in question, soil properties, and agronomic practices. Perhaps the most thoroughly studied example of soil suppressiveness, the decline of take-all spontaneously occurs in monocultures of susceptible wheat after 4–6 or more years of continuous cropping¹⁶. The build-up of antagonistic soil microbes, with fluorescent pseudomonads specifically implicated worldwide, is associated with take-all decline. Wheat, *T. intermedium*, *T. elongatum*, and several perennial grain germplasm lines are susceptible to take-all (C. Cox *et al.*, unpublished data) and if present in a perennial wheat crop, take-all would most likely decline as well. For example, as bacterial populations change within brown patches of turfgrass infected by *G. graminis* var. *avenae*, take-all declines and susceptible species can recolonize formerly diseased areas²⁰.

The take-all pathogen is a weak competitor in communities of saprophytes in plant residue²¹. Some of the dominant grasses of the tall and short grass prairies have no resistance to take-all (C. Cox and Garrett, unpublished data), although it may be that the established microbial community in the prairie ecosystem has a suppressive effect on take-all. *Cephalosporium gramineum* produces broad-spectrum fungal antibiotics that are thought to

Table 1. Common wheat diseases of the Great Plains, and pathogen characteristics as predictors of disease potential in a perennial wheat cropping system.

Disease	Characteristic ¹					
	Survives between crops in host residue or soil?	Competes well on residue or in soil?	Affects older roots?	Survives between crops in live tissue?	Increased with early fall planting date?	Worse with reduced tillage?
Wind-borne, leaf-infecting						
Leaf rust	-	N/A	-	+	-	-
Stripe rust	-	N/A	-	+	-	-
Stem rust	-	N/A	-	+	-	-
Powdery mildew	+	+/-	-	-	-	+
Flower-infecting						
Scab	+	+/-	-	-	-	+
Bunt and loose smut	- ²	-	-	- ³	+	-
Viruses						
Wheat streak mosaic	-	N/A	-	+	+	+
Barley yellow dwarf	-	N/A	-	+	+	- ⁴
Soilborne mosaic	+	+	-	-	-	-
Soil- or residue-borne						
Tan spot	+	+/-	-	-	-	+
Septoria	+	+/-	-	-	-	+
Take-all	+	-	+	+	+	+
Cephalosporium stripe	+	+/-	-	+	+	+
Common root rot, dryland foot rot	+	+/-	+	-	+	- ⁴
Strawbreaker foot rot	+	+/-	-	-	+	- ⁴
Pythium root rot	+	+	- ⁵	-	-	+

¹ +, Pathogen or disease has the characteristic, so increased disease potential is more likely with conversion from an annual to a perennial wheat cropping system assuming limited resistance. -, Pathogen or disease does not have the characteristic, so increased disease potential is less likely with conversion from an annual to a perennial wheat cropping system. +/- refers to an intermediate response. N/A = characteristic not applicable to the disease.

² Sometimes survives in soil as spores.

³ Spores or mycelium associated with dormant seed.

⁴ Disease decreases in reduced tillage.

⁵ Infects young roots.

exclude the more aggressive saprophytes from the substrate^{22,23}. The competitive saprophytic ability of *C. gramineum* may, therefore, make it more problematic on perennial wheat than the take-all pathogen.

Above-ground organs of perennial grasses may appear similar to seedlings during fall or spring regrowth, yet there are substantial, more mature plant roots and crowns present below ground throughout the year (Fig. 1). Root pathogens such as *Pythium* and *Rhizoctonia* are classic problems in no-till systems and may also be significant on perennial

wheat seedlings, especially during the establishment stage. Juvenile roots are particularly susceptible to infection and attack at the seedling stage can be devastating for plants²⁴. Mature plants, including older perennials, can also be adversely affected by root pathogens²⁵, especially since perennial plants continually replace old roots with new feeder roots.

For wind-dispersed, host-specific foliar pathogens, such as rusts and powdery mildews, there is ample evidence that mixing resistant host genotypes with susceptible genotypes



Figure 1. An illustration of the potential difference in root architecture between annual wheat and a perennial relative of domesticated wheat. The roots on the right are from the annual winter wheat cultivar Karl 92 and the roots on the left are from *Thinopyrum intermedium*. Plants were grown outdoors in 3 m long cylinders under similar growing conditions and excavated in late June. (Photo courtesy of Scott Bontz, The Land Institute, Salina, Kansas, USA.)

effectively reduces disease severity^{26–31}. In addition, such mixtures of genotypes may increase the durability of major gene resistance^{31,32}. Since inoculum of *Puccinia* species (the rust pathogens) seldom overwinters in much of the Great Plains, conversion from annuals to perennials may not affect these diseases. However, because the survival structures (ascocarps) of powdery mildew fungi survive between crops in and on plant residue, long-term effects of pathogen persistence should be considered when managing powdery mildew under a perennial production system.

Unforeseen minor diseases may become prevalent with the introduction of new perennial germplasm. Additionally, any dramatic shift in the microclimate, due to conversion from an annual to perennial grain crop, can have a significant positive, neutral, or negative impact on pathogens and disease development³³.

