Plant Pathology: A Story About Biology

Thomas R. Gordon and Johan H.J. Leveau

Department of Plant Pathology, University of California, Davis, California 95616;
email: trgordon@ucdavis.edu; jleveau@ucdavis.edu

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Abstract

Disease is a universal feature of life for multicellular organisms, and the study of disease has contributed to the establishment of key concepts in the biological sciences. This implies strong connections between plant pathology and basic biology, something that could perhaps be made more apparent to undergraduate students interested in the life sciences. To that end, we present an instructional narrative that begins with a simple question: Why are there diseases? Responses and follow-up questions can facilitate exploration of such topics as the evolution of parasitism, plant adaptations to parasitism, impacts of parasites on native plant communities, and ways in which human intervention can foster the emergence of aggressive plant pathogens. This approach may help to attract students who would not have found their way to plant pathology through traditional pathways. Packaging the narrative as a game may render it more interesting and accessible, particularly to a younger audience.

INTRODUCTION

Plant pathology was born of the need to mitigate impacts of diseases affecting agronomic crops, a mission that remains central to the rationale for this discipline. Of course, research in plant pathology has also contributed to science in a more general way, beginning with the work of Berkeley, deBary, and others, which helped to establish the germ theory of disease (41). This concept served as the foundation for innovations that improved the human condition by establishing the etiology of diseases affecting people and also by limiting the impact of plant pathogens on the supply of food. Many significant advances were to follow, including the identification of bacteria and viruses as disease-causing agents (41), demonstration of RNA as a genetic molecule (22), and the discovery of novel phenomena such as ice-nucleating bacteria (44) and gene silencing (43). Challenges posed by plant diseases have not abated. Movement of pathogens, changes in cultivars and crop production practices, and diminished availability of chemical treatment options provide ample opportunities for the emergence of new diseases and the reemergence of problems previously amenable to control. It is probably also true that opportunities for scientific discovery are no less than they have been in the past. Thus, it would seem quite reasonable to maintain a robust research effort on plant pathogens and the diseases they cause. However, the perceived benefits of the research enterprise are not by themselves sufficient to ensure the continued existence of plant pathology as a distinct discipline. This also requires a steady stream of interested students to justify teaching courses in plant pathology and to sustain the professional ranks in academia, government service, and industry. How do these students find their way to plant pathology?

Exposure through course work is one important means by which students develop a career interest in plant pathology (45). This suggests two obvious strategies for increasing the pool of graduate school applicants: (*a*) attract more students to plant pathology courses and (*b*) capture a larger proportion of students enrolled in those courses. A third possibility—though one over which plant pathologists generally have less control—is to embed more references to plant pathology in introductory level biology courses. Success in any of these approaches depends on an understanding of what the target audience is likely to find interesting. This review is predicated on the assumption that a subset of this group has a principal interest in biology. If so, it may be useful to introduce students to plant pathology in a way that emphasizes concepts of general interest to biologists. This is not to suggest that we should diminish the connection to agriculture, without which our identity would be lost, but rather that we need to tap more effectively into a broader pool of undergraduate students, relatively few of whom will find their way to plant pathology through agricultural connections. Thus, our aim should be to show aspiring young scientists that plant pathology offers excellent opportunities to study phenomena of interest to biologists.

Success in eliciting interest in any subject is determined to a large extent by the manner in which it is presented, and enhanced instructional methodologies are widely seen as critical to attracting more students to a career in science. A number of recent publications address this issue in the broad context of science education (1) and, more specifically, as it relates to (micro)biology (33) and plant pathology (61). These sources and others provide excellent points of entry to scholarly work on science education. Also of interest are presentations on the utility of various approaches specific to plant pathology that are available in the Education Center on the Web site maintained by the American Phytopathological Society (**http://apsnet.org/education/InstructorCommunication/TeachingArticles/Top.html**).

We will not attempt to cover the breadth of material that is available on teaching methodologies. Instead, we will show how the science of plant pathology can be introduced in a way that emphasizes opportunities for fruitful exploration of concepts central to the biological sciences. Thus, plant pathology is more than a problem-solving discipline and cannot be reduced to a checklist of pathogens and their characteristics. It is perhaps this simplistic view that encourages universities to submerge plant pathology into units with a focus on pest management. Such an approach fails to recognize that plant pathology is a robust and dynamic field of study that, like all scientific endeavors, can deepen our understanding of the natural world and provide insights and benefits that would not have been anticipated based on the initial motivation for an investigation. Sustaining this enterprise into the future requires that we provide undergraduates with a compelling introduction to our discipline. We can further this objective by helping the current generation of graduate students to develop the ability, willingness, and confidence to explain their field of research in terms that can be understood by the uninitiated and as a narrative that introduces established concepts in biology and invites new questions.

We propose the use of a narrative, based on a series of questions, to introduce plant pathology. We begin with questions concerning the origins of plant pathogens, followed by inquiry into the impacts of pathogens on their plant hosts in both native and managed ecosystems. Finally, we explore possible alternatives to parasitic relationships. Although this narrative is presented essentially as a monologue, it can (and should) be dialectic in practice, by incorporating the responses of students, which in turn would influence the choice of subsequent questions. Questions were an essential element in the Socratic mode of inquiry, and their heuristic value remains widely recognized today. Questions can elicit curiosity and prepare the mind to receive information. Furthermore, an instructional format based on a series of interrogatives lends itself very well to the construction of participatory exercises. Some of these exercises might take on the form of instructional or serious games in which students assume the role of a plant pathologist, farmer, or pathogen. Such immersive exercises provide a context for learning key concepts in biology and may build hypothesis-forming skills by offering opportunities for inquiry. Serious games specifically based on the plant pathology narrative will be further discussed in the final section of this review.

