

A Coevolutionary Framework for Managing Disease-Suppressive Soils

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Abstract

This review explores a coevolutionary framework for the study and management of disease-suppressive soil microbial communities. Because antagonistic microbial interactions are especially important to disease suppression, conceptual, theoretical, and empirical work on antagonistic coevolution and its relevance to disease suppression is reviewed. In addition, principles of coevolution are used to develop specific predictions regarding the drivers of disease-suppressive potential in soil microbial communities and to highlight important areas for future research. This approach brings an evolutionary perspective to microbial community management and emphasizes the role of species interactions among indigenous nonpathogenic microbes in developing and maintaining disease-suppressive activities in soil.

INTRODUCTION

Disease-suppressive soils represent an elusive but highly attractive goal for plant pathologists (for example, see References 4, 52, 75, 76, 98, 102, 131). For many soil-borne plant pathogens, the lack of effective resistance and limitations on the use and availability of pesticides impose significant challenges to crop production. However, suppressive soils, or soils in which little or no disease occurs under conditions that are seemingly favorable for disease development (4, 74, 101), have been identified for a wide variety of fungal and bacterial plant pathogens, including take-all on wheat (58), *Fusarium* on multiple crop hosts (2), scab on potato (67), *Phytophthora* on apple (74), black rot of tobacco (57), club root disease of Chinese cabbage (81), and for plant-parasitic nematodes (69, 127). Both natural and induced suppressiveness have been identified, and indigenous soil microbes are critical to plant disease suppression in both types. Natural disease suppression is not affected by plant host or cropping sequence, and is likely to be a function of the broad physical and chemical characteristics of the soil and their effects on soil microbial communities. In contrast, induced suppression depends not only on the characteristics of the soil but also on the plants grown in the soil, the cropping sequence, and the crop management strategies, and generally requires active management for maintenance (3, 12, 101).

Research on disease-suppressive soils has been summarized in multiple thoughtful review articles over the past decade (3, 12, 41, 53, 73, 75, 126). Central issues that scientists have focused on include (a) identifying the organisms responsible for disease suppression (6, 9, 14, 57), (b) characterizing the mechanisms by which indigenous microbes suppress target diseases, and (c) the impacts of crop management strategies on disease suppression (3, 21, 22, 45, 53, 60, 75, 84, 90, 108, 110, 129, 130). Several generalizations can be drawn from these suppressive systems and from efforts to generate suppression de novo: (a) agricultural management impacts soil microbial community

structure and function (for example, see References 19, 20, 134); (b) enhanced suppression is typically correlated with enrichment of antagonistic or competitive activities in one or more components of the soil microbial community (41, 53, 75, 126); (c) long-term monoculture can be a pathway to effective disease suppression (36, 126); (d) organic matter inputs can enhance disease-suppressive activities of soil microbial communities (3, 12, 82); and (e) the outcomes of management to achieve disease suppression are often highly variable (12). In particular, although the use of green manures, cover crops, crop rotation, composts, or other organic amendments has met with some successes (8, 55, 111), the predictability of particular strategies for inducing effective disease suppression remains poor (61). Thus, despite broad recognition of the tremendous potential for indigenous soil microbes to suppress plant pathogens and diseases, consistent, reproducible, and economically viable disease control via microbial community management has remained elusive.

Progress in managing soils to achieve disease suppression may require a new approach. To date, research on microbial community management to suppress plant pathogens has been vigorously empirical. Although this provides useful insight into the mechanisms of pathogen suppression and practical strategies for enhancing disease-suppressive activity in soil microbes, there has been little effort to develop a theoretical, ecological, or evolutionary framework for studying disease suppression. Consider that disease-suppressive soils are frequently characterized by high densities or diversities of soil microbes (42, 43, 77, 126), and, most notably, high densities, frequencies, or diversities of antagonistic populations (1, 13, 41, 53, 75, 126). Antagonistic phenotypes contributing to disease suppression include production of antibiotics, siderophores, and extracellular enzymes as well as other compounds that may enhance antagonistic phenotypes (e.g., signaling compounds and surfactants) (1, 25, 72, 78, 88). These phenotypes are all crucial to mediating species interactions in soil

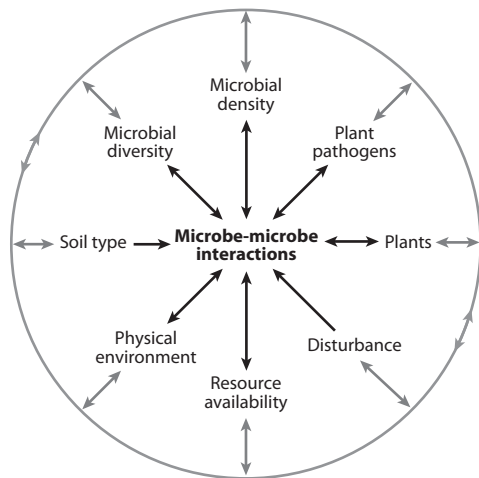


Figure 1

Ecological and coevolutionary interactions among microbes occur within the context of a variety of biotic and abiotic factors in the environment. Many of these factors are correlated and interact directly or indirectly, as signified by the outer connecting ring.

(48, 66). Thus, selection for these phenotypes is a function of the benefits these traits confer in interactions with coexisting microbes. Specifically, microbial interactions within the soil community are likely the primary force imposing selection for the enhanced antagonistic activities crucial to disease suppression. This suggests that a systematic consideration of the specific ecological and evolutionary forces likely to drive species interactions and selection for antagonistic populations may guide both empirical research and the development of quantitative and conceptual models for analyzing progress toward disease suppression.

Microbial interactions within the soil community are the explicit focus of the coevolutionary framework for disease suppression developed here (**Figure 1**). Thus, although a substantial body of research has documented the significance of plants to microbial communities (10, 18, 37, 47, 121), we argue here that, relative to disease suppression, plant host, soil type, and physical environment are all important primarily in setting a context within which microbial interactions occur. Plants

may, for examples, determine soil nutrient availability, but plant-microbe interactions are not conceived as directly responsible for the selection or enrichment of antagonistic activity. Plants may benefit significantly from enriched antagonist populations in soil, yet plant fitness benefits are not required for selection for antagonistic phenotypes. Similarly, although pathogen populations are often especially sensitive to antibiotic inhibition, interactions of microbial antagonists with the pathogen may or may not be significant to antagonist fitness (for examples, see References 46, 57, 100). Ironically, research related to suppressive soils may be hampered by an overemphasis on pathogen-antagonist interactions with little consideration of the bulk of microbial interactions in soil. Although negative impacts on pathogen populations are a desired outcome, the importance of direct interactions with pathogen populations in the development of microbial community characteristics that result in disease suppression is often unclear. The coevolutionary framework developed here casts the focus explicitly on microbial interactions within complex soil communities and considers other factors, including crop management, within the context of their direct or indirect impacts on microbial coevolutionary interactions in soil (**Figure 1**).

