

Applied Biodiversity Science: Managing Emerging Diseases in Agriculture and Linked Natural Systems Using Ecological Principles

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Summary

Pathogen reproduction tends to be host-frequency dependent, so that disease may be more problematic when particular crop species or genotypes are very common. Nonetheless, production agriculture is dominated by extensive monocultures. This is due partly to artifacts of agricultural policy and decision-making, but partly also to the real challenges of understanding and manipulating the ecological genomics of a single crop genotype, not to mention multiple species and genotypes. So there are trade-offs in investing agricultural research in many versus only a few agricultural species. Agricultural diseases may emerge or re-emerge for a number of reasons, including new pathogen introductions, new adaptation of pathogens to previously effective resistance genes, new types of host homogeneity (such as the widespread deployment of Texas male sterile cytoplasm in maize), trading policies that increase the economic impact of uncommon infections, and changes in the abiotic environment. Technological abilities in ecological genomics that are needed to support management of emerging and long-term disease include the ability to manipulate disease resistance genes in crops, the ability to devise crop plant communities at multiple spatial scales that are optimal for a range of agronomic traits, the ability to manipulate microbial communities for disease suppressive characteristics, and the ability to minimize undesired impacts on ecosystems surrounding agricultural systems. The construction of crop variety mixtures is an example of a technology that draws heavily on ecological ideas

and has also contributed greatly to our understanding of disease ecology through experiments examining the effects of patterns of host variability on disease through time and space. New forms of agricultural systems, such as perennial grains, may also offer environmental benefits such as reduced erosion and nutrient leaching, but will also challenge ecological genomics to provide effective methods of disease management since pathogens may more easily accumulate in long-term agricultural stands. While agricultural systems have typically grown less diverse over the past century, advances in ecological genomics are likely to make it feasible for systems to incorporate higher levels of diversity in the future as agricultural scientists are better able to influence and manage complex agricultural communities for reduced disease.

Introduction

Reproduction in plant pathogens tends to be host-frequency dependent and many pathogens are specific to one or a few crop species or genotypes. As a result, when susceptible genotypes of a particular species are present at higher frequency, covering a higher proportion of agricultural land, losses to disease for that species will tend to be higher (Garrett and Mundt 1999). Also, greater crop host abundance may lead to more rapid adaptation of pathogen populations to resistance genes so that the genes are useful for shorter periods of time (McDonald and Linde 2002). Yet a small number of species and genotypes dominate agricultural production (Strange and Scott 2005). It's not that careful evaluation has led agricultural scientists to the conclusion that the best human strategy is to deploy only a relatively small number of agricultural species and varieties. Rather, there are many factors that together lead to lower diversity in agricultural plant communities (Table 21.1). At each scale of decision-

making there are economic and political factors that push agriculture toward lower diversity, whether or not lower diversity is the best long-term strategy.

Decision makers	Forms of choices	Pressures away from agricultural diversity
Policy makers	What farming systems to subsidize through Farm bills	Lobbyists representing producers of major crop species are strongest
Agribusiness administrators	What crop varieties, biocontrol agents, and chemicals to produce and offer for sale	Specialization in particular crop species may be most profitable in the short run
Public research and extension scientists	What crop species to support with research and breeding programs	Researchers typically hired to specialize in one or two crop species
Farmers	Which crop species and varieties to grow	Limited availability of crop species with needed varietal and strategic development
Food processors	Which crop species and varieties to purchase	Specialization in particular crop species may be most profitable in the short run
Consumers	Which crop species and varieties to consume	Limited knowledge about and cultural support for other options

Table 21.1

Any of the strategies for managing diseases proposed by other authors in this book might also be usefully applied in some agricultural contexts. But, in contrast to the management of diseases of humans and natural systems, agricultural genotypes and individuals can, in theory, be completely replaced in order to increase disease resistance, with the main ethical concern being preservation of traditional varieties. Thus, agricultural scientists have emphasized manipulating

the genetic composition of agricultural species for disease management, often trying to perfect a single crop genotype. Improving even a single crop species has, in fact, often been a substantial challenge.