Parasite: an organism that derives all or part of its nutrition from another living organism

WHERE DO PATHOGENS COME FROM?

We begin our narrative by asking, why is there such a thing as disease? Obviously, there are many possible responses to this and to all the following questions, and in the interest of brevity and continuity, we will select only one or two to pursue. In this case, there are diseases because there are pathogens that cause disease. One might then ask why there are pathogens, and this would presumably lead to a request for a definition, of which many are possible. Assuming that we limit the scope of our discussion to infectious disease, it would be fair to say that a pathogen is—with rare exception—a parasite. Why are there parasites? One might respond, because organisms represent a resource that if effectively exploited can serve as a substrate for growth and reproduction. Thus, we might think of an organism or a part thereof as a habitat and a component of a niche that could be occupied by a successful parasite. Clearly, the line of inquiry could follow more than one course, and this could serve as a framework for student participation. For example, a student or group of students could be assigned to further develop the concept of a niche in the context of a host organism by addressing this question: What factors might be important in defining the spatial, temporal, and biochemical dimensions of niches available to parasites of a particular host species? Others could respond to evolutionary questions such as those described below.

Where a parasite succeeds in exploiting a host organism, it may ultimately propagate itself by some means and pass genetic coding for this capacity on to its progeny—or at least to some of them. Genetic combinations that confer the ability to grow and reproduce quickly and abundantly can be expected to increase in

Saprobe: an organism that derives all or part of its nutrition from the remains of once living organisms

frequency with each passing generation. Thus, because an organism is a potential source of nutrients, natural selection should favor parasites that exploit this resource. Given that such selective pressures have been in place for thousands of millennia, why were all organisms not long ago laid to waste through the ravages of parasitism? What countervailing influences have prevented this outcome? One might also inquire as to how the parasite-in-waiting was sustaining itself prior to its successful exploitation of a host organism. We will address the last question first, by exploring possible pathways to parasitism, and return to the other questions later.

We can begin this exercise by considering the role of microorganisms as decomposers. Decomposers are by definition saprobic, which is to say that they colonize the remains of formerly living organisms and are not themselves a cause of death. This is a process familiar to most, and fruits and vegetables forgotten in the refrigerator illustrate the capacity of microbes to engage in decomposition. Fully ripened fruit is little different from a microbial growth medium, a fact that can be easily demonstrated. Many fungi introduced into this substrate will grow quickly and sporulate profusely. So, it is reasonable to expect that many capable colonizers will compete for occupancy of this habitat. What determines the outcome of the competition? Many factors could be introduced at this point: triggers for germination, inherent differences in growth rate and the range of environmental conditions that influence it, and production and tolerance of antimicrobial metabolites. Proximity is also important because only fungi situated in, on, or very close to the fruit will be in a position to initiate colonization. Of course, many saprobic fungi produce airborne spores, so we can assume that most ripe fruits—not subject to treatment of some kind—will have viable fungal propagules on their surfaces. The cue for germination of those propagules may be a flush of nutrients released when fruit is wounded, perhaps by windblown soil particles, feeding by an insect, or simply from the impact when ripe fruit drops to the ground. With that, a race for acquisition of nutrients within the fruit has begun, and fungi better suited to growth and sporulation under prevalent conditions will be expected to leave more progeny for the next generation.

How do we get from competition among saprobes to the emergence of a pathogen? Perhaps one of the contestants cheats. It does not wait for the whistle but starts the race ahead of the others: It enters the fruit before it is fully ripened. Clearly, this would constitute a significant advantage over co-occurring saprobes. Thus, it is reasonable to suggest that selection would favor fungal decomposers able to access their substrate in advance of competitors. Through a logical extension of this process, the barrier between saprotrophy and parasitism would ultimately be breached, and thus derivation from a saprobe could explain the origin of a parasite capable of growing on fruit. This argument is readily extended to parasites of other plant organs, and it explains very well what the parasite was doing before it became a pathogen. But what sort of changes would allow this transition to occur? Here, we could explore various mechanisms utilized by saprobes to extract nutrients from a substrate and ask why these are not sufficient for parasitism. We can also draw on recent research to illustrate means by which fungi can manipulate the physiological status of their host so as to render it suitable for colonization sooner than it would be otherwise.

Fruit ripening involves alterations of the cell wall that are initiated coincident with maturation of the seed (27). Changes in structure of the fruit make it more palatable to animals serving as agents of dispersal, while also rendering fruit susceptible to exploitation by opportunistic pathogens (11) such as *Botrytis cinerea*. This fungus is commonly associated with senescing tissues and is a well-documented, competent saprobe (48). Consequently, *B. cinerea* is a good candidate for a pathogen that has been recently derived from saprobic antecedents. What mechanisms employed by *B. cinerea* allow this fungus to invade fruit in advance of strict saprobes? *B. cinerea* cannot colonize fruit until plant cell walls have been modified in a way that occurs naturally in ripening fruit. This process involves changes in gene expression, and recent work has shown that *B. cinerea* can upregulate the activity of plant genes whose protein products are required for ripening (10). This capability appears to constitute an adaptation that facilitates earlier access to fruit as a source of nutrients.