COEVOLUTION: THE CASE FOR TAKING A COEVOLUTIONARY APPROACH TO DISEASE SUPPRESSION

Coevolution is a primary force in generating and in organizing biodiversity on the Earth (51, 115). Darwin is widely credited with the concept of coevolution, as captured in this passage from *The Origin of Species*:

Thus I can understand how a flower and a bee might slowly become, either simultaneously or one after the other, modified and adapted to each other in the most perfect manner, by the continued preservation of all the individuals which presented slight deviations of structure mutually favorable to each other. (26)

Coevolution is the process of reciprocal genetic change between interacting populations (112). Critical to coevolution is the significance of species interactions to the fitness of each partner and the corresponding genetic changes that result from selection on each partner by the other. The idea of adaptation and counter-adaptation among interacting populations has been applied broadly to many types of interactions, but the most well-developed body of data, theory, and modeling related to coevolution is on host-parasite antagonistic coevolutionary interactions.

Plant pathologists have studied the dynamics of host-parasite coevolution for many decades. Flor's classic papers on gene-for-gene interactions between flax plants and the flax rust pathogen (32–34) provided the basis for some of the first quantitative modeling of gene-for-gene coevolution (11, 64, 79). This work in turn built conceptually upon the long-standing recognition by agricultural scientists of the role of host selection in generating rapid shifts in pathogen race abundance, contributing to the boom-and-bust cycles of wheat stem rust in the U.S. Great Plains (105). Furthermore, as early as the 1920s, agriculturalists worked actively to minimize variation in the wheat stem rust population, and therefore the pathogen population's capacity to respond to host selection pressure, by limiting sexual recombination through elimination of the alternate (sexual) host for the pathogen. Quantitative models developed by pathologists (for example, see References 64, 79) provided some of the earliest conceptualizations of the dynamics of host-parasite coevolution and how fitness costs and benefits of virulence and resistance impact coevolutionary trajectories. Overall, modern coevolutionary principles remain strongly grounded in the foundational concepts developed by plant pathologists studying host-parasite populations in agricultural and natural systems.

Coevolution offers a similarly compelling framework for studying microbial interactions and disease suppression in soil. Evolutionary change within soil microbial communities occurs over short time-scales and in response

to management practices (5). In fact, microbial evolution and coevolution are managed regularly, if unintentionally, by all crop management practices, and shifts in the relative abundance of distinct microbial genotypes or phenotypes are evident over timescales as short as a few weeks (129, 130). Moreover, microbial interactions within soil communities have been well documented to influence population densities and dynamics (48). Selection for antagonistic phenotypes crucial to disease-suppressive activity is a function of the benefits these traits confer in interactions with coexisting microbes. Ongoing coevolution among interacting microbial populations yields reciprocal selection for both resistance to antagonistic traits in sensitive populations, and, subsequently, for novel or enhanced antagonistic phenotypes. In this way, antagonist competitive dynamics may follow a coevolutionary trajectory similar to that of hosts and parasites, with adaptation and counter-adaptation common. Significant consequences of this coevolutionary dynamic include the potential for increases in the density, frequency, and diversity of antagonistic phenotypes within the soil microbial community.

Importantly, this coevolutionary dynamic may be vital for realizing long-term, stable pathogen or disease suppression. Specifically, ongoing coevolution among interacting populations provides the potential for continuing shifts in the frequencies of microbes producing particular antibiotics or antagonistic compounds, the amounts of antibiotic produced by individual microbes, and the diversity of antagonistic phenotypes or antibiotics sustained within the community. These ongoing shifts impose varying and diverse selection pressures on the pathogen population, thus minimizing directional selection, reducing the likelihood of pathogen resistance, and enhancing the stability of pathogen suppression over time. Although the concept of an antibiotic arms race analogous to a host-parasite arms race has been explored previously using mathematical models (23, 104), application of these concepts to the dynamics of pathogen-suppressive

communities may provide practical insights for agricultural management.

In total, what we know about soil microbial populations coupled with the significance of antagonistic phenotypes to both microbial fitness in soil and pathogen suppression suggests that microbial coevolutionary interactions are likely to play a significant role in determining the density, frequency, and diversity of antagonistic phenotypes in soil microbial communities. Thus, researchers focused on achieving disease suppression should consider carefully what existing coevolutionary data and theory suggest about the potential for managing microbial coevolutionary trajectories in soil.

DIFFUSE COEVOLUTION AND THE GEOGRAPHIC MOSAIC THEORY

The recognition that coevolution is a pervasive and significant force in nature has led to extensive research and quantitative modeling on the dynamics and principles of coevolution. If microbial populations in soil are relentlessly coevolving and we hope to manage the coevolutionary process to achieve disease suppression, what crucial aspects of coevolution should be considered?

One critical fact is that, within complex soil communities, target populations or species interact with a potentially diverse collection of coexisting populations (112, 116). Thus, rather than the simple model of tightly-linked, pairwise coevolutionary dynamics that applies to many host-parasite systems, the concept of diffuse coevolution (7) is most appropriate for thinking about coevolutionary dynamics within soil microbial communities. Diffuse coevolution emphasizes that selection for a specific trait may be imposed by interactions with multiple coexisting species or members of a community rather than by only a single population (54, 106, 107). Although research on suppressive soils often focuses on one or a few readily culturable microbial taxa, recent work has shown that disease suppression is correlated with broad and complex shifts in microbial community

composition (57, 75, 97). This is consistent with the concept of diffuse coevolution, i.e. the idea that interactions occur within a network involving many members of the community.

Spatial variability in coevolution is a second fundamental factor to consider. Although microbial interactions and selection occur within localized populations, in aggregate, the long-term dynamics of coevolution occur across a broad spatial landscape. For microbes in agricultural fields, management is imposed at the field-scale, but the field consists of a network of localized communities within which species interactions occur. Thompson proposed the Geographic Mosaic Theory of Coevolution to describe the dynamics of coevolution across a landscape of discrete populations (112–114). Variation among locations in the specific subset of interacting species present and in the abiotic characteristics of the location and in the genetic diversity available for selection provide a platform for variation in the outcomes of the ecological and coevolutionary interactions. The result is a geographic mosaic of coevolving populations and coevolutionary outcomes across an agricultural field. There are likely to be coevolutionary hot spots in which coevolution has a significant influence on the interacting species, and cold spots where there may be either no interaction or no reciprocal selection.