Ecologists have long been intrigued by the relative fitness of specialist and generalist organisms and the question of how to partition agricultural research effort can be framed similarly: are agricultural specialists or agricultural generalists better adapted? (Or, since agriculture is embedded in a complex economic system that requires the cooperation of large numbers of people, the question might also be posed as whether agricultural societies are better off as generalists or specialists.) Many agricultural specialists work with only a single crop species. Investing a great deal of effort in a single agricultural species makes it possible to understand all the major pathogens of the species fairly well and makes it easier to develop more or less effective disease resistance and other strategies for managing diseases. By contrast, an agricultural generalist might develop many crop types, though each type might be less modified and characterized than would otherwise have been possible. These decisions could be viewed through the lens of economic portfolios, but the typical approach of agricultural researchers might more aptly be termed “insider trading” in that, rather than simply observing and predicting the characteristics of crop genotypes and systems, crop genotypes are directly manipulated in ways that may make their performance easier to predict. And the process of gaining knowledge can, itself, be accelerated, so that more resources are available or the same resources can be used to produce more information. For example, genetic markers can now be used to rapidly screen seedling trees to determine whether they have disease resistance genes that are only expressed in adults (Collard et al. 2005).

A goal of this chapter is to demonstrate both how agricultural research and agricultural systems have contributed to disease ecology and how new insights into community ecology could greatly benefit agricultural disease management. Agricultural plant pathology has pioneered the study of the effects of biological diversity on disease ecology and agricultural systems. Though production agriculture is often characterized by strikingly low biological diversity, agriculture offers excellent model systems for studying the effects of biodiversity on ecological processes, since agricultural pathogens are relatively well-understood and techniques for handling them in studies of spatial and temporal diversity have been developed. Agricultural research is also making extensive contributions to the field of ecological genomics, including characterizations of how plant and pathogen genomes and gene expression influence the community ecology of host-pathogen interactions (Garrett et al. 2006b). Here we discuss forms of human technology available for managing disease, how agricultural homogeneity and other factors may contribute to the emergence of disease, how crop diversity can be manipulated to manage disease, how the composition of soil microbial communities may be manipulated to suppress disease, and the effects of agricultural adaptations to disease on surrounding systems. We emphasize plant-based agricultural systems, which are most readily manipulated through breeding programs and management strategies.

Human agricultural technology and information base

Human agriculture differs from, for example, the fungus gardening of leaf-cutter ants in the huge role of intentional information accumulation and transfer. This information takes both genetic forms, such as improved varieties, and strategic (memetic) forms, such as strategies for reducing inoculum loads. Even ant agriculturalists may distribute biocontrol agents (Currie et al. 1999), thus transmitting genetic information for disease management.

Components of current human technological ability include the ability to manipulate genetic disease resistance, to manipulate non-pathogen microbial communities to enhance disease-suppressiveness of soils (discussed more below), to manipulate acquired and induced disease resistance (through chemical agents or microbial communities), to develop pesticides and biocontrol agents (Fravel 2005), to develop cultural practices such as sanitation (removal of diseased tissues) to reduce inoculum levels, and to develop uses of crop biodiversity such as rotation schemes, intercropping, and variety mixtures (discussed more below). Boudreau and Mundt (1997) have reviewed the principles of many disease management practices that have an ecological basis, including modifications to plant density and microclimate. Some of these technologies are currently marginal and all can be improved upon through better understanding of community ecology. Genetic engineering is a new tool that can potentially bring in forms of genetic information that are completely new to crop systems.

Information is a particular challenge for agricultural disease management in developing countries. Loss of traditional information, in traditional varieties and land races, wild crop relatives (which may be important sources of resistance genes for breeding programs), and traditional management methods, is a common risk (e.g., Hijmans et al. 2000). Useful information is particularly needed for orphan crops (Nelson et al. 2004), crops such as finger millet which may be of particular important to resource-poor farmers but in which little recent genetic or strategic investment has been made.