It is clear that perennial grain production will present challenges for disease management. But in typical

agricultural environments, disease pressures are a reality in any crop, whether annual or perennial, and may greatly limit yield potential and management strategies. Many crops are grown successfully even though significant disease problems exist. Disease epidemics of annual wheat remain common despite decades of focused research to prevent outbreaks. Although disease reduces average annual wheat yields in Kansas by more than 13% each year³⁴, Kansas remains the leading wheat producer in the nation. Herbaceous perennials such as Kentucky bluegrass (*Poa pratensis*), switchgrass (*Panicum virgatum*), and alfalfa (*Medicago sativa*) are also important agricultural crops, despite disease and pest problems.

Resistance, Gene Deployment and Durability

Although ecological studies are, and will be, sorely needed to further examine pathogenic relationships in a perennial grain crop, development of genetic resistance to economically important diseases through plant breeding programs is necessary. Wild plants with inherently slow growth rates, such as most perennials, tend toward large investments in antiherbivore defense compared to plants with fast growth rates, such as most annuals^{35,36}. A limited number of studies have also compared annual versus perennial life histories in terms of pathogen defense. For example, in response to six maize viruses, three annual teosinte (*Zea* spp.) lines were susceptible to all of the viruses, whereas perennial diploid and tetraploid teosintes were each susceptible to only one of the six viruses³⁷. These differences in susceptibility probably developed because perennial plants have evolved in the context of longer-term exposure to pests and pathogens in natural ecosystems than have annual plants. Despite this greater exposure, perennials dominate most native landscapes and constitute roughly 80% of North America's native flora³⁸. In other words, the pressure of disease has not led to the downfall of perennials.

Wheatgrasses (*Thinopyrum* spp.), the wild relatives of modern wheat, and hybrids of wheatgrass × wheat show high levels of resistance to many common wheat diseases, including Cephalosporium stripe, wheat streak mosaic (and its wheat curl mite vector), stripe, stem and leaf rust, barley yellow dwarf, eyespot^{39–43} and tan spot (C. Cox and Garrett, unpublished data). Indeed, finding *Thinopyrum* lines highly susceptible to common cereal diseases for purposes of ecological studies has been challenging (C. Cox, personal observation).

Resistance to diseases in natural systems is often heterogeneous within plant populations and dynamically coevolves with virulence genes in the pathogen population. For example, in the Fertile Crescent where oat (*Avena* spp.) and oat crown rust diversity are high, only 30% of individuals within populations tested were resistant to oat crown rust²⁶. In populations of *Linum marginale*, an herbaceous perennial flax found abundantly in Australia,

patterns of resistance varied with patterns of virulence in the associated populations of the rust pathogen *Melampsora lini*^{44,45}. Broadly virulent pathogens dominated highly resistant host populations, whereas weakly virulent, more aggressive pathogens dominated susceptible populations. In other words, in the susceptible host populations, rust pathogen isolates had few virulence genes that could overcome specific plant defense and allow disease to occur (virulence), but were highly fit and capable of causing high disease severity on the plant genotypes they could infect (aggressiveness). Aggressiveness was most likely mediated by among-pathotype competition and favored over virulence in susceptible host populations. On the other hand, greater virulence, or the ability to infect multiple host genotypes, was favored over aggressiveness in resistant populations. Part of this explanation relies on the assumption that there is a cost to carrying extra virulence genes.

In agriculture, host-plant genetic resistance is not always available for every potential disease, and it is difficult to incorporate resistance genes that target all specific pathogen populations into a single crop cultivar. Further, genes deployed in monocultures of single cultivars may be more vulnerable to 'boom and bust' cycles. The numerous examples of defeated major gene resistance are evidence that 'selection [for pathogen virulence] is efficient in agricultural ecosystems that are based on monoculture and genetic uniformity'³². Deployment of a major resistance gene specific for a virulence gene in the pathogen population in monoculture over a large geographical area imposes a change in the selection pressure within the pathogen population. Mutant (or migrated) virulence alleles not recognized by the resistance genes are favored, thus the frequency of virulence increases over time and resistance breaks down³². The coevolutionary arms race between resistance genes in host populations and virulence genes in the corresponding pathogen populations also occurs in natural ecosystems and predates agriculture.

McDonald and Linde³² suggest four characteristics of a pathogen that pose the greatest risk for defeating resistance genes: both sexual and asexual reproduction, high potential for genotype flow, large effective population sizes, and high mutation rates. Mixtures of different crop cultivars or species, among other noteworthy methods such as gene pyramiding and gene rotation, may disrupt directional selection, so that the rate of increase of pathogen mutant alleles or genotype frequencies slows^{31,32}. However, wide-scale deployment of a single mixture comprised of only a few component genotypes could also ultimately prove to be undesirable in terms of pathogen selection pressures, major gene conservation, and effective disease control³¹.