EVOLUTIONARY POTENTIAL, SELECTION, AND DISEASE-SUPPRESSIVE SOIL COMMUNITIES

The rate and trajectory of coevolution within any localized community are determined by the evolutionary potential of the interacting populations and the strength of selection (11, 35, 39, 64). The evolutionary potential of a population reflects its ability to incorporate novel genotypes/phenotypes and is a function of both population size and diversity. Larger population sizes, shorter generation times, and higher rates of mutation, recombination, or dispersal all contribute to greater evolutionary potential for a population (39). Greater evolutionary

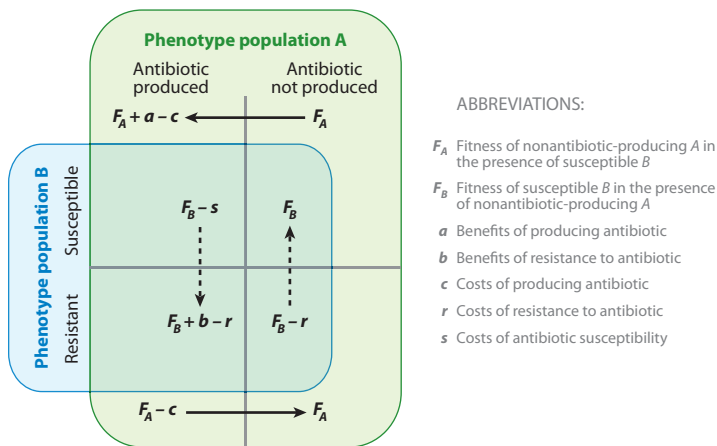


Figure 2

Relative fitness costs and benefits drive changes in antibiotic inhibitory and resistance phenotypes. Population A (solid arrows) produces an antibiotic that acts on population B (dashed arrows). There is selection on population A for antibiotic production where susceptible competitors are present and benefits outweigh costs of production. Population B experiences reciprocal selection for resistance due to the fitness costs imposed by the antibiotic. Development and spread of resistance exert reciprocal selection on A, reflecting the costs of antibiotic production. In coevolving populations, selection is also a function of the relative and absolute abundances of each phenotype, which are not incorporated here. *Modified from Leonard, 1977.*

potential suggests a greater capacity for adaptation within the population, critical to the process and rate of coevolution.

The strength of selection is a function of the costs of species interactions to the fitness of a population. Greater fitness costs impose stronger selection and consequently greater potential for shifts in population phenotypes. As coevolution proceeds, the balance of costs and benefits of a particular phenotype varies depending upon the phenotypes of the interacting species. Modifications of Leonard's simple model exploring selection pressures for plant pathogens (64) provide a useful template for describing the balance of fitness costs and benefits that influence antagonistic coevolution within soil communities. Consider a simple case with the potential for antibiotic production in one population and the potential for antibiotic resistance in a coexisting population (Figure 2). Selection for antibiotic-producers in population A is a function of the costs of the competitive interaction with the nonpro-

ducing population B as well as the costs and benefits of antibiotic production (Figure 2a,c). Simplistically, if $(a - c) > 0$, then there should be directional selection for antibiotic production in population A, resulting in increasing frequencies of antibiotic producers within the community. Subsequently, selection for antibiotic resistance within population B is a function of the costs of antibiotic inhibition to the population (s) as well as the potential costs and benefits of resistance (r and b , respectively). If $(b - r) > (s)$, then there should be directional selection for antibiotic resistance in population B, and corresponding increases in resistance frequency. Note that selection is a statistical phenomenon acting at the level of the populations, and reflected in shifts in the relative abundance of particular phenotypes within the population (Figure 3a). As the two populations continue to interact, stabilizing selection may result in reductions in both the frequencies of antibiotic producers within population A (Figure 3a) and, subsequently, the frequencies of resistance within population B. Ongoing coevolution imposes recurrent cycles of directional and stabilizing selection and corresponding increases and decreases in the frequency of antibiotic production and resistance genes in populations A and B, respectively (Figure 3a).

Among bacterial populations with the capacity to produce multiple antibiotics or diverse antagonistic phenotypes (e.g., siderophores and antimicrobial enzymes), selection may act successively or simultaneously on distinct antagonistic or resistance phenotypes or alleles (e.g., see Figure 3b,c). Both the density and the frequency of antibiotic production and resistance phenotypes are important to determining the relative fitness benefits of antibiotic resistance and production phenotypes, respectively. Intuitively, antibiotic production genes are likely to confer a greater fitness benefit within high as compared with low density communities because the frequency of competitive encounters is greater in high density locations (density-dependent selection). Furthermore, because rare antibiotics are likely to confer a greater fitness benefit than commonly