Information requirements for good management are even greater at the interface between agricultural and natural (or unmanaged) systems. Some native systems, like tallgrass prairie, do require management choices in human landscapes about factors such as burning frequency. These choices could be adjusted to take into account effects on adjacent agricultural systems if,

for example, more frequent burning reduced pathogen emigration to agricultural fields from prairie, as long as such decisions did not affect the integrity of the natural system. Conversely, agricultural systems should be managed to minimize spread of pathogens to natural systems. This can be challenging, even for well-publicized diseases such as sudden oak death, which has been widely distributed via nursery stock (Rizzo et al. 2005). Knowledge about the nature of exchanges of plant pathogens between managed and unmanaged systems is generally rare.

Causes of emergence, or re-emergence, of agricultural diseases

Agricultural diseases may emerge through several well-known, though not necessarily easily predictable, mechanisms. Exotic invasive pathogens may be introduced, such as the introduction of the soybean rust fungus to the US in 2004, probably via a hurricane (Stokstad 2004). Familiar pathogens may re-emerge in the classic boom and bust cycle that often characterizes deployment of major resistance genes in agriculture, with analogies in co-evolution in natural systems but with the added potential for human strategy to delay evolution of pathogens that can overcome resistance (Clay this text, Clay and Kover 1996, Leach et al. 2001). New forms of host population heterogeneity may unexpectedly support rapid pathogen reproduction. For example, Texas male sterile cytoplasm was widely used in US maize breeding programs and had become common throughout US maize varieties in the early 1970s. This cytoplasm surprisingly conferred susceptibility to a new form of the southern corn leaf blight pathogen, causing widespread losses in maize production (Ullstrup 1972). Trading policies can “produce” emergent diseases even when yield losses are minimal. For example, though Karnal bunt is a minor wheat disease, many countries refuse wheat imports from regions where the disease is present, so the introduction of this pathogen into new areas has important economic

impacts (Rush et al. 2005). Changes in the abiotic environment may also be associated with emergence of diseases (Garrett et al. 2006a). In an intriguing study of dried wheat specimens sampled across 160 years, Bearchell et al. (2005) found that the ratio of abundance of two wheat pathogens was closely correlated with environmental SO₂ levels.

Agricultural diversity for disease management

Agricultural biodiversity can have important effects on diseases at multiple scales. Within a field, the use of crop variety mixtures or intercropping can be used to reduce disease. Diverse landscapes of agricultural and natural systems are also assembled, though with less intentionality, by communities of land managers. On a larger scale, a mixture of agricultural and unmanaged fields have the potential to dilute available host tissue for specific pathogens or provide additional hosts and “green bridges” through time and space for more host-generalist pathogens

Mitchell et al. (2002) demonstrated that decreased plant species diversity in grassland plant communities increased pathogen load for the overwhelming majority of foliar fungal diseases evaluated. Indeed, Harper (1977, 1990) 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.”

The effects of diversity in nature are often multilateral. Increased diversity at one trophic level often results in increased diversity at other levels (Armbrecht et al. 2004). For example, an increased number of plant species in a community is frequently correlated with an increased number of insect species (Murdoch et al. 1972, Andow 1991, Armbrecht et al. 2004). More diverse pathogen populations or communities are found in natural ecosystems where plant

diversity is high compared to monocultures in conventional agroecosystems (Browning 1974, Gilbert 2002, Mundt 2002).

In an agricultural field, perhaps the simplest way we can increase plant diversity is through the mixing of different cultivated varieties (cultivars) within a crop species. Mixtures of at least two crop cultivars increases the genetic diversity and has shown to be effective at reducing disease and pest severity, increasing yield stabilities, and strengthening resilience of the crop to physiological stresses (e.g., Power 1999, Bowden et al. 2001, Mundt 2002, Cox et al. 2004). Kansas wheat farmers are increasingly planting seed blends typically composed of three cultivars (Bowden et al. 2001). According to the Kansas Agricultural Statistics Service, cultivar mixtures currently cover 15.2% of the wheat acreage in Kansas, USA, covering more land than any single unblended wheat cultivar other than the extremely popular wheat cultivar Jagger. Wheat mixtures are also commonly grown in the Pacific Northwest, USA (Mundt 2002). It makes sense to decrease the dependence on one cultivar, since even a “superior” cultivar has its flaws. Combining cultivars that have complementary characteristics reduces risks of crop failure and increases stability.

