Emerging Plant Diseases: What Are Our Best Strategies for Management?

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The impact of plant disease can be stark. Famine can result if no systems are in place to replace lost crops. Notorious famines precipitated by plant disease include the Irish potato famine of the 1840s due to potato late blight, the Bengal famine of 1943 due to rice brown spot, and famines in Uganda in the 1990s due to cassava mosaic disease. Whole ecosystems can be altered when ecologically important plant species are decimated by invasive pathogens with which they have not coevolved. For example, the generalist pathogen *Phytophthora cinnamomi* has wreaked havoc in Australian natural areas, its relative *Phytophthora ramorum* threatens temperate forests worldwide, and the eastern United States has been altered by the removal of native chestnut stands by *Cryphonectria parasitica*. There are also many less dramatic diseases that produce a cumulative 10% reduction in crop yield (Strange and Scott 2005; Savary, et al. 2006). While some parts of the world take food availability for granted, the recent jump in food prices has brought new attention to food security and the factors that threaten it.

Our objective in this essay is to make readers more aware of the factors that drive emerging plant pathogens as a risk factor for food

security and for the biological integrity of natural areas. We would also like to share some of the excitement of applied plant pathology, a field in which scientists work with fascinating microbes, "worthy adversaries" in work to protect agriculture and wildlands. Consider the range of strategies that a country's plant pathologists are responsible for developing. Some diseases are already established in areas where they potentially cause yield loss every year. They may be costly to manage, but management strategies are available. For agricultural species, resistance genes may be available for incorporation in breeding programs. The Red Queen from Alice in Wonderland has often been invoked as a symbol of the coevolution of plants and pathogens, where plants need to keep running just to stay in place in terms of evolving new forms of resistance to pathogens that are also continuously evolving. In agricultural systems, plant breeders developing resistant crop varieties take the side of the crop species in the "arms race" with pathogens. Resistance strategies may include partial resistance, where the direct selection pressure for new pathogen types is lower. In cases where resistance genes are not available or not sufficient for disease management, strategies for the use of other cultural methods, such as changing planting times to avoid pathogens, or pesticides may be used. Plant pathologists work to optimize these systems by, for example, minimizing unnecessary pesticide use through weather-based disease forecasting to guide when pesticides would and would not be useful. But diseases that are new to a region are generally the most problematic, because neither plants nor plant pathologists have had sufficient opportunity to adapt to them.

Decisions about plant-disease management, just like decisions about medical treatment, consist of a series of compromises. Plantdisease risk is a complicated function of the characteristics of the host, pathogen, and environment. Some controversies in plant pathology arise when there is not enough information to know how to weight different risk components. There is an old joke about risk managers using license-plate numbers in the parking lot outside their office as a source of parameters for their risk analyses. The fact is that decisions about how to manage plant diseases generally need to be made with a level of information that is unsatisfactory to scientists. For example, most plant pathologists would agree that having a homogeneous planting of a particular crop species could pose a risk if the genotypes deployed are unexpectedly susceptible to a disease, or if the acreage exerts selection pressure for new pathogen types to overcome resistance. But estimating the magnitude of these two types of risk is difficult, so if there is a cost to avoiding the homogeneity, it is difficult to know how to balance the different types of costs. Similarly, it is clear that international trade in plant species provides many benefits but also an increased risk of introduction of a new pathogen. Because it is difficult to estimate the risk precisely, it is difficult to determine how much to restrict plant movement. The new science of characterizing ecosystem services and their economic value offers to help with such decisionmaking processes (Cheatham, *et al.* 2009). For example, if tillage can be used to reduce disease risk but it also increases the risk of soil loss, it would be useful to be able to compare these two risks from an economic standpoint. But for the moment, the ecosystem-services concept only offers a framework for evaluating the costs and benefits of strategies. For now, in most cases, the actual economic value of more complex services can only be loosely defined.

What Are Plant Pathogens and What Causes Them to "Emerge"?

Plant diseases can be caused by a combination of biotic and abiotic agents. Unfavorable environmental conditions, such as an excess or deficiency of nutrients, humidity, light, toxic chemicals, and so on, can damage plants. Infectious plant diseases can be caused by nematodes, viruses, bacteria, fungi, and protozoa (Agrios 2005). The classic plant-disease triangle of host, pathogen, and environment is often used to illustrate how the interaction of these components determines the occurrence and impact of plant disease in time and space (Madden, *et al.* 2007).