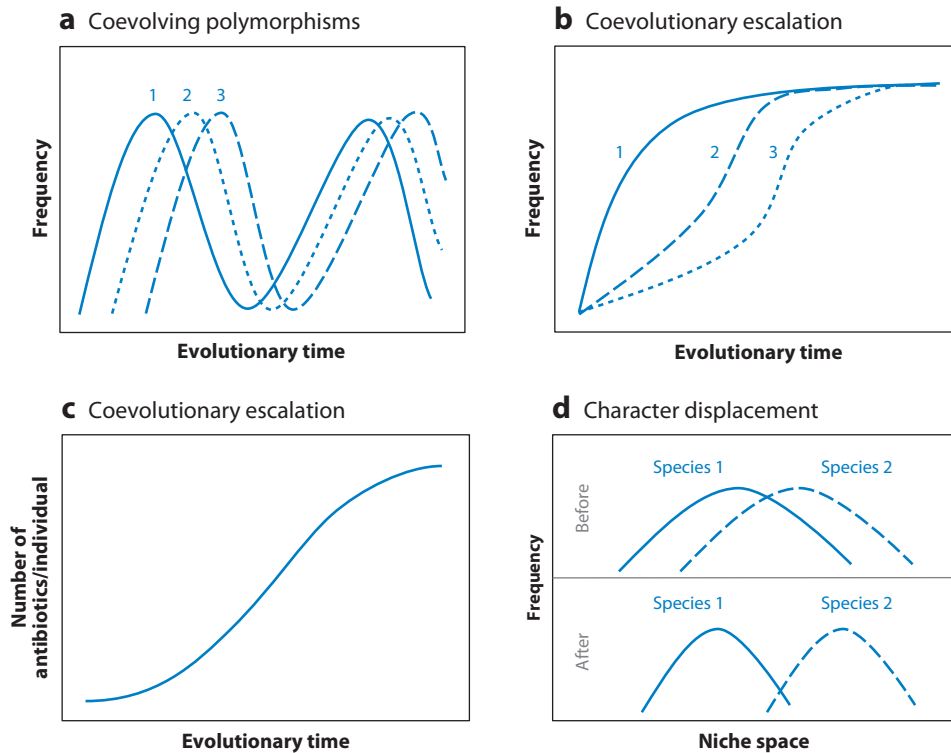


Figure 3

Variation in the frequency of individual alleles, phenotypes, or populations in response to coevolution over time. Lines with different dash patterns represent distinct alleles, phenotypes, or populations. Dynamics represented include (a) coevolving polymorphisms: The frequency of antagonistic phenotypes 1, 2, or 3 fluctuates over time; dominant antibiotic phenotypes undergo serial replacement in response to the development of resistance; (b) coevolutionary escalation: The frequency of individuals able to produce antibiotic 1, 2, or 3 increases over time; (c) coevolutionary escalation: The mean number of antibiotics produced per individual increases over time; and (d) coevolutionary displacement: Some individuals of species 1 and species 2 occupy overlapping niche space; among competitors, niche overlap decreases over time.

produced antibiotics, frequency-dependent selection is also likely to be important. Specifically, because a bacterium is resistant to antibiotics that it produces, commonly-produced antibiotics have more widespread resistance within the community and therefore provide a smaller fitness benefit than rare antibiotics to which there is little resistance. This rare advantage (frequency-dependent selection) contributes to the generation and maintenance of a diversity of antagonistic phenotypes within coevolving communities.

The coevolutionary framework suggests that effective management of disease-

suppressive potential is enhanced by increased understanding of the fitness costs and benefits of antibiotic production and resistance in soil microbes. However, there is little empirical data on the costs or benefits of antibiotic production or resistance phenotypes for microbial populations in soil communities [although note that toxin production by *Saccharomyces cerevisiae* was estimated to impose a fitness cost of 3% (132)]. In fact, one major concern with antibiotic resistance phenotypes within clinical populations is that there is strong evidence that the costs of antibiotic resistance can be mitigated over time by compensatory

mutations so that resistance may be maintained within bacterial populations with little apparent fitness costs (89). In a similar manner, compensatory mutations have the potential to reduce the costs of antibiotic production, potentially contributing to the long-term stability of antibiotic-producing populations despite a high frequency of resistance in competing populations. This suggests that the simple parameters noted in **Figure 2** may not be stable over time or among communities (for example, r or c may decline due to compensatory mutations). Furthermore, there is evidence that antibiotics may serve multiple functions in the ecology of microbes in natural environments, not only to mediate antagonistic interactions but also, for example, as signaling molecules that mediate gene expression within complex communities (27, 31, 65, 135). The potential multifunctionality of antibiotics or other antagonistic phenotypes suggests that these phenotypes may be maintained in the population even in the presence of high frequencies of resistant competitors. The possibilities of compensatory mutations and multifunctionality of antagonistic phenotypes may be important contributors to the long-term stability of pathogen-suppressive soils and may highlight critical questions for the study of antagonistic coevolution. More detailed insights into the fitness costs and benefits of antagonistic and resistance phenotypes are crucial to understanding the potential for active management of disease suppression.

COEVOLUTIONARY OUTCOMES AND DISEASE SUPPRESSION

There is a range of possible outcomes of coevolution based upon both empirical and modeling studies (112). Perhaps the most important to consider for soil microbial communities are coevolving polymorphisms, coevolutionary escalation, and coevolutionary displacement.

Coevolving polymorphisms refer to continual fluctuations in the relative frequency of different interaction phenotypes within coevolving populations, with serial replacement

of alleles (**Figure 3a**). Coevolving polymorphisms are widespread among interacting host-parasite populations, and have been suggested to be likely for antagonistic coevolution among antibiotic-producing bacteria (23). For disease-suppressive soils, coevolving polymorphisms may produce sequential dominance of antagonistic phenotypes, with the predominant phenotype at any given time likely to vary across the geographic mosaic. The temporal and spatial variation in the predominant phenotype produce complex selection on pathogen populations, enhancing the stability of disease suppression.

Coevolutionary escalation describes the case in which interacting populations make ever greater investments in attack and defense (**Figure 3b,c**). Relative to disease suppression, coevolutionary escalation focuses on selection for either increasing quantities or numbers of antagonistic compounds (for example, see **Figure 3b,c**). Increasing quantities of a single antibiotic may enhance disease-suppressive potential while increasing selection for resistance among coexisting soil microbes. Increasing diversity of antagonistic phenotypes imposes simultaneous selection for multiple resistance capabilities or for resistance phenotypes that confer protection against multiple antibiotics [e.g., efflux pumps (91)]. The requirement for simultaneous resistance against multiple antagonistic traits represents a significant challenge to coexisting microbes, including pathogens, and may contribute to the stability of disease suppression over time.

Coevolutionary displacement acts to reduce the frequency and/or intensity of antagonistic interactions. Among competitors, coevolutionary character displacement describes interactions that lead to niche differentiation, such as nutrient use specialization or shifts in nutrient use phenotype (**Figure 3d**). Coevolutionary character displacement minimizes the negative effects of interspecies interactions on fitness, and, consequently, antagonistic phenotypes are less likely to confer fitness benefits and accumulate in the community. In this way, coevolutionary character displacement is likely

to have negative effects on the development of disease-suppressive microbial communities. Coevolutionary displacement may also result in the elimination of one species from habitats where another species or set of species is present, specifically in cases where one population may lack the capacity to respond to a novel antagonistic phenotype in another. Across the geographic mosaic, however, spatial heterogeneity in the presence and absence of antagonistic phenotypes permits the maintenance of sensitive populations (16, 24), thus contributing to the maintenance of microbial diversity despite local coevolutionary displacement.