An example of striking success of cultivar mixtures is the use of mixtures of high-value rice varieties that are susceptible to the disease rice blast with lower-value resistant varieties (Zhu et al. 2000). Use of this strategy has dramatically reduced fungicide use through a large area of China. The success of this system for disease management may be due in part to the unusually large scale at which it is deployed, since the success of smaller scale mixtures may be reduced if high levels of inoculum are supplied from adjacent plots or fields (Garrett et al. 2001).

Although mixture effectiveness against residue- and soilborne diseases remains less predictable, there is little doubt that mixtures of small grains can substantially reduce the severity

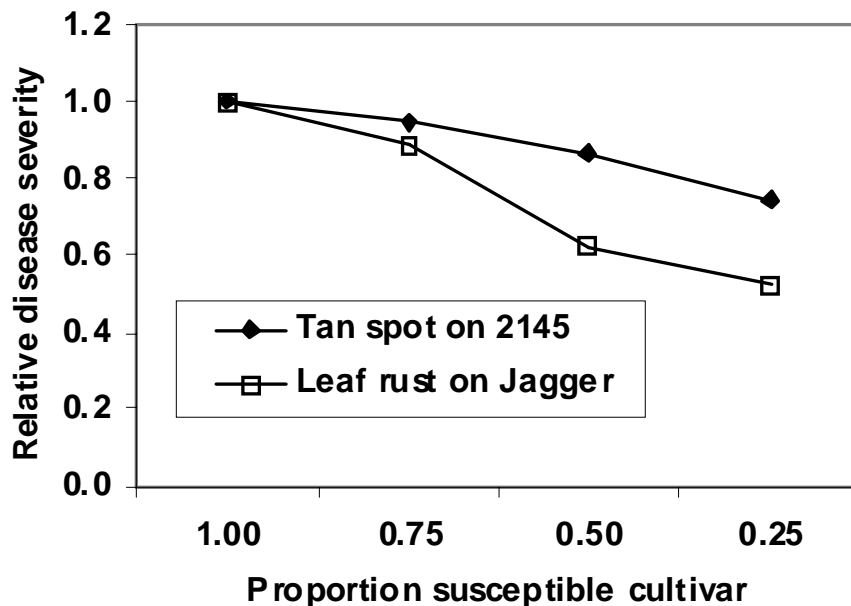
of foliar diseases caused by polycyclic, specialized, wind-dispersed pathogens, such as those causing rusts, powdery mildews, and rice blast (Browning 1974, Wolfe 1985, Browning 1988, McDonald et al. 1988, Mahmood et al. 1991, Garrett and Mundt 2000, Mundt 2002, Cox et al. 2004). Infection by viruses may also be reduced in grass mixtures if the pathogen population is partitioned between grass types or vector behavior markedly changes. 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 virus strain (Garrett et al. 2004). Further, aphid vectors of BYDV exhibited shorter feeding times in oat mixtures compared to oat monocultures, with associated lower rates of virus transmission (Power 1999). Some of the mechanisms proposed for reduced disease severity include dilution of inoculum due to the wider spatial distance between susceptible genotypes (Burdon and Chilvers 1977, Chin and Wolfe 1984, Wolfe 1985), induced resistance (Lannou et al. 1995), and compensation by the resistant cultivar through increased tiller number (Finckh and Mundt 1992).

Mixture effectiveness largely depends on the plant host and life history of the pathogen. Garrett and Mundt (1999) suggest that the effects of host diversity will tend to be greatest when the host genotype unit area is small (defined as the area occupied by an independent unit of host tissue of the same genotype (Mundt and Browning 1985)), 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 the course of an epidemic is large (i.e., several cycles of inoculum is produced). Using these criteria diseases can be compared according to the magnitude of host diversity effect predicted (Garrett and Mundt 1999, Cox et al. 2004, Cox et al. 2005a).