There are many reasons why a plant disease may "emerge," or increase in importance: (1) The introduction of a new pathogen species or a new type within a species may be the most obvious source of emergent pathogens. An example of the latter is race Ug99 of the wheat stem rust pathogen, discovered in East Africa and moving north through important wheat-growing regions. Wheat stem rust has caused little yield loss in the United States in recent years because of effective resistance in common wheat varieties. But U.S. varieties do not generally have resistance to Ug99, so there is great urgency to develop effective resistance in U.S. cropping systems before Ug99 arrives through contaminated plant materials or even on the clothes of tourists. (2) An increase in the availability of susceptible crop acreage may lead to pathogen emergence. A classic example of a surprising emergent disease is southern corn leaf blight (SCLB). While the disease was known in the United States, it had typically not been a serious problem. When corn breeders switched to a particular form of male sterile cytoplasm for varieties grown throughout the United States in the 1970s, SCLB suddenly became much more important, and scientists realized that this cytoplasm conferred susceptibility to SCLB. Homogeneity of resistant plant varieties can also support disease emergence through the selection pressure for pathogen genotypes that can overcome that resistance. (3) New pathogens may arise through hybridization of existing pathogen species when they come into contact through changing geographic distributions; hybridization may have contributed to Dutch elm disease epidemics (Brasier 2001); (4) In some cases, it is the introduction of an arthropod vector that makes a pathogen more important. For example, between 1927 and 1930, Citrus tristeza virus (CTV) was introduced into South America, but only in 1950 with the introduction of the aphid vector *Toxoptera citricidus* was this pathogen considered economically important (Anderson, et al. 2004). A similar situation was seen in California for *Xylella fastidiosa*. This bacterium caused Pierce's disease for a century in this state, but with the introduction of new insect vector species, Pierce's disease spread rapidly, causing significant losses (Anderson, et al. 2004).

What Strategies Can Reduce the Risk of Disease Emergence?

The potential use of plant population or community heterogeneity is an interesting and controversial option to reduce the risk of disease emergence. For example, Margosian, *et al.* (2009) analyzed the connectivity of the U.S. agricultural landscape and concluded that the large connected acreage of major crop species, such as maize or soybean, increases the risk of impact from introduced pathogens. Disease impact may be greater both because pathogens can more readily move throughout large areas of crop acreage and because attempts to limit or eradicate new pathogens are less likely to be successful. However, such an assertion is very difficult to test because of the large spatial scales involved, and thus the limited number of "replicate invasions" that can be studied, and because of the likelihood that a number of different factors influence the success of a pathogen invasion. Thus, the risk imposed by large acreages of single plant species is difficult to quantify. If policy makers concluded that it would be important to reduce connectivity of major crop species acreage, implementation of plans to restrict planting in particular areas would likely be highly controversial. But in the case of U.S. agriculture, where government subsidies sometimes support only a limited range of crop species, policies that instead support greater heterogeneity in cropping systems could have some benefits for reducing disease and pest risk.

Another controversial approach to reducing disease risk would be implementation of stronger policies to reduce the movement of plant materials (food, fiber, genetic material, horticultural species, packing materials, etc.) between regions. While this would undoubtedly reduce the risk of disease spread, it would also impose a high "opportunity cost" in terms of reducing the benefits that might have been gained by making plant materials available across regions. Anthropogenic introductions of pathogens may be the primary route through which new infectious diseases emerge (Daszak, et al. 2000; Anderson, et al. 2004). In some cases, emerging plant pathogens can be excluded from a country by regulatory actions at the nation's borders. A number of regulatory strategies are in place in, for example, the European Union and the United States, with umbrella guidelines established by the World Trade Organization that oversees the international trade of plant materials. Although plant-health inspections and quarantine mechanisms continuously improve, some (e.g., Brasier 2008) consider them ineffective or flawed. The main criticisms are that the regulatory mechanisms focus on visual inspections of the plant materials in both the exporting and importing countries. These inspections may, however, cover only a small proportion of the transported materials and therefore likely miss infrequent but viable disease agents. Furthermore, visibly symptomless plants may harbor disease agents in their tissues or in the substrates with which they are transported. This latter issue is further exacerbated by the fact that while many disease agents may be benign in their native environments and in association with their coevolved hosts, their behavior in a new environment with new hosts is unpredictable. This issue may be best exemplified by a number of severe, introduced plant pathogens that apparently cause only little concern in the location of origin (e.g., C. parasitica-causing extensive damage to native chestnuts when introduced to North America and Europe, in contrast to the more resistant Asian species). Whether the issue is the regulatory bodies' inability to detect the pathogens be-

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cause of inadequate screening, the pathogens' undetectability during the inspections, or simply our inability to predict the risk of importing infectious agents that cause no severe threat in the location of their origin, the bottom line remains that the control of international borders may be inadequate to stop potential pathogens (Brasier 2008).