Host Diversity and Lessons from the Ghost of Disease Past

Increased diversity at one trophic level often begets increased diversity at other levels⁴⁶. For example, an increased number of plant species in a community is

frequently correlated with an increased number of insect species⁴⁶⁻⁴⁸. Similarly, more diverse pathogen populations are found in natural ecosystems where plant diversity is high, compared to monocultures in conventional agroecosystems^{26,31,49}. Pathogen diversity even increases in mixtures of annual grains³¹. Thus, not only can perennial roots increase soil microbial diversity, as previously discussed, but increasing plant species or genotype diversity can also increase microbe and insect diversity.

The accumulation of detrimental pathogens in plant rhizospheres can affect both annuals and perennials in natural and agroecosystems. In natural ecosystems, the build-up of pathogens can profoundly affect plant community structure. At the plant population and community levels, this interaction may alter host-plant competitive abilities, facilitate existence of tolerant or non-host-plant species, and prevent domination of strong competitors⁴⁹⁻⁵³. As a result, these plant-pathogen relationships may facilitate successional processes, enhance genetic diversity and structure of host populations, and maintain plant (and pathogen) biodiversity in natural ecosystems. From the perspective of a plant pathologist working on agronomic problems, pathogen build-up seems natural in any plant stand, especially perennials. However, lessons from plant ecology suggest that the problems of genetic uniformity may become too great within a perennial cropping system. Indeed, Harper^{54,55} concluded, 'host specific pathogens appear to penalize a population that becomes dominated by a single species', and therefore, 'diversity in plant communities may reflect the failure of pure stands'. This phenomenon is often described as 'the ghost of disease past'. Mitchell et al.⁵⁶ estimated the effects of different plant species diversity levels on foliar fungal diseases in grassland plant communities, and observed that for the overwhelming majority of the diseases evaluated, decreased plant species diversity increased pathogen load. Increasing host diversity in a perennial cropping system may increase the resilience and resistance to attacks by pests and pathogens.

The ability of small-grain cultivar mixtures to substantially reduce the severity of foliar disease caused by polycyclic, specialized, wind-dispersed pathogens, such as rusts, powdery mildews and rice blast, has been well demonstrated^{26-31,57-59}. Infection by viruses may also be reduced in grass mixtures if the pathogen population is partitioned between grass types, or if vector behavior changes markedly. For example, barley yellow dwarf virus (BYDV) infects three major prairie grasses, but the dominant virus strains appear to differ among these species and also to differ from the dominant wheat strain⁶⁰. Further, aphid vectors of BYDV exhibited shorter feeding times in oat mixtures compared to oat monocultures, with associated lower rates of virus transmission⁶¹.

Additional study is needed to better understand the effects of mixtures on soil-borne, monocyclic and/or splash-dispersed pathogens. Collectively, results of these empirical studies are less consistent^{31,59,62-66}. Garrett and

Table 2. Common wheat diseases of the Great Plains and inherent characteristics of host–pathogen system as predictors of host-diversity effect for reduced disease.

Disease	Characteristic ¹			
	Shallow dispersal gradient	Small lesion size	Many pathogen generations per epidemic	Strong host specialization
Wind-borne, leaf-infecting				
Leaf rust	++	++	++	++
Stripe rust	++	+	++	++
Stem rust	++	+	++	++
Powdery mildew	+	+	++	++
Flower-infecting				
Scab	+/-	-	-	-
Bunt and loose smut	--	--	--	++
Viruses				
Wheat streak mosaic	+/-	--	-	-
Barley yellow dwarf	++	--	-	-
Soil- or residue-borne				
Soilborne mosaic	--	-	--	+/-
Tan spot	+/-	+/-	+/-	+/-
Septoria	+/- ²	+/-	+/-	+/-
Take-all	--	-	--	-
Cephalosporium stripe	--	--	--	-
Common root rot, dryland foot rot	--	+/-	-	-
Strawbreaker foot rot	-	-	-	+
Pythium root rot	--	+/- ³	+/-	--

¹ ++, Pathogen system strongly exhibits the characteristic, so a host-diversity effect of reduced disease is most likely. +, Pathogen system exhibits the characteristic, so a host-diversity effect of reduced disease is more likely. -, Pathogen weakly exhibits the characteristic, so a host-diversity effect of reduced disease is less likely. --, Pathogen system does not exhibit the characteristic, so a host-diversity effect of reduced disease is even less likely. +/-, Pathogen system moderately exhibits the characteristic.

² Dispersal gradient is initially shallow at the origin of the epidemic, but steep in subsequent cycles.

³ Lesion size is relatively small on older roots and large on young roots and seeds.

Mundt⁶⁷ suggest that the effects of host diversity depend on the life history of the pathogen and will tend to be greatest when the host genotype unit area is small, there is strong host–pathogen specialization, the pathogen’s dispersal gradient is shallow (i.e., inoculum levels drop off after relatively long distances versus a steep gradient in which inoculum levels drop off after relatively short distances), characteristic lesion sizes are small, and the number of pathogen generations over an epidemic is large. Using these criteria, diseases can be compared according to the magnitude of host diversity effect predicted (Table 2).