As a test of this hypothesis, Cox et al. (2004) directly compared the relative effectiveness of wheat cultivar mixing for two wheat diseases, tan spot and leaf rust, in a field experiment over two growing seasons at two different locations in Kansas. In contrast to leaf rust, caused by a highly specialized, polycyclic, wind-borne pathogen with a shallow dispersal gradient, the tan spot pathogen survives in plant residue and has a steep dispersal gradient (Sone et al. 1994). Two annual wheat cultivars, one susceptible to leaf rust (Jagger) and the other susceptible to tan spot (2145), were mixed in different proportions 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 ($P < 0.0001$) more effective at reducing the severity of leaf rust compared to tan spot (Fig. 21.1, reproduced from Cox et al. 2004).

Determining the necessary level of plant diversity required (Main 1999) and the manner in which mixtures are best deployed for effectively reducing disease is a complex task. Small

Fig. 21.1



increases in host diversity within annual wheat populations, such as two cultivar mixtures in which one cultivar is resistant to disease, have substantially reduced disease severity (e.g., Cox et al. 2004). Even though these systems are much simpler than most natural plant communities, there are still many complicated competitive interactions and host-microbe interactions that need to be understood to optimize use of agricultural diversity. For example, wheat mixtures developed to decrease stripe rust severity were more effective at intermediate than at higher or lower planting densities (Garrett and Mundt 2000), though there is no clear reason for this result. Higher levels of diversity, such as polycultures of different plant species, may be also desirable for reasons that go beyond the scope of plant pathology, such as more efficient moisture and nutrient management, especially for perennial crops (Main 1999, Crews 2005).

Diverse landscapes of agricultural and natural systems are also assembled, though with less intentionality, by communities of land managers. The spread of pathogens between these systems has received little attention because of the difficulty in conducting such large studies. Barley yellow dwarf virus is one pathogen that moves between agricultural and natural systems such as tallgrass prairie (Garrett et al. 2004); invasive grasses play a role in increasing its abundance and so spill-over effects on other species (Malmstrom et al. 2005). Invasive plant species may also impact agricultural epidemics. For example, kudzu may play an important role as an additional host in the new epidemic of soybean rust in the USA. The combination of widespread soybean plantings and invasive kudzu stands may also have significant effects on native legumes susceptible to the soybean rust fungus.

Enhancing Soil Microbial Communities to Suppress Disease

Definitions of biological control range from strict to inclusive. For the most conservative definition, the introduction of one or a few organisms to control a targeted plant pathogen, commercial success is still a challenge (Weller 1988, Fravel 2005). As an anonymous observer has put it, “it’s like releasing poodles on the Serengeti”. Perhaps a more enlightened ecological approach relies not on a single or a few introduced antagonists for disease suppression, but rather on enhancing the resident soil microbial community (Mazzola 2004).

Disease suppressive soils in which indigenous microflora collectively protect plants against soilborne pathogens have been described for many soilborne pathogens (reviewed in Weller et al. 2002, Garbeva et al. 2004, Mazzola 2004). General suppression refers to the total soil microbial biomass which limits the fitness of a plant pathogen through competition for resources or through more direct forms of antagonism (Weller et al. 2002). Suppression of this type is often enhanced by practices that increase soil microbial activity and diversity, such as the addition of organic amendments, crop rotation, cover crops, organic farming, reduction of or abstinence from pesticides, and the buildup of soil fertility (Weller et al. 2002, Garbeva et al. 2004, Mazzola 2004). Indeed, indicators for soil health may be indicators of a soil’s ability to suppress disease caused by soilborne pathogens (van Bruggen and Semenov 2000).

Plant type is also one of the major determinants of microbial community structure in soil (Garbeva et al. 2004). Plant species and genotypes culture microflora differentially within their rhizospheres and surrounding soil (Grayston et al. 1998, Kaiser et al. 2001, Berg et al. 2002, da Mota et al. 2002, Mazzola and Gu 2002). Monocultures of certain crops and cultivars have been indicated as building up soil suppressiveness either to the continuing crop over time (e.g., take-all

disease of wheat (Weller et al. 2002)) or to the following crop as part of a rotation (Mazzola and Gu 2000, 2002).