MICROBIAL COEVOLUTION IN SOIL: IMPLICATIONS FOR DISEASE SUPPRESSION AND MANAGEMENT

The goals of management to induce disease suppression are to increase the densities, frequencies, antagonistic abilities, and/or diversities of indigenous antagonist populations in soil. Antagonistic coevolutionary trajectories, either coevolving polymorphisms or coevolutionary escalation, offer possible pathways to accomplishing one or more of these goals. In contrast, coevolutionary displacement may constrain the capacity of soil microbial communities to antagonize or suppress plant pathogens. Coevolution provides a framework for considering the effects of microbial density, microbial diversity, limiting nutrient availability, nutrient diversity, and disturbance on population trajectories (Figures 4 and 5), and may provide practical insight into conditions likely to optimize the potential for achieving disease-suppressive, antagonistic microbial communities in soil.

Coevolution Across a Microbial Density Gradient

Density is a key factor in determining the evolutionary potential of a population (39). Larger population sizes generally have a greater diversity of genotypes and more potential for

mutation or recombination; this variation is the raw material for coevolution. Consequently, coevolutionary potential increases with increasing population densities (Figure 5a). Population density also influences the frequency and intensity of species interactions: Higher local densities increase the frequency of and the intensity of competitive interactions. This increases the potential fitness benefits and, ultimately, the expected prevalence of competitive phenotypes (for example, see References 1, 87).

This suggests two important considerations regarding microbial density in soil. First, managing communities in soil to sustain high microbial population densities enhances rates of coevolution and, assuming a trajectory of coevolving polymorphisms or escalation, increases the potential for disease suppression. Although density is often considered a possible correlate of disease suppression (for examples, see References 63, 83, 95), it is typically regarded as having a direct impact on interactions with pathogens: More antagonists equal more suppression (15, 29, 96, 103). However, greater attention should be given to the influences of microbial density on the competitive and coevolutionary interactions that generate and sustain antagonistic microbial communities. Second, and perhaps more importantly, where a community starts, or initial density, is likely to have a significant impact on the effectiveness of management to induce suppression. In particular, all other things being equal, management imposed upon initially high density communities should offer greater potential for inducing disease suppression than low density communities. Moreover, initial community densities, although rarely considered as an experimental factor, may provide a crucial pretreatment predictor of the potential effectiveness of management practices in inducing disease suppression (87, 129, 130). Furthermore, significant management-induced increases in population densities in soil may be an important step in the development of pathogen-suppressive soil communities, even if disease suppression is not immediately observed. Coevolutionary theory suggests that systematic research exploring the

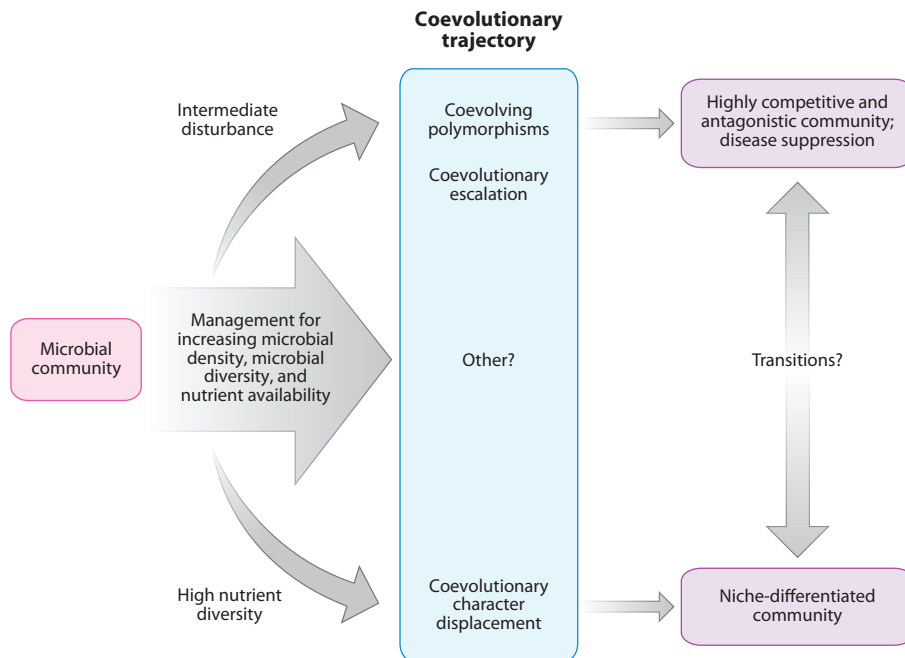


Figure 4

Coevolutionary dynamics as drivers of pathogen suppression. Microbial density, microbial diversity, and nutrient availability are hypothesized to primarily influence the rate of coevolution directly (through their influences on evolutionary potential) and indirectly (through their influences on the frequency and intensity of competitive interactions). A significant challenge for the future is to determine factors that influence the specific trajectory of coevolutionary dynamics towards antagonistic coevolution (coevolving polymorphisms or escalation leading to disease suppression) or niche differentiation (coevolutionary character displacement). We hypothesize that intermediate disturbance may favor coevolving polymorphisms and coevolutionary escalation, contributing to the development of a highly competitive and antagonistic community effective at suppressing plant pathogens. In contrast, we hypothesize that a high diversity of nutrient inputs may favor a coevolutionary trajectory towards niche differentiation, resulting in a less antagonistic microbial community. Future research should consider alternative possible trajectories and the selective forces that may mediate transitions from niche-differentiated to antagonistic soil microbial communities.

relationships between initial microbial densities and management-induced progress toward disease suppression among soil types and cropping systems provides substantial insight into the process of creating disease-suppressive microbial communities in soil.

Coevolution Across a Microbial Diversity Gradient

Both local, within-community and cumulative field-scale diversity contribute to coevolutionary potential. Locally, more diverse populations

have a greater array of phenotypes upon which selection can act, magnifying the potential for recombination to generate novel phenotypes (39, 59, 86, 136). Diversity among locations across a field generates the geographic mosaic of coevolution or spatially variable coevolutionary trajectories. The resulting collection of coevolutionary hot spots and cold spots, coupled with regular dispersal among locations (mediated by plowing, see below), can contribute to the maintenance of a diverse array of antagonistic phenotypes across the landscape.

This suggests that management to sustain diverse microbial communities contributes to the potential for coevolution and disease suppression within agricultural fields (Figure 5b), and, as with density, that initial diversities are significant in determining the effectiveness of management in inducing suppression. Diversity has been previously suggested to be an important attribute of healthy soils and a contributor to disease suppression (53, 95, 120, 133). However, microbial community diversity has been traditionally understood to be beneficial for disease suppression primarily because of the direct effects of a diverse pool of antagonists and competitors on pathogen populations (for example, see Reference 42). Use of a coevolutionary framework suggests diversity is also fundamental to the processes that generate and maintain disease-suppressive phenotypes. However, the effects of diversity on the potential for antagonistic competition (coevolving polymorphisms or coevolutionary escalation) versus niche differentiation (coevolutionary displacement) are more difficult to predict (Figure 4). The implications of alternative coevolutionary trajectories for disease suppression are substantial. This suggests that research to systematically characterize the relationships between diversity and the potential for antagonistic versus niche-differentiated coevolutionary outcomes in response to management is crucial both for understanding the processes that lead to consistent disease suppression and for development of effective management strategies.