Wheat has a relatively small host genotype unit area—defined as the area occupied by an independent unit of host tissue of the same genotype⁶⁸—compared to sorghum, corn

and Illinois bundle flower. Wind-dispersed pathogens are often more effectively reduced in mixtures than splash-dispersed pathogens, probably due to the shallower dispersal gradients of the former. A shallower dispersal gradient tends to result in more movement of propagules away from the susceptible host plant, provided that an influx of inoculum does not saturate a field⁶⁷. In light of these assumptions, cultivar mixtures would be expected to have less effect (over one growing season) on diseases that are monocyclic, splash-dispersed and/or soil-borne, compared to highly specialized, wind-borne diseases such as leaf rust and powdery mildew.

As a test of this hypothesis, the relative effectiveness of wheat cultivar mixing for tan spot versus leaf rust was

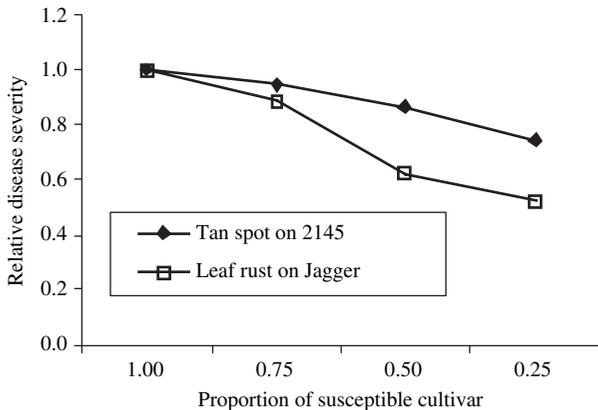


Figure 2. Relative effects of cultivar mixtures for leaf rust and tan spot on susceptible annual wheat cultivars, Jagger and 2145, respectively. This illustrates the greater effectiveness of mixtures to reduce severity of leaf rust compared to tan spot. Means combine site-years and treatments inoculated with both leaf rust and tan spot or either leaf rust alone (Jagger) or tan spot alone (2145). Relative disease severity of each mixture is expressed as a proportion of the severity in the monoculture of the susceptible cultivar. The two slopes are significantly different ($P < 0.0001$). (Reproduced from C. Cox et al., 2004⁵⁹.)

directly compared in a four site-year field experiment⁵⁹. In contrast to leaf rust, a highly specialized, wind-borne pathogen with a shallow dispersal gradient, tan spot is residue-borne with a steep dispersal gradient⁶⁹. Two annual wheat cultivars, one resistant to leaf rust and the other resistant to tan spot, were mixed in different proportions of 0.25, 0.50, 0.75 and 1.00 and inoculated with each pathogen alone and in combination. For both tan spot and leaf rust, disease severity decreased substantially on the susceptible cultivar as the proportion of that cultivar decreased in mixture. However, as predicted, mixtures were significantly more effective at reducing severities of leaf rust than tan spot (Fig. 2), supporting the above premise. In the absence of resistance genes, it may be that a better method of reducing soil- and residue-borne diseases is by increasing the diversity of soil microorganisms and saprophytes on plant residue. This would potentially facilitate competition between microbes and reduce the risk of a small number of pathogens dominating and, therefore, proliferating. In a perennial crop, this could be accomplished by increasing the diversity of perennial plants beyond two or three cultivars of the same species, so that the biological differences among plants effectively cultures diverse microbial communities. Perhaps the perennial nature of the roots may be an advantage when considering this objective¹⁴.

Although much research with mixtures focuses on annual grain hosts, we do not expect disease responses within mixtures of perennials to differ from annual mixtures within a single growing season. However, the relationship between a perennial wheat crop and its pathogens is on a different temporal scale than an annual crop. An epidemic affecting an annually planted or rotated crop is generally

short-lived and over when hosts are dead, or in less than 1 year. On the other hand, an epidemic could potentially affect a perennial crop over its lifetime, spanning many years. Depending on host-plant susceptibility and environmental conditions, this potentially increases the number of generations of pathogens that survive on host-residue over the duration time of the epidemic (which could be years) on the perennial crop compared to an annually planted crop. With more pathogen generations per epidemic, the ability of mixtures to reduce disease may increase over time (Table 2), provided the field does not become saturated with inoculum. This means that mixtures could have a greater effect on some diseases in perennial grain systems than in annual systems. This could hold especially against pathogens that have relatively few generations per year, such as many of the soil- and residue-borne and splash-dispersed pathogens. An experiment is in progress testing this hypothesis, using different biculture combinations of susceptible and resistant cool-season perennial grasses and alfalfa, and different epidemic ages (C. Cox and Garrett, unpublished data).

Determining the necessary level of diversity of cultivar or species mixtures, and the manner in which mixtures are best deployed for effectively reducing disease, is a complex task. Several factors influence the relative effectiveness of diversity, including the levels of resistance available, the environment, the disease in question, and the agronomic goals of the grower. Small increases in host diversity within annual wheat populations, such as two cultivar mixtures in which one cultivar is resistant to a disease, have substantially reduced the effects of disease⁵⁹. In Kansas, mixtures consisting of 2–3 different cultivars covered 7% of the wheat acreage in 2001, 11.5% in 2002, and 12.8% in 2003, according to the Kansas Agricultural Statistics Service. Intercropping of two or more species is also desirable if there are no cultivars available within a species resistant to a particular disease, and may be important in a perennial grain crop. Also, increased diversity within a perennial grain cropping system may be desirable for reasons that go beyond the scope of plant pathology, such as more efficient moisture and nutrient management (see Crews, this issue).