Diversity at one trophic level often results in diversity at other levels. For example, higher numbers and greater complexity of antagonist isolates against the soilborne pathogen *Rhizoctonia solani* AG 3 were found in species-rich permanent grassland compared to arable land under rotation or monoculture of maize (van Elsas et al. 2002). Moreover, higher densities of particular antibiotic producing genes were detected in the grasslands, whereas these genes were present at low densities or absent from the arable land planted to annuals.

Effects of agriculture on other systems and the challenge of developing perennial agriculture

Because of the unique degree of control humans potentially have over their food web (Cohen, this book), the effects of diseases on agroecosystems include their effects on human decision-making. Decisions about management often involve trade-offs: use of minimum tillage systems, and even more dramatically, perennial systems, reduces erosion but tends to increase disease risks for pathogens that survive in senesced plant material (Bockus and Shroyer 1998, Cox et al. 2005a). The common use of annuals in agriculture has resulted in increased erosion and potential for movement of nitrogen and other agricultural inputs to neighboring natural systems.

Much of the ongoing degradation of 15 of the 24 ecosystem services examined in the United Nations-sponsored *Millennium Ecosystem Assessment* (MEA), in particular sudden changes in water quality, creation of “dead zones” along the coasts, and shifts in regional climate, are linked to agriculture. The MEA report has labeled agriculture the “largest threat to biodiversity and ecosystem function of any single human activity”. Because of the seamlessness

of borders between natural and agricultural ecosystems, conservation efforts that ignore agriculture will lack impact.

The development of herbaceous perennial grains for human consumption would reduce the agricultural impacts outlined in the MEA report. Crop species currently being developed include wheat, rice, corn, sorghum, sunflower (oil crops), and legumes (Moffat 1996, Pimm 1997, Glover 2005). Although decidedly controversial and still in the toddler stage, the development of perennial grains suitable for agriculture is well underway and prospects are excellent (Scheinost 2001, Cox et al. 2002ab, DeHaan 2005). The challenges of and potential for disease management of perennial grain crops were reviewed by Cox et al. (2005a).

A limited number of studies have compared annual vs. perennial life histories in terms of pathogen defense. In response to six maize viruses, three annual teosinte (*Zea*) lines were susceptible to all of the viruses, whereas perennial diploid and tetraploid teosintes were each susceptible to only one of the six viruses (Nault et al. 1982). Wheatgrasses (*Thinopyrum* spp.), the perennial relatives of modern wheat (*Triticum aestivum*), and perennial hybrids of wheatgrass x wheat show high levels of resistance to many common wheat diseases, including Cephalosporium stripe, wheat streak mosaic (and its wheat curl mite vector), stripe and leaf rust, barley yellow dwarf, eyespot (Jones et al. 1995, Friebe et al. 1996, Juahar and Peterson 1996, Cox et al. 2002a), and tan spot (Cox et al. 2005b). 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 flora (Hart 1977).

Conclusions

Changes in current policies could support management of disease in agriculture. Artificial incentives could be removed from farm policies that support lower agricultural diversity. Interestingly, current political pressures for reduced trade protectionism may act to reduce farm subsidies that support production of only a small number of specific crop species. Some research in agriculture should be directed back reflectively to include the development of theory about how best to allocate resources for agricultural research. While a great deal of research effort is invested in understanding and manipulating the genomes of a small number of crop species, more investment is needed in understanding the broader context of optimal crop plant communities and microbial communities for disease management. A more diverse agricultural system is likely to be more stable in the face of new or newly important diseases.

Ecological theory, including ecological genomics, can contribute greatly to the development of better agricultural systems. A new area of ecology could focus on how to adapt theory in community ecology to incorporate the role of human decision-making about the use of genetic and strategic information for disease management. Agroecology would benefit from an increased ability to predict the outcomes of interactions between and among plants, microbes, and pathogen vectors. Ecological genomics could contribute a better understanding of the genetic basis of these interactions so that better crop mixtures can be developed, for disease management as well as other desirable outcomes. In microbial ecology, better theory is needed for the prediction and manipulation of microbial interactions to facilitate soils that inhibit disease.