The ability to influence the developmental program in a potential host is a remarkably subtle and effective means of facilitating pathogenesis, but it does not obviate the need for a wound in order for the fungus to access host tissue. Certainly, selection should favor any mechanism for more direct entry. Asking how this might be achieved leads us into an extensive body of literature that details mechanical and biochemical processes involved in active penetration of host tissue. This includes release of degradative enzymes (39) and formation of appressoria (19), within which elevated pressure allows mechanical force to be focused on a small surface area (4). As might be expected, a pathogen such as *B. cinerea*, which is perhaps only recently derived from strict saprobes, has appressoria that are relatively unsophisticated and appear to generate only moderate pressures (67). Hence, *B. cinerea* may be more heavily reliant on enzymatic means of breaching the cell wall. Many of these same enzymes would be required by a simple decomposer in order to assimilate monomeric components of structural carbohydrates, so even recently derived pathogens should be well equipped along these lines. In this respect, they might be regarded as preadapted for parasitism.

How does one test a hypothesis concerning the need for a degradative enzyme or an appressorium to penetrate a host surface? One approach would be to deprive the pathogen of a specific capability and determine if that affects its ability to gain access to a host. This can be done biochemically (39) or genetically. As an example of the latter approach, a mutant strain of *Colletotrichum lagenarium* that lacked a fully functional appressorium was shown to be incapable of host penetration and pathogenesis, whereas complementation with a wild-type gene restored these capabilities (54). Likewise, inactivation of a gene involved in host recognition prevented formation of appressoria by *C. trifolii* and also prevented infection (21). However, this mutant strain was capable of colonizing its host and inducing typical symptoms if inoculated into a wound. These findings support the hypothesis that an appressorium can be critical to the infection process and hence may be regarded as an adaptation for a parasitic mode of existence.

Adaptation: a characteristic of an organism that evolved into its present state because it performed a function that enhanced the organism's fitness

Appressorium: a swelling of a hyphal tip that functions to generate pressure, which facilitates penetration of a plant cell wall

Tragedy of the commons: multiple individuals, acting independently, will tend to deplete a shared, limited resource, to the ultimate detriment of all those utilizing the resource

HOW DO PLANTS RESPOND TO PARASITISM?

Now let us return to a question posed earlier that can be rephrased as follows: What have been the consequences of selection for parasitism on host species that are targets of these depredations? If, as we have argued, natural selection favors parasitism, would it not also favor aggressive parasitism, such that those exploiting a host more quickly and completely ultimately displace less aggressive forms? This is not unlike the tragedy of the commons (46), in which a public resource is degraded because each individual is motivated to extract what he or she can as quickly as possible before it is lost to others. And yet, plant life on earth has flourished, and so perhaps we need to reexamine our assumption about selection for parasitism, which is now exposed as unduly simplistic. Parasitism that begets elimination of a host will certainly be selected against. So, let us add that qualification: Natural selection should favor parasitism, and even aggressive parasitism, up to the point that it impacts host availability. Thereafter, negative feedback, in the form of reduced availability of hosts, should serve as a brake on the drive toward parasitism. This suggests a more complex and dynamic process, and we now consider some of the possible outcomes.

In one scenario host species A is so severely damaged by a parasite that it cannot produce progeny in numbers sufficient to sustain itself. Even relatively moderate damage might, over time, achieve this result, where species A competes for the same habitat as co-occurring

Apparent competition: one species gains advantage over another species that is detrimentally affected by a parasite to which it is differentially susceptible

Alloinfection: infection initiated by a propagule not produced on the individual sustaining the infection

Autoinfection: infection resulting from a propagule produced on the individual sustaining the infection

Systemic induced resistance (SIR): the phenomenon in which prior infections or injuries in a plant induce resistance in previously noninfected parts of the plant

species B, which is unaffected by the parasite (apparent competition). If species A is represented by a single population, the result could be extinction, but if the host species has a broader distribution and includes a number of disjunct subpopulations, there may be more to the story. Perhaps only a single population is eliminated, with others, where the parasite does not occur, remaining unaffected. In that case, seed dispersal might allow recolonization of the lost habitat. Thus, unless a plant species is comprised of one continuous population, it may tolerate aggressive parasitism simply by sacrificing populations to perhaps be reestablished later, much as an individual plant sheds parts to be replaced by others serving the same function. The demise of a host population will of course impact the parasite, which may itself disappear or at least decline in abundance. Either outcome improves the odds of successful recolonization by species A. This scenario suggests that the distribution of a plant species might constitute an adaptation to a parasite or to parasites generally, with natural selection favoring species with discontinuous distributions.

If broadly applicable, this type of selection would promote diversity, a concept that is captured in the Janzen-Connell hypothesis (36), which predicts that each plant is a reservoir of species-specific natural enemies and consequently, that conspecific seedlings suffer a risk of mortality proportional to their proximity to a mother plant (26). In contrast, seedlings of different species will be less affected and hence favored. Thus, host-specific pathogens should promote diversity on a local scale. A number of researchers have sought to test this hypothesis, with a particular emphasis on tropical rain forests (3, 5). Their studies reveal many challenges inherent in achieving a definitive test, not least of which is confirming the critical assumption that pathogens manifest the necessary degree of host specificity (23), yet much of the published data are at least consistent with operation of the type of selection predicted by the Janzen-Connell hypothesis (8). Further support for the importance of plant pathogens as drivers of diversity in native plant communities derives from the observed fate of monocultures in tropical rain forests.