Fire

Thus far, resistance and host diversity have been suggested as disease management tools in a perennial wheat cropping system. However, increased plant diversity may not be highly effective against every disease, especially those caused by pathogens that are relatively immobile, such as residue- and soil-borne pathogens (Table 2). Burning of the tallgrass prairie in the Great Plains is common and can increase plant productivity and affect plant community structure⁷⁰. Burning is also well-known to increase seed yields of Kentucky bluegrass and other perennial grasses produced for seed. At this time, effects of fire on grain yield of wheatgrass and related perennial wheat materials is not

known, although potential increases in yield are possible by appropriate timing and frequency of burning. Limited research also suggests that burning can decrease disease potential by decreasing the amount of infested plant litter that would otherwise serve as inoculum sources. Burning decreases severity of Phoma and Ascochyta blights in alfalfa seed production fields⁷¹, stripe rust in Kentucky bluegrass seed production fields⁷², ergot in perennial ryegrass cultivation⁷², rice stem rot⁷³, rice sheath blight⁷¹ and Cephalosporium stripe of wheat⁷⁴. Studies in the tallgrass prairie of Kansas also suggest that leaf rust is less common on *Erigeron strigosus* in annually burned sites compared to unburned sites (Dendy and Garrett, Dept. of Plant Pathology, Kansas State University, personal communication, September 2004). Although burning is largely prohibited in the Pacific Northwest, where perennial wheat is also being considered^{42,75}, fire may prove a critical tool in managing diseases of perennial grain crops in the Great Plains.

In addition to burning, grazing by cattle and bison in the tallgrass prairie is also important for plant productivity and maintenance of species biodiversity⁷⁰. Rotational grazing may prove a critical tool in the productivity of perennial grain crops, and it would be worthwhile to examine its impact on disease and grain yields.

Conclusions

Sustainable disease management in perennial grain systems will require both the application of ecological principles and breeding expertise. The use of host genetic resistance to disease, host diversity, and field burning may prove critical management tools. Breeding for perennial species is a time-consuming, laborious task, and the release of suitable cultivars is still perhaps 25 years away. In the meantime, germplasm must be continually evaluated for disease resistance, among other agronomic traits, including perennial habit. Therefore, more ecological disease studies are needed, using perennial germplasm or analogues that examine resistance gene deployment in plant populations, host diversity, pathogen and microbial diversity, burning and rotational grazing. Additionally, lessons from plant ecology and the ghost of disease past must not be ignored. Understanding the cropping system as an ecosystem is important, perhaps more so when considering the management of perennial crops.

Acknowledgements. We would like to thank J. Glover (without whom this manuscript may not have been written), T. Todd, S. Dendy, J. McCarron, S. Travers, W. Jiang, W. Wilhelm and anonymous reviewers for helpful comments on the manuscript. Special thanks also go to Wes Jackson for his support and stimulating this discussion. This work was supported by a graduate fellowship from The Land Institute awarded to C.M.C.; by the National Science Foundation under Grant No. DEB-0130692; by NSF Grant No. EPS-9874732, with matching support from the State of Kansas; by NSF Grant No. EPS-0236913, with matching funds from the Kansas Technology Enterprise Corporation; by USDA Grant No. 2002-34103-11746; and by

Regional Research Funds from North Central Project NC-125. This is Kansas State Experiment Station Contribution No. 04-244-J.