We close this discussion with two forms of technology optimism, as illustrated in Figure 21.2. First, there is continuing great potential for humans to develop technological abilities that

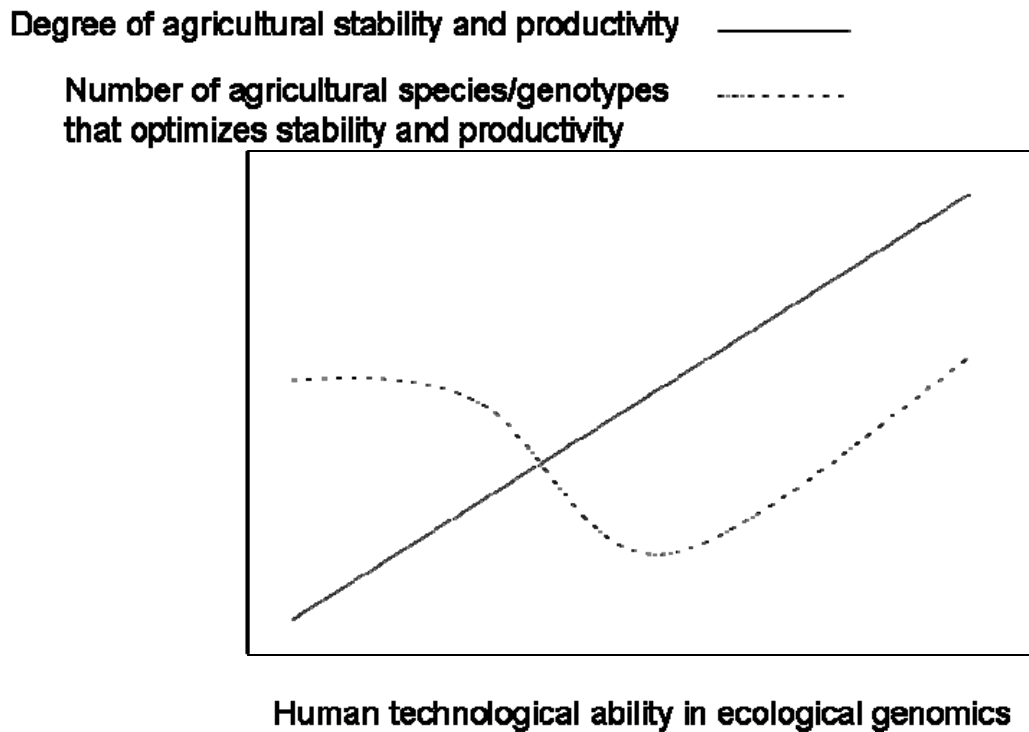


Fig. 21.2

will support better disease management as well as enable transitions to new types of cropping systems such as perennial grains. This is illustrated in Figure 21.2 as a straight line, indicating that technological abilities are defined here as those that lead to desirable outcomes such as productivity and stability, as well as reduced undesirable impacts on surrounding ecosystems. Second, as humans gain new technological abilities in ecological genomics, they will be able to effectively influence and manage a wider range of agricultural species and genotypes (collectively, “crop types”) to enhance agricultural productivity and stability. Previously, a diverse portfolio of crop types was probably necessary to optimize agricultural systems. We may currently be at a low point in deployed agricultural diversity in temperate regions and

approaching a low point in tropical regions, as agriculture industrializes and research focuses on a small number of crop types. This may be a useful short-term approach, as great strides are made in understanding the ecological genomics of some particularly important crop species and developing tools that may be applied to other systems. Deployment of variety mixtures and intercropping is often limited by an incomplete understanding of the genomic basis for interactions such as competition between crop types and for differential responses to climatic heterogeneity that may result in undesirable differences in maturity rates for different crop types. Similarly, more complete understanding is needed for optimal deployment of crop types to exert desired selection pressures on pathogens and beneficial microbes. And also, at larger scales, deployment of greater agricultural diversity is often limited by an inability to simultaneously develop many crop types to a high level of performance and economic competitiveness. However, as it becomes easier to develop and implement strategies for the use of agricultural diversity through multiple crop types, rather than continuing toward a single “super genotype”, the benefits of agricultural systems may be optimized by making use of the complementary traits of many crop types.

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