Coevolution Across a Nutrient Availability or Environmental Productivity Gradient

Environmental quality or productivity is a key contributor to sustaining both a high density and a diverse soil microbial community. Thus, maintaining high environmental productivity, with particular emphasis on nutrient availability, is important to maintaining a high evolutionary potential, as described above (Figure 5c). Empirical research has confirmed

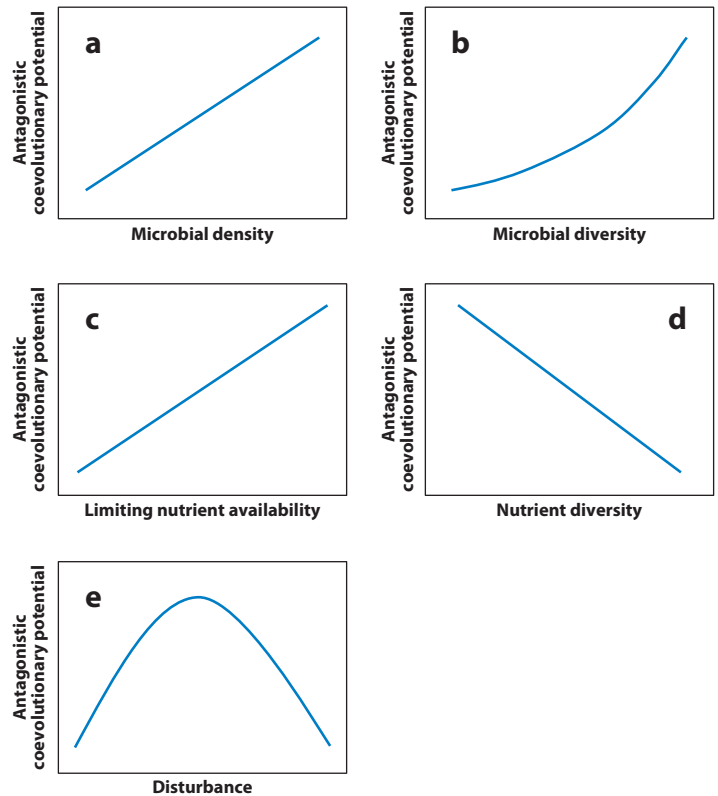


Figure 5 Antagonistic coevolutionary potential along gradients of (a) microbial density; (b) microbial diversity; (c) limiting nutrient availability; (d) nutrient diversity; and (e) disturbance.

the theoretical prediction that increasing productivity accelerates the rate of coevolution for host-parasite associations (70). Moreover, increasing nutrient availability can enhance the feasibility of making antibiotics or other costly antagonistic compounds (70, 71), thus contributing to the potential for achieved fitness benefits or disease suppression (70). Similarly, experimental research on the costs and benefits of microbial toxin production showed that the fitness benefits of toxin production were greatest at high nutrient availabilities (132). Finally, in soil communities, antibiotic-producing *Streptomyces* communities were both larger and more inhibitory when following large rather than small nutrient inputs (99). In total, there

is compelling experimental evidence that nutrient availability is likely to have a significant positive effect on microbial densities, rates of coevolution, and the relative fitness benefits of antagonistic phenotypes, all of which are critical to the development of disease-suppressive microbial communities.

Nutrient inputs have long been recognized as useful for enhancing disease suppression in soil, yet there is substantial variability in the effects of different inputs on disease suppression (49, 60, 93) and on the effects of the same input on disease suppression in different fields or the same field in different growing seasons (83, 110). This variability is a constraint to the practical use of organic inputs for disease management. Coevolutionary theory suggests that initial community density, diversity, or composition may be one source of the variation in the effectiveness of organic inputs in enhancing antagonistic activities in soil. For example, in cases where communities start at very low densities, successive or very high nutrient inputs may be needed to increase population densities to the point where competitive interactions are significant to fitness before disease suppression can be induced. This suggests that studying only disease suppression as a response to nutrient inputs may miss important steps or benchmarks in the development of disease-suppressive potential. In contrast, within communities that already support a reasonably high density and diversity of antagonists, nutrient inputs may have only small effects on densities but may play a critical role in enhancing the fitness benefits or capacity of populations to express antagonistic phenotypes (70). In either case, greater nutrient inputs are predicted to have a relatively larger effect on microbial community size or antagonistic activity, although there are likely to be limits to the capacity of communities to respond to single-event, inundative nutrient inputs. Sustained management of nutrient inputs should focus on supporting high community densities and diversities while providing consistent resources to enhance capacities for antagonistic phenotypes. Further research should focus on the interactions between initial community

characteristics (density and/or diversity) and the effects of varying inputs on disease suppression.

Coevolution Across a Nutrient Diversity Gradient

Nutrient availability is likely to interact significantly with nutrient diversity in its influences on coevolution. In particular, high nutrient diversity may maximize the potential for character displacement and niche differentiation among competitors as a means to reduce the significance of competition to fitness (92, 125) (**Figure 5d**). Rather than competing for many different resources and engaging in potentially costly production of antibiotics or other competitive tools, niche differentiation may optimize fitness via nutrient specialization. Coevolutionary character displacement, yielding a community of niche-differentiated, nonantagonistic microbial specialists, is substantially less effective in creating disease-suppressive soil communities than coevolutionary escalation.

If high nutrient diversities are more likely to result in coevolutionary character displacement, perhaps low nutrient diversities are especially likely to generate coevolutionary escalation or coevolving polymorphisms that yield strongly antagonistic populations. This may partly explain the consistency of long-term monoculture in achieving disease-suppressive soil communities (94, 100, 126). Long-term monoculture may work because it imposes strong directional selection for microbes that specialize on a very specific set of nutrients associated with a single host plant over sustained periods of time. By limiting the potential for niche differentiation, the low nutrient diversity establishes the context for coevolutionary interactions that maximize the fitness benefit of antagonistic phenotypes. This raises questions about the extent to which crop rotation, which provides a varying array of nutrients to microbial communities over time, influences the long-term coevolutionary trajectories of competing populations in soil. Although valuable for impeding the buildup of pathogen

populations in soil, rotation may also constrain the potential for coevolutionary escalation or coevolving polymorphisms. Future research exploring the tradeoffs between niche differentiation and antagonistic phenotypes among soil microbial populations, and how these are influenced by management strategy, is needed to enhance our capacities to manage microbial coevolution to achieve consistent disease suppression.