References

- 1 Tilman, D. 1999. Global environmental impacts of agricultural expansion: The need for sustainable and efficient practices. *Proceedings of the National Academy of Science* 96: 5995–6000.
- 2 Jackson, W. and Jackson, L.L. 1999. Developing high seed yielding perennial polycultures as a mimic of mid-grass prairie. In E.C. Lefroy, R.J. Hobbs, M.H. O'Connor, and J.S. Pate (eds). *Agriculture as a Mimic of Natural Ecosystems*. Kluwer, Dordrecht, The Netherlands.
- 3 Moffat, A.S. 1996. Higher yielding perennials point the way to new crops. *Science* 274:1469–1470.
- 4 Pimm, S.L. 1997. In search of perennial solutions. *Nature* 389: 126–127.
- 5 Cox, T.S., Bender, M., Picone, C., Van Tassel, D.L., Holland, J.B., Brummer, E.C., Zoeller, B.E., Paterson, A.H., and Jackson, W. 2002. Breeding perennial grain crops. *Critical Reviews in Crop Science* 21:59–91.
- 6 Wilhelm, W.W., Mielke, L.N., and Fenster, C.R. 1982. Root development of winter wheat as related to tillage in western Nebraska. *Agronomy Journal* 74:85–88.
- 7 Buyanovsky, G.A. and Wagner, G.H. 1987. Carbon transfer in a winter wheat (*Triticum aestivum*) ecosystem. *Biology and Fertility of Soils* 5:76–82.
- 8 Gordon-Werner, J. and Dorffling, K. 1988. Morphological and physiological studies concerning the drought tolerance of the *Secale cereale* × *Secale montanum* cross Permontra. *Agronomy and Crop Science* 160:277–285.
- 9 Warembourg, F.R. and Estelrich, H.D. 2001. Plant phenology and soil fertility effects on below-ground carbon allocation for an annual (*Bromus madritensis*) and a perennial (*Bromus erectus*) grass species. *Soil Biology and Biochemistry* 33: 1291–1303.
- 10 Mathre, D.E. and Johnston, R.H. 1990. A crown barrier related to Cephalosporium stripe resistance in wheat relatives. *Canadian Journal of Botany* 68:1511–1514.
- 11 Lindstrom, M.J., Schumacher, T.E., and Blecha, M.L. 1994. Management considerations for returning CRP lands to crop production. *Journal of Soil and Water Conservation* 49: 420–425.
- 12 Gebhart, D.L., Johnson, H.B., Mayeux, H.S., and Polley, H.W. 1994. The CRP increases soil organic carbon. *Journal of Soil and Water Conservation* 49:488–492.
- 13 Huggins, D.R., Allen, D.L., Gardner, J.C., Karlen, D.L., Bezdicek, D.F., Rosek, M.J., Alms, M.J., Flock, M., Miller, B.S., and Staben, M.L. 1997. Enhancing carbon sequestration in CRP-managed land. In R. Lal, J.M. Kimble, R.F. Follett, and B.A. Stewart (eds). *Management of Carbon Sequestration in Soil*. CRC, Boca Raton, FL. p. 323–334.
- 14 Neher, D.A. 1995. Biological diversity in soils of agricultural and natural ecosystems. In R. Olson, C. Francis, and S. Kaffka (eds). *Exploring the Role of Diversity in Sustainable Agriculture*. American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, Madison, WI. p. 55–71.
- 15 Rovira, A.D. and Wildermuth, G.B. 1981. The nature and mechanisms of suppression. In M.J.C. Asher and P. Shipton