For example, many attempts have been made to establish plantations of *Hevea brasiliensis*, the source of natural rubber, within the native range of this species. These plantations were all eventually devastated by rubber leaf blight, caused by *Microcyclus ulei* (18). This fungus is a native associate of *H. brasiliensis* that otherwise causes relatively little damage. Does the natural distribution of *H. brasiliensis*, approximately two trees per hectare, provide some protection against a leaf-infecting fungus? Certainly, it would reduce the rate of alloinfection, and perhaps autoinfection proceeds gradually enough that systemic induced resistance (SIR) (32) can limit the success of subsequent infection attempts. In contrast, when inoculum is sufficiently abundant, as would be the case in a monotypic stand, the frequency of infection attempts may be high enough to overwhelm host defenses before they are sufficiently elevated by SIR (6). Whether or not SIR plays a role in this story remains to be determined, but the failure of efforts to establish plantations of *H. brasiliensis* certainly justifies the hypothesis that the pathogenic potential of *M. ulei* imposes limits on the density of *H. brasiliensis* stands within its native range.

To place it in a more refined form, our hypothesis can be expressed as follows: Leaf-infecting pathogens can play an important role in determining the distribution of the species on which they are parasitic. Admittedly, this hypothesis does not lend itself to a definitive experimental test, but it does allow us to make predictions that can be tested against experience. For example, we could predict that high-density plantings of *H. brasiliensis* should thrive in the absence of rubber leaf blight, and indeed this has been the case. Exotic plantations are highly productive in Malaysia and Thailand and in other locations where *M. ulei* does not occur (18).

Is the impact of plant pathogens on host distribution limited to tropical environments or can we find evidence of these effects in other plant communities? One affirmative indication may be gleaned from a survey of diseases affecting native conifers in temperate forests on North America's Pacific coast (59). Twelve of 14 canker diseases are described as being more severe on trees growing on poor sites and/or subjected to drought stress. These observations suggest that the range of a species may be limited to habitats wherein a tree's physiological status and/or environmental limitations on a pathogen allow the host to avoid significant disease impacts. Outside of this range, disease pressure increases and host trees, if not killed, are significantly less productive and a population cannot be sustained. This concept also finds support in observations that trees moved outside of their native range may be prone to disease problems caused by pathogens with which they co-occur but which are ordinarily not damaging. The differential effects of *Diplodia pinea* on *Pinus radiata* (66) and of *Fusarium circinatum* on *Pinus patula* (72), in exotic plantations as compared to their respective native ranges, provide good illustrations of this contrast.

Why is it that trees are more susceptible to co-occurring pathogens outside of their native range? It is not necessarily because trees grow poorly. In fact, the opposite may be true. For example, Monterey cypress (*Cupressus macrocarpa*), which is native to cool areas near the coast in California, is commonly planted in warmer inland areas, where it grows rapidly and will thrive if provided with adequate moisture. However, these off-site plantings of Monterey cypress are highly susceptible to cypress canker (29), caused by *Seiridium cardinale*, which causes little or no damage in the native range of this species. This differential effect of a pathogen may reflect allocation of resources to growth at the expense of defense (34). Carbon directed toward the construction of vegetative structures is unavailable for synthesis of antimicrobial compounds. Thus, *S. cardinale* may exert an effect on the range of its host by targeting individuals that are composed of tissue more amenable to colonization.

To summarize, we have developed an argument that plants adapt to parasitism in part through limitations of the density and distribution of their populations so as to minimize opportunities for pathogenesis. But is this really sufficient? Isn't it possible for a parasite to be capable of causing disease even where the host is growing under conditions that maximize its capacity for defense? What then?

HOST RESISTANCE TO DISEASE

Up to this point, with respect to susceptibility, we have effectively treated the host as a static entity. Should we not consider the possibility that natural selection will favor genetically resistant individuals? If genetic resistance can negate the effects of a parasite, the range of habitats open to a plant species may be considerably expanded. In fact, genetic differences in susceptibility to disease are well documented in nonagricultural plant populations (9). Resistance is typically not absolute and will often be represented by multiple genotypes, each of which manifests some level of resistance to a subset of the parasite population. Thus, genetic variation in host resistance may be mirrored by corresponding differences in virulence within populations of a parasite. Over time, adaptations conferring resistance may be countered by selection for pathogen traits that restore virulence. In this type of arms race (17, 63), will one ultimately prevail over the other, or will some sort of balance be achieved? In a simple system, the relative frequencies of host genotypes might be expected to fluctuate according to the prevalence of the pathotype(s) to which they are susceptible (55). Thus, the most abundant host genotype, as defined by determinants of susceptibility, favors pathogen genotypes capable of parasitizing it, which in turn acts to limit the abundance of this host genotype. As the once prevalent host genotype declines as a proportion of the population, its parasites are disadvantaged accordingly and consequently should also occur at a lower frequency. In natural ecosystems, these patterns may be difficult to discern, owing to numerous complexities that are likely to be overlaid on gene-for-gene or genotype-for-genotype interactions (7). Consideration

Genetic transformation: introduction of a gene into the genome of an organism, which consequently gains the characteristic(s) conferred by that gene

of the various factors that might preclude detection of a simple relationship between resistance and virulence genotypes could serve as the basis for an instructive group exercise.