Coevolution Across a Disturbance Gradient

One hallmark of agricultural production systems is regular disturbance of soil communities. Plowing is perhaps the most dramatic disturbance event for most localized soil microbial communities, and disperses soil microbes. Movement or dispersal of organisms among the geographic mosaic of local populations has been shown to have dramatic impacts on coevolution across the landscape (39, 40, 71, 112, 118, 119, 123, 124, 132) (**Figure 5e**). Very high levels of movement can homogenize distinct communities, reducing the total diversity and thus the evolutionary potential across the landscape. In contrast, low levels of movement among local communities can significantly limit genetic diversity within any one site, similarly constraining coevolutionary potential. Intermediate levels of population mixing are optimal for enhancing the rate of coevolution, specifically by maximizing the evolutionary potential within local communities (17, 38, 39, 68, 80, 123). This suggests that experimental work on the impacts of plowing frequencies or intensities on rates of coevolution or the development of disease-suppressive soil communities may help to devise optimal plowing strategies for agricultural fields.

In disrupting locally adapted communities via plowing, coevolutionary hot spots, where significant reciprocal selection and coevolution have taken place, are likely to have a disproportionate impact on coevolution across the landscape (44, 50, 71, 124). In fact, coevolutionary hot spots in areas of high productivity may

largely drive landscape-scale dynamics (71). This suggests that the deliberate development of a series of microbial coevolutionary hot spots, established with very high nutrient availability, microbial density, and microbial community diversity, may offer a significant means for jump-starting the creation of disease-suppressive soil communities in agricultural fields. This idea is consistent with research showing that suppressive soils can be established or spread by mixing small volumes of already suppressive soils into nonsuppressive soils, or via targeted inoculation of soils with antagonists (for example, see References 56, 94, 102, 117, 128). Further work to consider the optimal density and spatial pattern of coevolutionary hot spots for sustaining disease suppression across an agricultural landscape, and how this interacts with plowing or dispersal dynamics, may contribute practical strategies for managing coevolution to achieve disease suppression.

Plowing may also contribute to the maintenance of an antagonistic versus a niche-differentiated coevolutionary trajectory. Regular dispersal may have more negative consequences for niche-differentiated, specialist microbes than for strongly antagonistic microbes. Although dispersal to a new community where there has been little selection for resistance may substantially increase the fitness benefits of antagonistic phenotypes, movement may place a specialist microbe in a habitat that lacks the optimal substrates it requires for growth or where its niche preferences overlap significantly with other microbes. Thus, following dispersal, maladaptation of coexisting microbes may serve to benefit the antagonist while penalizing the niche specialist (28, 85, 109). This suggests that plowing may help sustain a coevolutionary escalation or coevolving polymorphism trajectory that favors antagonistic generalists, thereby increasing the potential for developing disease-suppressive soils. This prediction is consistent with work showing that microbial niche breadth increases with dispersal (122). Wloch-Salamon et al. (132) also showed that the advantages of toxin production to microbial fitness are maximized at intermediate levels of dispersal, again

suggesting benefits of plowing to the development of disease-suppressive soils. Unfortunately, most field studies confound the effects of plowing on soil nutrient inputs (residue) and microbial movement. Future work to determine the specific impacts of the frequency, timing, and patterns of microbial movement on antagonistic phenotypes and disease suppression independent of the effects of plowing on nutrient availability will enhance understanding of microbial coevolutionary dynamics and the development of practical management strategies.

Coevolution and Management

In total, use of a coevolutionary framework for managing the dynamics of disease-suppressive activity in soil suggests the following:

1. Microbial density and diversity matter. In addition to managing communities to sustain high microbial densities and diversities, initial density and diversity should be considered as important variables influencing the effectiveness of management in enhancing disease suppression. Systematic research on the relationships between initial microbial density or diversity and management-induced progress towards disease suppression may identify threshold initial population densities/diversities required for successful pathogen suppression in different soil types or cropping systems. Initial densities may be significant predictors of the success of management to enhance disease suppression, potentially serving as pretreatment decision aids for the use of green manures or compost amendments.
2. Nutrient quantity is important, but is likely not independent of nutrient diversity in its effects on microbial coevolutionary dynamics. Further work is needed to explore the short- and long-term effects of nutrient diversity on suppressive activity and to understand the ways in which nutrient quantity and diversity in-

teract with microbial density and soil type in inducing disease suppression. In particular, understanding the nutrient conditions under which communities follow an antagonistic coevolutionary trajectory versus a coevolutionary displacement trajectory is crucial for effective management of disease-suppressive potential.

3. Creation of coevolutionary hot spots may provide a practical means to jump-start or sustain the development of suppressive soils across an agricultural field.
4. Soil tillage, and particularly its impacts on microbial movement, may have significant effects on the spread and fitness benefits of antagonistic phenotypes; further work should consider how varying frequencies or timing of tillage may alter trajectories towards disease suppression.
5. Basic information on the costs and benefits of antagonistic phenotypes for soil microbes within complex soil communities and on temporal shifts in the diversity and abundance of distinct antagonistic phenotypes in agricultural soils provides important insight into the dynamics and stability of disease suppression.

Finally, it is important to note limitations of the microbial coevolutionary framework for studying disease suppression. Not all disease suppression is mediated via soil microbes (62). For example, brassicaceous crops inhibit plant pathogens directly through production of glucosinolates. Moreover, although not considered here, plants may participate directly in coevolutionary interactions with their soil microbes by selection for specific antagonistic phenotypes and by altering gene expression among soil microbes. Future work should incorporate these interactions explicitly into multi-trophic coevolutionary models. There is not a single pathway to comprehensive suppression against all pathogens. Effective antagonistic populations or phenotypes are likely to vary for different plant pathogens, suggesting that distinct evolutionary and coevolutionary trajectories may be significant to disease suppression in different cropping systems.