Natural phenomena, such as severe storms, can also introduce new agents across borders. Soybean rust (caused by Phakopsora *pachyrhizi*) is an example of the rapid long-distance dispersal of a plant pathogen. Originally identified in Asia in the early 1900s, soybean rust has spread through Africa and South America since the mid-1990s and recently to the United States. The large potential economic losses caused by soybean rust and its rapid emergence in the new world motivated forecasting of soybean rust dispersal. The Integrated Aerobiology Modeling System (IAMS)—a modeling tool to forecast pathogen dispersal from meteorological data—was developed by Isard, et al. (2005). Simulations with IAMS suggested that a storm, Hurricane Ivan, could transport rust spores from Colombia to the United States. Subsequent analyses suggested that such severe weather events might be a common cause of long-distance dispersal. Prevailing strong winds and favorable humidity allowed soybean-rust establishment more than 1,000 km from the closest known inoculum sources within the United States (Isard, et al. 2007). These data indicate that in our changing environment, in which severe weather events are predicted to increase, long-distance-possibly even cross-oceanicpathogen dispersal may become more frequent.

Post-Introduction Strategies

We conclude that the introduction of new plant pathogens is nearly inevitable. Now, we ask if the control of these pathogens is possible once they have been introduced. Some diseases, such as Dutch elm disease (caused by *Ophiostoma ulmi* and its close relative *O. novoulmi*), may have spread across continents at a speed that has precluded any control. We use examples of diseases where environmental forecasting may allow preemptive action and where a detailed understanding of the organisms' biology may provide tools for (biological) control. We conclude with examples of regulatory action to limit a pathogen's spread within the western United States.

Soybean rust (above) exemplifies predictive modeling combined with preemptive action. The IAMS predicts whether or not climatic conditions support the dispersal, germination, and establishment of the disease, which migrates annually from the southern United States to the north (Isard, *et al.* 2007). The ability to predict movement, combined with fungicide applications during the early colonization, can reduce crop losses as well as save in fungicide costs. Pathogen establishment can be costly as can be its control after establishment. Yorinori, *et al.* (2005) estimated that losses to soybean rust were \$759 million in the main soybean production regions of Brazil in 2003, in addition to \$500 million spent on fungicides. Effective ecological forecasting tools, such as IAMS for soybean-rust establishment, help reduce the costs of subsequent pathogen control.

Chestnut blight (caused by *C. parasitica*) provides an example of biocontrol, the use of a parasite or other natural enemy to manage an undesirable organism. In this severe fungal pathogen of U.S. native chestnut, a virus is passed between two strains of the pathogen. The virus infects the fungus and reduces its ability to cause disease (hypovirulence). The use of a pathogen of a fungus to control a disease in plants is appealing, as the establishment of a virus-bearing fungal population provides a long-term reduction in the disease symptoms. In the case of C. parasitica, the hypovirulent strains have established adequately well for chestnut recovery in tests in Europe and North America (Fulbright, et al. 1983; Heiniger and Rigling 1994). Unfortunately, the introduction of hypovirulence has not been universally successful (MacDonald and Fulbright 1991). Although the potential biocontrol using the virus-bearing fungi has been well-documented and is worth consideration, it is only available because of a fortuitous well-studied system. Many introduced plant pathogens have not had similar research emphasis, and the basic research to develop biocontrol tools often requires decades of research.

P. ramorum—the causal agent of sudden oak death (SOD)—is an example of a recent newcomer. This plant pathogen was identified in 1995 from German rhododendrons (Werres, *et al.* 2001) and was soon detected in the western United States, where its spread has been devastating to many native plants. The concern about the pathogen's impacts on forestry in California and Oregon led to a monitoring program and diligent quarantine regulations that included destruction of infected plants and their neighbors in nurseries and native stands (Goheen, *et al.* 2004; Rizzo, *et al.* 2005). Regardless of these aggressive measures, Prospero, *et al.* (2007) concluded that inoculum persisted after the eradication measures. The response to *P. ramorum*

exemplifies the near-impossible task of controlling some plant pathogens. Furthermore, the success of regulatory actions and quarantine measures remains dependent on citizens' voluntary submission to restrictions.

Several controversies persist for the development of strategies for managing new plant diseases. Increasing agricultural heterogeneity may decrease risk, as may decreasing the movement of plant materials. In both cases, it is difficult to quantify the costs and benefits of the actions so that the political will can be developed to implement needed policies. In the mean time, pathogens continue to spread to new areas with the potential for developing new pathogen types through hybridization and the potential to develop new vector associations through newly overlapping pathogen and vector ranges. As a result, threats to food security and to natural ecosystems increase. One certainty is that society would benefit from investing more effort in understanding these processes so that better strategies can be implemented.

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