- (eds). *Biology and Control of Take-all*. Academic Press, London, UK. p. 385–415.
- 16 Weller, D.M., Raaijmakers, J.M., McSpadden-Gardener, B.B., and Thomashow, L.S. 2002. Microbial populations responsible for specific soil suppressiveness to plant pathogens. *Annual Review of Phytopathology* 40:309–348.
 - 17 van Elsas, J.D., Garbeva, P., and Salles, J. 2002. Effects of agronomical measures on the microbial diversity of soils as related to the suppression of soil-borne plant pathogens. *Biodegradation* 13:29–40.
 - 18 Clapperton, M.J., Lee, N.O., Binet, F., and Conner, R.L. 2001. Earthworms directly reduce the effects of take-all (*Gaeumannomyces graminis* var. *tritici*) on soft white spring wheat (*Triticum aestivum* cv. Fielder). *Soil Biology and Biochemistry* 33:1531–1538.
 - 19 van Bruggen, A.H.C. and Semenov, A.M. 2000. In search of biological indicators for soil health and disease suppression. *Applied Soil Ecology* 15:13–24.
 - 20 Sarniguet, A. and Lucas, P. 1992. Evaluation of populations of fluorescent pseudomonads related to decline of take-all patch on turfgrass. *Plant and Soil* 145:11–15.
 - 21 Asher, M.J.C. and Shipton, P.J. (eds). 1981. *Biology and Control of Take-all*. Academic Press, London, UK.
 - 22 Bruehl, G.W. and Lai, P. 1968. The probable significance of saprophytic colonization of wheat straw in the field by *Cephalosporium gramineum*. *Phytopathology* 58:464–466.
 - 23 Bruehl, G.W., Millar, R.L., and Cunfer, B. 1969. Significance of antibiotic production by *Cephalosporium gramineum* to its saprophytic survival. *Canadian Journal of Plant Science* 49: 235–246.
 - 24 Bockus, W.W. 1987. Diseases of roots, crown, and lower stems. In E.G. Heyne (ed.). *Wheat and Wheat Improvement*. American Society of Agronomy, Madison, WI. p. 510–527.
 - 25 Cook, R.J., Sitton, J.W., and Haglund, W.A. 1987. Influence of soil treatments on growth and yield of wheat and implications for control of Pythium root rot. *Phytopathology* 77: 1192–1198.
 - 26 Browning, J.A. 1974. Relevance of knowledge about natural ecosystems to development of pest management programs for agroecosystems. In *Proceedings of the First International Wheat Genetics Symposium*, Manitoba, Canada. p. 12–27.
 - 27 Wolfe, M.S. 1985. The current status and prospects of multiline cultivars and variety mixtures for disease resistance. *Annual Review of Phytopathology* 64:148–155.
 - 28 Browning, J.A. 1988. Current thinking on the use of diversity to buffer small grains against high epidemic and variable foliar pathogens: problems and future prospects. In N.W. Simmonds and S. Rajaram (eds). *Breeding Strategies for Resistance to the Rusts of Wheat*. CIMMYT, Mexico, D.F. p. 76–90.
 - 29 McDonald, B.A., Allard, R.W., and Webster, R.K. 1988. Responses of two-, three-, and four-component barley mixtures to a variable pathogen population. *Crop Science* 28:447–452.
 - 30 Mahmood, T., Marshall, D., and McDaniel, M.E. 1991. Effect of winter wheat cultivar mixtures on leaf rust severity and grain yield. *Phytopathology* 81:470–474.
 - 31 Mundt, C.C. 2002. Use of multiline cultivars and cultivar mixtures for disease management. *Annual Review of Phytopathology* 40:381–410.
 - 32 McDonald, B.A. and Linde, C. 2002. Pathogen evolution genetics, evolutionary potential, and durable resistance. *Annual Review of Phytopathology* 40:349–379.
 - 33 Bockus, W.W. and Shroyer, J.P. 1998. The impact of reduced tillage on soilborne plant pathogens. *Annual Review of Phytopathology* 38:485–500.
 - 34 Bockus, W.W., Appel, J.A., Bowden, R.L., Fritz, A.K., Gill, B.S., Martin, T.J., Sears, R.G., Seifers, D.L., Brown-Guedira, G.L., and Eversmeyer, M.G. 2001. Success stories: breeding for wheat disease resistance in Kansas. *Plant Disease* 85: 453–461.
 - 35 Coley, P.D., Bryant, J.P., and Chapin, F.S. III. 1985. Resource availability and plant antiherbivore defense. *Science* 230: 895–899.
 - 36 Bazzaz, F.A., Chiariello, N.R., Coley, P.D., and Pitelka, L.F. 1987. Allocating resources to reproduction and defense. *Bioscience* 37:58–67.
 - 37 Nault, L.R., Gordon, D.T., Damsteegt, V.D., and Iltis, H.H. 1982. Response of annual and perennial teosintes (*Zea*) to six maize viruses. *Plant Disease* 66:61–62.
 - 38 Hart, R. 1977. Why are biennials so few? *The American Naturalist* 111:792–799.
 - 39 Jones, S.S., Murray, T.D., and Allan, R.E. 1995. Use of alien genes for the development of disease resistance in wheat. *Annual Review of Phytopathology* 33:429–443.
 - 40 Friebe, B., Gill, K.S., Tuleen, N.A., and Gill, B.S. 1996. Transfer of wheat streak mosaic virus resistance from *Agropyron intermedium* into wheat. *Crop Science* 36:857–861.
 - 41 Juahar, P.P. and Peterson, T.S. 1996. *Thinopyron* and *Lophopyrum* as sources of genes for wheat improvement. *Cereal Research Communications* 24:15–21.
 - 42 Cox, C.M., Murray, T.D., and Jones, S.S. 2002. Perennial wheat germplasm lines resistant to eyespot, *Cephalosporium* stripe, and wheat streak mosaic. *Plant Disease* 86:1043–1048.
 - 43 Cox, C., Bockus, W., Garrett, K., Cox, T.S., and Peters, T. 2004. Reaction of selected perennial grass accessions to barley yellow dwarf, 2003. *Biological and Cultural Tests for Control of Plant Diseases* Vol. 19. Published online at www.apsnet.org/online/BCtests/ (verified 18 January 2005).
 - 44 Burdon, J.J. and Thompson, J.N. 1995. Changed patterns of resistance in a population of *Linum marginale* attacked by the rust pathogen *Melampsora lini*. *Journal of Ecology* 83:199–206.
 - 45 Thrall, P.H. and Burdon, J.J. 2003. Evolution of virulence in a plant host–pathogen metapopulation. *Science* 299:1735–1737.
 - 46 Armbrrecht, I., Perfecto, I., and Vandermeer, J. 2004. Enigmatic biodiversity correlations: ant diversity responds to diverse resources. *Science* 304:284–286.
 - 47 Murdoch, M.W., Evans, F.C., and Peterson, C.H. 1972. Diversity and pattern in plants and insects. *Ecology* 53: 819–829.
 - 48 Andow, D.A. 1991. Vegetational diversity and arthropod population response. *Annual Review of Entomology* 36:561–586.
 - 49 Gilbert, G.S. 2002. Evolutionary ecology of plant diseases in natural ecosystems. *Annual Review of Phytopathology* 40: 13–43.
 - 50 Dinoor, A. and Eshed, N. 1984. The role and importance of pathogens in natural plant communities. *Annual Review of Phytopathology* 22:443–466.
 - 51 Bever, J.D. 1994. Feedback between plants and their soil communities in an old field community. *Ecology* 75: 1965–1977.
 - 52 Mills, K.E. and Bever, J.D. 1998. Maintenance of diversity within plant communities: soil pathogens as agents of negative feedback. *Ecology* 79:1595–1601.