Genetic resistance is one of several topics that can provide a bridge to practical questions of interest to plant pathologists and relevant to human welfare. As a solution to disease problems, genetic resistance is appealing because it can be both completely effective and environmentally benign. What does it take to endow a commercial variety with disease resistance? Where a major gene for resistance has been cloned, it may be possible, using genetic transformation (38), to incorporate the trait conferred by that gene directly into a preferred horticultural type. This obviates the need for a protracted series of crosses, followed by screening for the desired trait, backcrosses, and further screening, as would be required where one is reliant on conventional breeding alone. Thus, genetic transformation can save time and money (assuming we exclude costs of commercialization engendered by current regulatory requirements), and does not degrade highly selected genotypes, as commonly occurs where resistance genes are introgressed into elite germplasm (35). Furthermore, it results in a completely defined genotype, with respect to determinant(s) of resistance, in contrast to the traditional approach, which introduces not only the targeted gene(s) but also many genes of unknown function. Why is the product of the former process referred to as a genetically modified organism (GMO) but the latter is not? This requires consideration of sociopolitical issues outside the scope of this review but which might well be an appropriate topic for discussion, depending on the context of the presentation (24). For example, courses that link science to societal issues could assess the merits of deploying corn transformed to produce a bacterial protein that is toxic to certain insects. Corn plants so modified suffer less insect damage and less growth of the mycotoxin-producing fungus *Fusarium verticillioides* (51). Are the perceived environmental concerns associated with GMOs sufficient to outweigh the benefits of reduced pesticide use and a lower mycotoxin load in the human food supply?

By whatever means genetically resistant varieties are developed, they represent an important tool for disease management. Does deployment of a major gene for resistance constitute the final solution to a disease problem? Not surprisingly, the answer will depend on the particulars of the pathosystem, because the durability of resistance can be influenced by a number of factors (49). However, it is often the case that the genetic capacity to overcome major gene resistance resides in a pathogen population, and so the corresponding allele or allelic combination may increase in frequency over time. It is worth noting that spatial and temporal dynamics at work in native plant communities will help to buffer natural selection for aggressive parasites. However, this is not the case in modern agroecosystems. Contemporary agricultural practices favor uniformity—to gain production efficiencies and meet consumer expectations—thus stripping away the ecological dimensions of resistance and allowing the full force of natural selection to drive host-parasite relationships toward a destructive end. How can we respond to this? Can we restore some features of the natural world that will enhance the durability of disease resistance? The use of multilines, in which several different genes for resistance are incorporated into an otherwise common genetic background, is one affirmative step toward that goal (13, 50).

WHAT ARE THE ALTERNATIVES TO PARASITISM?

All the above scenarios effectively place the burden of accommodation on the host. Must it always be so? What about attenuation of a pathogenic strain? If lower pathogen virulence extends the life span of a host, it would increase the time available for a parasite to produce propagules that might come into contact with uninfected plants. Thus, a case could be made for selection favoring less aggressive strains. This might be viewed as a contradiction of what has already been presented, but can also be seen simply as an alternative path open to plant-associated microbes. If so, where might this pathway lead? A number of well-characterized pathosystems could be viewed as the present-day result of such a process, one of which we will consider here: *Fusarium verticillioides* in corn (*Zea mays*).

Research conducted by Desjardins et al. (20) documented recovery of *F. verticilloides* from seed of wild teosintes (*Zea* spp.) in Mexico and Central America. This apparently commensal relationship was perhaps the starting point for the present association between *F. verticillioides* and the agronomic derivative of teosinte known as corn. Whatever its origin, it is clear that *F. verticilloides* is now a common internal inhabitant of corn, with variable consequences for its host. This fungus is recovered from seed at a high frequency and, following germination, proceeds to colonize the developing seedling and may establish a systemic infection that reaches kernels at maturity (52). Thus, the fungus can be found within a corn plant throughout its life history, often without any visible impact. This type of relationship can be viewed as an alternative to destructive parasitism. Like parasitism, it offers a competitive advantage relative to strict saprobes that must await death of the plant before accessing the resources available within, but rather than breaching the barriers by destructive means, the endophytic microbe instead employs stealth. That is to say, it does not provoke a response from its host and extracts only enough nutrients to sustain limited growth, while allowing the plant to remain productive. When the host dies, the endophyte can switch to a saprophytic mode of growth, with the advantage of already being inside the substrate to be exploited.

Is this strategy superior to the more direct approach of overt parasitism? The biological world rarely offers such a categorical endorsement. Rather, the spatial and temporal heterogeneity inherent in native ecosystems allows a diversity of ecological and evolutionary strategies to flourish, at least for a time. Life histories may be viewed as hypotheses about the future in an uncertain world (68). Some will fail catastrophically, and others will succeed to varying degrees, while undergoing continual revisions over evolutionary time. Although we cannot identify a clearly superior strategy, we can assess their relative merits based on what we observe in nature. For example, we can ask what presently appears to be more common: fully exploitative and destructive parasitism or weakly parasitic/commensal relationships? If we focus on native plant communities, examples of destructive parasitism are relatively few, with a suite of ecological and genetic adaptations imposing limits on the expression of this potential in most cases. In contrast, endophytes appear to be quite numerous, having been found in nearly every plant examined (12, 57). Furthermore, because endophytes tend to be cryptic, we have presumably identified a smaller proportion of the total than would be the case for parasites that have conspicuous effects on their hosts.