SUMMARY, CONCLUSIONS, AND FUTURE DIRECTIONS

Our goal in this review has been to synthesize and apply concepts of coevolution to the development and management of disease suppression within soil microbial communities. Development of a conceptual framework for managing microbial antagonistic activities in soil can provide a fundamentally different collection of research questions and management objectives than a purely empirical approach. In particular, by considering the impacts of management on coevolution and the likelihood of an antagonistic coevolutionary trajectory, this framework suggests a new focus on the impacts of microbial density, diversity, and movement on the success of management strategies in inducing disease suppression. Furthermore, this approach offers the potential for identifying density or diversity benchmarks or management targets that may be crucial steps in the development of disease suppression, offers insight into possible reasons for failure of management to achieve suppression, and provides a foundation for predictions of the success of management in inducing suppression as a function of the initial characteristics of a site. Finally, the

coevolutionary framework integrates studies of disease suppression with the fundamental ecology and evolutionary biology of indigenous soil microbes, and raises important basic questions about the fitness costs and benefits of antagonistic phenotypes that are crucial to the long-term stability of disease suppression.

Coevolution has been argued to be “one of the most important ecological and genetic processes organizing earth’s biodiversity” (112). For soil microbes, microbial coevolutionary dynamics are a primary driver for the accumulation of antagonistic activities within communities. Evolutionary change within soil microbial communities occurs over short time scales and in response to management. Thus, our capacities to effectively utilize management to achieve specific coevolutionary outcomes require more detailed understanding of microbial coevolutionary dynamics in soil. Rapid advances in our capacity to study complex soil microbial communities will contribute significantly to this process (for example, see Reference 30). Future work to manage and sustain disease-suppressive activities within soil microbial communities will be enriched by adoption of a coevolutionary perspective.

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Contents

Not As They Seem <i>George Bruening</i>	1
Norman Borlaug: The Man I Worked With and Knew <i>Sanjaya Rajaram</i>	17
Chris Lamb: A Visionary Leader in Plant Science <i>Richard A. Dixon</i>	31
A Coevolutionary Framework for Managing Disease-Suppressive Soils <i>Linda L. Kinkel, Matthew G. Bakker, and Daniel C. Schlatter</i>	47
A Successful Bacterial Coup d'État: How <i>Rhodococcus fascians</i> Redirects Plant Development <i>Elisabeth Stes, Olivier M. Vandeputte, Mondher El Jaziri, Marcelle Holsters, and Danny Vereecke</i>	69
Application of High-Throughput DNA Sequencing in Phytopathology <i>David J. Studholme, Rachel H. Glover, and Neil Boonham</i>	87
<i>Aspergillus flavus</i> <i>Saori Amaike and Nancy P. Keller</i>	107
Cuticle Surface Coat of Plant-Parasitic Nematodes <i>Keith G. Davies and Rosane H.C. Curtis</i>	135
Detection of Diseased Plants by Analysis of Volatile Organic Compound Emission <i>R.M.C. Jansen, J. Wildt, I.F. Kappers, H.J. Bouwmeester, J.W. Hofstee, and E.J. van Henten</i>	157
Diverse Targets of Phytoplasma Effectors: From Plant Development to Defense Against Insects <i>Akiko Sugio, Allyson M. MacLean, Heather N. Kingdom, Victoria M. Grieve, R. Manimekalai, and Saskia A. Hogenbout</i>	175
Diversity of <i>Puccinia striiformis</i> on Cereals and Grasses <i>Mogens S. Hovmøller, Chris K. Sørensen, Stephanie Walter, and Annemarie F. Justesen</i>	197

Emerging Virus Diseases Transmitted by Whiteflies <i>Jesús Navas-Castillo, Evvira Fiallo-Olivé, and Sonia Sánchez-Campos</i>	219
Evolution and Population Genetics of Exotic and Re-Emerging Pathogens: Novel Tools and Approaches <i>Niklaus J. Grünwald and Erica M. Goss</i>	249
Evolution of Plant Pathogenesis in <i>Pseudomonas syringae</i> : A Genomics Perspective <i>Heath E. O'Brien, Shalabb Thakur, and David S. Guttman</i>	269
Hidden Fungi, Emergent Properties: Endophytes and Microbiomes <i>Andrea Porras-Alfaro and Paul Bayman</i>	291
Hormone Crosstalk in Plant Disease and Defense: More Than Just JASMONATE-SALICYLATE Antagonism <i>Alexandre Robert-Seilaniantz, Murray Grant, and Jonathan D.G. Jones</i>	317
Plant-Parasite Coevolution: Bridging the Gap between Genetics and Ecology <i>James K.M. Brown and Aurélien Tellier</i>	345
Reactive Oxygen Species in Phytopathogenic Fungi: Signaling, Development, and Disease <i>Jens Heller and Paul Tudzynski</i>	369
Revision of the Nomenclature of the Differential Host-Pathogen Interactions of <i>Venturia inaequalis</i> and <i>Malus</i> <i>Vincent G.M. Bus, Erik H.A. Rikkerink, Valérie Caffier, Charles-Eric Durel,</i> <i>and Kim M. Plummer</i>	391
RNA-RNA Recombination in Plant Virus Replication and Evolution <i>Joanna Sztuba-Solińska, Anna Urbanowicz, Marek Figlerowicz,</i> <i>and Jozef J. Bujarski</i>	415
The <i>Clavibacter michiganensis</i> Subspecies: Molecular Investigation of Gram-Positive Bacterial Plant Pathogens <i>Rudolf Eichenlaub and Karl-Heinz Gartemann</i>	445
The Emergence of Ug99 Races of the Stem Rust Fungus is a Threat to World Wheat Production <i>Ravi P. Singh, David P. Hodson, Julio Huerta-Espino, Yue Jin, Sridhar Bhavani,</i> <i>Peter Njau, Sybil Herrera-Foessel, Pawan K. Singh, Sukhwinder Singh,</i> <i>and Velu Govindan</i>	465
The Pathogen-Actin Connection: A Platform for Defense Signaling in Plants <i>Brad Day, Jessica L. Henty, Katie J. Porter, and Christopher J. Staiger</i>	483

Understanding and Exploiting Late Blight Resistance in the Age of Effectors <i>Vivianne G.A.A. Vleeshouwers, Sylvain Raffaele, Jack H. Vossen, Nicolas Champouret, Ricardo Oliva, Maria E. Segretin, Hendrik Rietman, Liliana M. Cano, Anoma Lokossou, Geert Kessel, Mathieu A. Pel, and Sophien Kamoun</i>	507
Water Relations in the Interaction of Foliar Bacterial Pathogens with Plants <i>Gwyn A. Beattie</i>	533
What Can Plant Autophagy Do for an Innate Immune Response? <i>Andrew P. Hayward and S.P. Dinesh-Kumar</i>	557

Errata

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