- 53 Holah, J. and Alexander, H.M. 1999. Soil pathogenic fungi have the potential to affect the coexistence of two tallgrass prairie species. *Journal of Ecology* 87:598–608.
- 54 Harper, J.L. 1977. *Population Biology of Plants*. Academic Press, London, UK.
- 55 Harper, J.L. 1990. Pests, pathogens, and plant communities: an introduction. In J.J. Burdon and S.R. Leather (eds). *Pests, Pathogens, and Plant Communities*. Blackwell Scientific Publications, Oxford, UK. p. 3–14.
- 56 Mitchell, C.E., Tilman, D., and Groth, J.V. 2002. Effects of grassland plant species diversity, abundance, and composition on foliar fungal disease. *Ecology* 83:1713–1726.
- 57 Garrett, K.A. and Mundt, C.C. 2000. Effects of planting density and cultivar mixture composition on stripe rust severity in wheat: an analysis accounting for limits to the replication of controls. *Phytopathology* 90:1313–1321.
- 58 Zhu, Y., Hairu, C., Fan, J., Wang, Y., Li, Y., Chen, J., Fan, J., Yang, S., Hu, L., Leung, H., Mew, T.W., Teng, P.S., Wang, Z., and Mundt, C.C. 2000. Genetic diversity and disease control in rice. *Nature* 406:718–722.
- 59 Cox, C.M., Garrett, K.A., Bowden, R.L., Fritz, A.K., Dendy, S.P., and Heer, W.F. 2004. Cultivar mixtures for the simultaneous management of multiple diseases: tan spot and leaf rust of wheat. *Phytopathology* 94:961–969.
- 60 Garrett, K.A., Dendy, S.P., Power, A.G., Blaisdell, G.K., Alexander, H.A., and McCarron, J.K. 2004. Barley yellow dwarf disease in natural populations of dominant tallgrass prairie species in Kansas. *Plant Disease* 88:574.
- 61 Power, A.G. 1999. Virus spread and vector dynamics in genetically diverse plant populations. *Ecology* 72:232–241.
- 62 Vilich-Meller, V. 1992. *Pseudocercospora herpotrichoides*, *Fusarium* spp. and *Rhizoctonia cerealis* stem rot in pure stands and interspecific mixtures of cereals. *Crop Protection* 11: 45–50.
- 63 Mundt, C.C., Brophy, L.S., and Schmitt, M.S. 1995. Disease severity and yield of pure-line wheat cultivars and mixtures in the presence of eyespot, yellow rust, and their combination. *Plant Pathology* 44:173–182.
- 64 Halloin, J.M. and Johnson, D.J. 2000. Reduction of sugarbeet losses from *Rhizoctonia* crown and root rot by use of mixtures of resistant and susceptible varieties. *Phytopathology* 90:S33 (abstract).
- 65 Hariri, D., Fouchard, M., and Prud'homme, H. 2001. Incidence of soil-borne wheat mosaic virus in mixtures of susceptible and resistant wheat cultivars. *European Journal of Plant Pathology* 107:625–631.
- 66 Cowger, C. and Mundt, C.C. 2002. Effects of wheat cultivar mixtures on epidemic progression of *Septoria tritici* blotch and pathogenicity of *Mycosphaerella graminicola*. *Phytopathology* 92:617–623.
- 67 Garrett, K.A. and Mundt, C.C. 1999. Epidemiology in mixed host populations. *Phytopathology* 89:984–990.
- 68 Mundt, C.C. and Browning, J.A. 1985. Development of crown rust epidemics in genetically diverse oat populations: effect of genotype unit area. *Phytopathology* 75:607–610.
- 69 Sone, J., Bockus, W.W., and Claassen, M.M. 1994. Gradients of tan spot of winter wheat from a small area source of *Pyrenophora tritici-repentis*. *Plant Disease* 78:622–627.
- 70 Knapp, A.K., Briggs, J.M., Hartnett, D.C., and Collins, S.L. (eds). 1998. *Grassland Dynamics: Long-term Ecological Research in Tallgrass Prairie*. Oxford University Press, New York.
- 71 Hardison, J.R. 1976. Fire and flame for plant disease control. *Annual Review of Phytopathology* 14:355–380.
- 72 Hardison, J.R. 1963. Commercial control of *Puccinia striiformis* and other rusts in seed crops of *Poa pratensis* by nickel fungicides. *Phytopathology* 53:209–216.
- 73 Bockus, W.W., Webster, R.K., Wick, C.M., and Jackson, L.F. 1979. Rice residue disposal influences overwintering inoculum level of *Sclerotium oryzae* and stem rot severity. *Phytopathology* 69:862–865.
- 74 Bockus, W.W., O'Conner, J.P., and Raymond, P.J. 1983. Effect of residue management methods on incidence of *Cephalosporium* stripe under continuous winter wheat production. *Plant Disease* 67:1323–1324.
- 75 Scheinost, P.L., Lammer, D.L., Cai, X., Murray, T.D., and Jones, S.S. 2001. Perennial wheat: The development of a sustainable cropping system for the U.S. Pacific Northwest. *American Journal of Alternative Agriculture* 16:147–151.