Admittedly, our assessment is based only on a snapshot in time. We cannot exclude the possibility that destructive parasitism has been more common in the past, but we can, from our present vantage point, infer that such relationships have tended not to persist. So, we have the basis for an argument that plant-associated microbes have more commonly evolved into endophytes than destructive parasites. Of necessity, endophytes are parasitic and would be regarded as commensal associates if their impact appears to be negligible. It is also possible that endophytic microbes provide a benefit to their host, which might be difficult to detect. For example, endophytes may limit opportunities for microbes with more destructive potential, either through induction of resistance in their host (53) or by more directly competing with would-be pathogens (42). This suggests a trajectory toward mutualism, with nutrients surrendered to a parasite being repaid in the form of protection against greater losses, not unlike the human concept of insurance.

Endophyte: a microorganism that resides in a plant, without any obvious detrimental impact on its host; it may or may not confer a benefit on the host plant

Mutualism: two organisms of different taxa living in close association in a way that benefits both participants under most circumstances

Latent pathogen: a microorganism that colonizes a plant without evident impact for some period of time before causing disease

WHICH PARTICIPANTS BENEFIT AND UNDER WHAT CIRCUMSTANCES?

Is the relationship between *F. verticillioides* and corn best regarded as parasitic, commensal, or mutualistic? The answer depends on the circumstances under which the relationship is allowed to develop. Numerous studies confirm that *F. verticillioides* can be a cause of seedling disease, stalk rot, and ear rot (40). These activities are an unambiguous expression of parasitism. This same fungus is commonly isolated from symptomless corn (52), which is indicative of a commensal relationship, and it has also been shown to be potentially protective of infection by other pathogens (42), suggesting mutualism. How can we explain this diversity? Many factors may contribute to the observed variation, and one that can play a determinative role is water stress (60). Water stress results in lower photosynthetic rates, and as a consequence, the plant may mobilize starch reserves in order to meet the need for growth and development not satisfied by current photosynthate. These physiological changes apparently trigger more aggressive growth of *F. verticillioides*, contributing to the development of stalk rot. This type of response may be adaptive for an endophyte, to the extent that it facilitates more rapid exploitation of a resource, for which other endophytes and saprobes may eventually compete. It also serves to illustrate the relative ease with which a relationship can move between the categories to which we seek to assign them.

This example invites a question concerning the consequences of agricultural practices. Have our production systems enhanced opportunities for plant-associated microbes that are pre-adapted for pathogenesis? Selection for maximal yields will naturally push plants toward the limits of what can be supported by their photosynthetic capacity, increasing the risk that suboptimal environmental conditions will engender utilization of stored reserves. Endophytes might respond to biochemical signals associated with this process and initiate aggressive growth, as though the plant was near the end of its productive life. Endophytes engaged in this type of exploitation should be self limiting under natural circumstances, to the extent that they compromise their host's ability to reproduce. However, this limitation will not be operative in agroecosystems, where the same crop is grown more or less continuously over time. Thus, agriculturalists may be providing the selection pressure for endophytes to become latent pathogens with ever shorter latent periods. This phenomenon may explain the occurrence of many pathosystems presently of concern to agriculture, including diseases caused by wilt pathogens (28).

In its association with corn, *F. verticillioides* appears to occupy an ambiguous status, with the consequences for the host plant being contingent on environmental conditions. Can we identify relationships that have traveled further along the path toward mutualism? The answer of course is yes, and the realm of plant-microbe interaction provides many examples, such as the association of *Epichloe* spp. (and their asexual derivatives in the genus *Neotyphodium*) with temperate grasses in the subfamily Pooideae (58). In these relationships, the fungus grows throughout vegetative structures of the plant without eliciting symptoms. These endophytic fungi may also colonize floral primordia and remain viable within mature seeds, allowing for efficient vertical transmission (71). The benefit to the fungus is obvious: Its host plant provides a habitat and is the source of all required nutrients. How does the plant benefit from this relationship? Infected plants can be more productive and drought tolerant (30), and they generally out-compete conspecifics that lack the endophytic association. In addition, the endophyte may confer on its host a degree of resistance to root-feeding nematodes (37) and herbivorous insects (16).

Deterrence of feeding by herbivores has been attributed to specific secondary metabolites produced by *Ephichloe* spp. (58). Could the plant not achieve the same end by producing those (or similar) metabolites itself? Yes, but perhaps it is more efficient for a plant to subcontract for metabolic services, rather than to develop them de novo. By analogy, a computer manufacturer might find it more cost-effective to purchase such peripheral items as batteries and power cords from suppliers already in the business of producing them, rather than creating the capacity to do so internally. In this way, a firm can focus its resources on technologies that provide a competitive advantage. Likewise, plants can benefit by drawing on the metabolic repertoire available to fungi. In fact, this may be more common than has been recognized, as many endophytic fungi are not readily cultured, and hence could easily be missed. For example, fungal symbionts were recently shown to be a source of ergot alkaloids found in members of the Convolvulaceae (47). Of course, plants too can synthesize metabolites that serve as feeding deterrents or inhibitors of microbial growth, which suggests that evolution has not consistently favored plants that co-opt preexisting biosynthetic pathways from fungi over those that elaborate their own defensive compounds. It is probably more reasonable to view the two approaches as alternative solutions to a problem, with neither constituting an inherently superior strategy. From this perspective, microbes simply expand the reservoir of genetic diversity on which natural selection can act to construct plant adaptations to environmental challenges.

MUTUALISM FROM/TO PARASITISM

Some adaptations might be achieved equally well through a mutualistic association or by a plant independently, but are there mutualisms that manifest capabilities that could not have been achieved in any other way? One candidate for this exclusive status would be the mycorrhizal association between fungi and plant roots (2). In this case, the benefit accruing to the plant derives from a number of uniquely fungal attributes that might never have developed independently in the plant kingdom. This includes the mycelial mode of growth, which is characterized by an environmentally responsive, variable hyphal diameter and branching pattern that allows for more effective exploration of soil than is possible for multicellular plant roots, coupled with the capacity to endure periods of drying (62). Thus, it has been suggested that only by utilizing these pre-existing capabilities were vascular plants able to colonize terrestrial environments (69), which required extraction of moisture and nutrients from a dense and periodically dry substrate. Similarly, the ability of legumes to fix atmospheric nitrogen in root nodules through the agency of bacterial metabolism has never been achieved by a plant not participating in a mutualistic association (70). Because mutualisms are common and can be quite powerful, they may be seen as a natural outcome of evolution, with one-sided parasitic relationships being aberrations that flare up spontaneously, only to expire of natural causes shortly thereafter or to remain constrained by any of various ecological and/or genetic adaptations in the host species. However, parasitism remains critically important as a driver of genetic diversity. This is evident at the species level, as outlined in the Red Queen hypothesis (15, 31), and in the structure of plant communities (14, 26). And of course, parasitism is not necessarily an evolutionary end point. Many relationships presently regarded as mutualisms were likely initiated through parasitic intrusions, and likewise, mutualistic relationships can quickly shift toward parasitism in response to genetic changes in either symbiont or when environmental conditions compromise the host plant. Indeed, the biosphere exists in a state of dynamic stability, poised to respond to disturbances through a cascade of changes that may diminish the prospects for some organisms while favoring others. Disturbances of various magnitudes, on local, regional, and global scales, have beset the living world since its inception, yet life has adjusted and endured. Whereas global impacts have been associated with singular, violent events such as volcanic eruptions and impacts with extraterrestrial bodies, the more protracted process of exploitation by humanity may constitute the greatest disturbance yet wrought upon the earth. A central

Red Queen hypothesis: the proposition that species must change continuously over evolutionary time in order to evade the consequences of parasitism element in our transformation of the planet is agriculture. The biospheric tremors that have followed from this ongoing trauma provide a wealth of opportunities for the expression of evolutionary innovations and for inquisitive biologists who seek to understand and manage them.

Our objective in this review has been to show that a conversation initiated by simple questions about plant diseases can capture many topics of general interest to biologists and that plant pathology provides a quite useable framework for introducing students to biology. Whereas a straightforward narrative may effectively engage students already interested in biology, broader appeal, and potentially more effective delivery of the concepts, may be achieved with more creative packaging, as described in the next section.

SERIOUS GAMES AND THE PLANT PATHOLOGY NARRATIVE

Serious games are teaching tools that aim to motivate and engage students in ways that are different from but complementary to traditional methods for the achievement of learning objectives (56). These games compress time, scale, and sometimes reality, such that a concept can be better understood. Effective games teach skills that are useful and applicable outside the game's setting. Typically, serious games provide an immersive environment and a first-person perspective that, in combination, make players feel like they are part of the game and infuse them with a sense of commitment to their newly assumed identity (25). Because of the requirement to deliver specific learning outcomes, serious games rely on a structured presentation of events, actions, and consequences, which can be thought of as the narrative underlying the game (56). A good narrative promotes greater engagement, encourages longer participation, stimulates peer-to-peer teaching, and promises better learning outcomes. There are several excellent examples of plant pathology–based serious games, some of which have been reviewed recently (61). An early one was DIAGNOSIS, developed at Massey University (64, 65). It is a classic example of a detective story, which confronts players with a problem that requires gathering and piecing together clues in order to identify the cause of disease on an infected plant. This forensics concept is likely to resonate well with a current generation of students who are growing up with popular TV shows such as "CSI: Crime Scene Investigation," and its numerous videogaming spin-offs (e.g., **www.csigamer.com**). Developed in the era of text-based adventure games, DIAGNOSIS is no longer available (at least online). A similar but visually much more mature game is Plant Pathology vLab (**http://courses.ncsu.edu/ww201/common/game/index.html**). This game is part of undergraduate class PP 315 (Principles of Plant Pathology), offered at North Carolina State University. Following the same whodunit scenario, the player assumes responsibility as a technician in a plant pathology testing lab and is given the task of identifying the pathogen responsible for having caused disease symptoms on a tomato plant brought in by a concerned farmer. The player has many tools at his/her disposal to aid in the diagnosis, including a microscope, growth media, antibody tests, and reference books. Navigation in this game is visual, much more mouse/click- than type-based, and provides the opportunity to walk around in the lab and learn about different lab stations through instantly available video presentations. This exercise can be a wonderful simulator of the frustration and excitement that characterize the scientific discovery process. Students find themselves going back and forth between hypotheses, based on the outcome of their test results. Getting to the right answer, i.e., the correct diagnosis, is a very satisfying experience, and the desire to find the answer has the potential to emotionally attach a player to the game, which is an important feature of experiential learning (25).

In another type of game, players assume the role of a farmer or farm advisor. An example is the aMaizing Plant Disease Game, which was originally developed at the University of Aberdeen with the aim to teach about decision making in agriculture. The player's task is to grow a virtual crop all the way to a profitable harvest. Along the way, important decisions need to be made, such as what variety to sow and when to apply fungicides to combat disease. A major difference with the previously described whodunit approaches is that the player now becomes an active contributor to the game's end point. By choosing from several crop varieties and fungicides, or fungicide application practices, there are many different outcomes to this story, not like the disease diagnostic games that offered only one possible ending (i.e., the correct diagnosis). This type of game is in essence about economics: in this case, how to balance the costs and benefits of disease control in the face of more or less unpredictable factors, such as weather conditions. Although the designer of the game has laid out rules for the costs and benefits of each decision that can possibly be made, it is the user of the game who determines what decisions are actually made and when. This provides the player with a feeling of control, and perhaps more importantly, it fosters an appreciation for the possibility of being held accountable for the outcome of one's actions. A third type of game is one that has not been fully explored yet, at least not as far as we know, in plant pathology. It involves players taking on the role of a plant-associated microbe, with the aim to maximize survival in a simulated plant environment. Perhaps closest in spirit is Spore, a video game that lets players move microbes and have them evolve into more sophisticated beings by giving them certain properties that confer increased survival skills. Because different properties come at different costs, this too is essentially a game in economics (i.e., resource allocation), as it lets players experience the concept that in order to survive, no single strategy is necessarily the best. Instead, tradeoffs in cost and benefit will give rise to many, not mutually exclusive solutions for maximal survival. We envision that a similar approach can be used to convey the concept of microbial diversity, more specifically, the diversity of interactions that microorganisms can have with their host plants. These could cover the entire gamut, from commensalism to mutualism to parasitism, and could accommodate many stories of plant pathology in its narrative, including those featured in this review article.

Commensalism: two organisms of different taxa living in close association with one another in a way that benefits one participant but has no evident beneficial or detrimental impact on the other

Another option in serious gaming is to focus on foliar pathogens to exploit the remarkable parallels that exist between these microbes and characters in the popular board and computer game Settlers of Catan (**http://www.catan.com/**). In both cases, players represent pioneers or settlers, trying to colonize an uninhabited finite space, i.e., a plant leaf or an island. The latter is laid out randomly at the beginning of each game from terrain hexes representing topographical features, each providing the settlers with natural resources in a fashion that is determined by properties inherent to those features, chance, and a player's decisions. Natural resources may be used for settler activities such as engineering the local environment, which might increase survival but can also erode the plant leaf or island to a point where it can no longer sustain the settler population. Such game scenarios are likely to leave students with some understanding of why aggressive parasitism might not be a common strategy in nature. In more sophisticated versions of the game, the player might be confronted with other inhabitants of the plant leaf, each with unique survival strategies that are differentially compatible with those of the player's, thus entering further into the realm of game theory and the concept of arms races, and the relative merits of cooperation versus confrontation. Incidentally, the use of war-like language that sometimes typifies plant pathology jargon might actually work to our benefit in engaging at least some students, given the popularity of this particular genre in contemporary videogaming.

CLOSING REMARKS

The study of host-microbe interaction embraces a remarkably diverse array of organisms and interactions, and thus presents a wealth of research opportunites for students interested in biology. We propose that these opportunities could be made more apparent by presenting the subject matter in a way that emphasizes its centrality within the biological sciences. The practical value of information generated by research in plant pathology should be appealing as well, but this dimension of the discipline is likely not visible to most without an agricultural background and so may remain unduly limiting as a point of entry to plant pathology. The dialectic approach we have described might help to capture the attention of students potentially interested in biology and could be structured to suit any level of instruction from precollege through graduate study. Likewise, serious games can be designed to illustrate concepts at an introductory level but may also provide productive challenges for more advanced students. Although not explored here, the design of serious games could itself be an instructive exercise. In sum, we offer these ideas in the hope they might encourage further development of methods that can be used to more effectively present concepts of plant pathology and thereby enhance our educational efforts and encourage more students to seek careers in this field.

SUMMARY POINTS

1. The study of plant diseases can invite exploration of issues of general interest to biologists. This fact can be conveyed to the uninitiated as a narrative, which could focus, among other possibilities, on the evolution of parasites and the consequences of their interactions with host plants.
2. Parasites can be represented as having evolved in response to selection for earlier access to the resource represented by a living plant. Manipulation of host physiology and elaboration of structures to facilitate penetration of intact tissue may be seen as adaptations that facilitate parasitism.
3. Plant species adapt to parasitism, in part, through limitations on the density and distribution of their populations, so as to minimize opportunities for pathogenesis. Thus, pathogens may exert a significant influence on the structure of native plant communities.
4. Plants may manifest resistance to disease, and genetic resistance is a useful management tool in agroecosystems. The durability of resistance is variable and may be limited by the fact that the uniformity favored by modern agriculture has largely eliminated the ecological dimensions of resistance. This allows natural selection to drive host-parasite relationships toward a destructive end.
5. Accommodation between host and parasite may be realized through the establishment of mutualisms, wherein both participants gain some benefit. Arguably these relationships are more common than those causing severe damage to the host plant. However, the relative benefits to mutualists may be contingent on environmental conditions, and agricultural practices can facilitate conversion of endophytic mutualists to latent pathogens.
6. The global disturbance known as agriculture provides excellent opportunities for aggressive pathogens and for biologists interested in studying them. Making more students aware of these opportunities may be achieved by using games to introduce concepts and promote understanding.

DISCLOSURE STATEMENT

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