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Effects of phytopathogens on plant community dynamics: A review

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ABSTRACT

The impacts of phytopathogens on agricultural systems, disease controls and economic losses caused by the pathogens are internationally important research subjects. Recently, increasing evidence has shown that phytopathogens play a critical role in mediating competitions among their host plant species. According to Chesson's coexistence framework, niche differences (i.e., species differences in resource use, host-specific pathogen loads, and other ecosystem processes) are more associated with intra-specific limitation than with inter-specific limitation. However, fitness differences (i.e., variations in competition abilities among plant species) can determine the dominance of plant species. An increase in niche differences tends to promote the coexistence of plant species, whereas an increase in fitness differences tends to exclude competing species. In this review, two types of pathogen mechanisms that could affect plant communities are discussed based on the coexistence framework. Type I is the density-dependent pathogen mechanism, in which disease occurrence in a community is related to the density of host species. In this mechanism, disease transmission increases niche differences as a host species becomes common, and/or reduces niche differences as a host species becomes rare. Type II is the density-independent pathogen mechanism, in which disease transmission does not depend on host plant density. This mechanism mainly focuses on fitness differences. When competitively dominant host plants are more susceptible to pathogens, pathogens can reduce fitness differences among species and thereby improve plant diversity. Alternatively, if the competing species are more resistant than other species to pathogens, fitness differences are prone to be increased.

The Janzen–Connell effect (JC effect) and plant–soil feedback theory are characterized by Type I phytopathogen mechanism and are discussed here in details. The JC hypothesis has been mostly applied to forest ecosystems, whereas the plant–soil feedback theory has been applied more widely in several ecosystems. The JC hypothesis assumes that seeds/seedlings around the mother plant are most susceptible to host-specific pathogens. Since seed/seedling mortality caused by pathogens is related to plant density, the JC effect is an example of negative density dependence. The plant–soil feedback theory illustrates the interactions between plants and soil. Plants can alter soil properties through the input of organic matter and chemicals, and provide habitats and nutrients for soil organisms, which in turn can affect plant performance. This feedback can be either negative or positive, depending on whether it leads to a net reduction or an enhancement of plant growth when comparing the plant species cultured in soil conditioned by the plant to that in mixed soil.

This review summarizes phytopathogen effects on plant diversity, plant invasion, community succession, and addresses some future research challenges. Several research goals are highlighted; for instance, studies of pathogens with multiple hosts and host plants with multiple pathogens are necessary for a better understanding of the role of phytopathogens in plant community dynamics. Research on the interactions of plant pathogen with soil legacy (priority) could provide new insights into the influences of phytopathogen on plant communities during climate change. In addition, a combination of theoretical modeling and field studies would be an effective way to examine the function of phytopathogens in plant community dynamics.

1. Introduction

In agricultural ecosystems, plant pathogens not only negatively affect seedling survival and growth, but also reduce crop production and quality, which results in a great economic loss [1–2]. Until now most of the work on plant pathogens has been focused on how to control and lower disease occurrences, while the function of pathogens in natural ecosystems has not been thoroughly investigated.

Plant pathogens can transmit horizontally via vectors such as soil, water and insects, as well as vertically via mother plants [3]. Some pathogens are specific for certain plant species, while others that are non-specific have a broad range of hosts. Hence, plant pathogens may play different roles among species within a community [4–5]. In this paper,

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we summarized the available mechanisms by which plant pathogens affect species composition and community dynamics, reviewed recent research developments in this area, and discussed the possible directions for future research.

2. General roles of plant pathogens in plant communities

The interactions between plants and pathogens can promote or exclude species coexistence. Plant pathogens can influence community stabilities when their impact on plant growth relies on host relative abundance [6]. For example, host-specific pathogens increase as their preferred host becomes abundant in a community, thus limit further growth of the host, which is beneficial to the stabilization of the community [7–8]. When the impact of pathogens on communities does not depend on host abundance, it often alters fitness differences among plant species and indirectly affects species coexistence [6]. For instance, some pathogens that have a broad range of hosts can transmit among a variety of plant species. When the infection of these pathogens on rare species exceeds that on dominant species, it will lead to the further growth of highly competitive species, and cause the increase of fitness differences that might destabilize the whole community [9].

3. Mechanisms of plant pathogen effects on plant communities

In a community, plant species have niche differences that promote coexistence and fitness differences, which exclude coexistence. Niche differences should overrule fitness differences, if plant species coexist persistently in an ecosystem. This is referred to as Chesson's coexistence framework [10] (Fig. 1). Here we synthesized the major theories on how pathogens influence plant communities based on this framework. The theories include density-dependent mechanism that affects niche differences of plant species, and density-independent mechanism that affects fitness differences (Table 1).

3.1. The Janzen–Connell hypothesis

Janzen (1970) and Connell (1971) hypothesized that specific enemies can maintain rainforest diversity by controlling the density of dominant species. That is, specific enemies such as predators or pathogens can effectively infect hosts and limit their further growth as host abundance increases in the community. In tropical ecosystems, seed dispersal from seed rains leads to a high seed density near the mother plant, which makes the seeds more susceptible to specific enemies and causes high seed and/or seedling mortality. This phenomenon is called the Janzen–Connell effect (JC effect). The JC effect is also known as negative density dependence (NDD), as the effect is associated with density of a population and the population was negatively mediated by the enemies.[11–12].

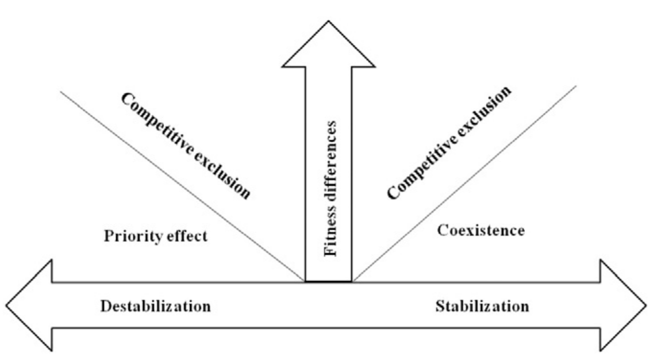

Fig. 1. The theoretical framework describing how interactions of plants with pathogens influence plant community dynamics [10]. The figure is adapted and substantially modified by Mordecai [6]. The x-axis measures the strength of stabilization or destabilization, and the y-axis measures the fitness differences between species.

Table 1
Mechanisms by which pathogens affect plant community dynamics.

Mechanisms	Plant community
A) Density-dependent pathogens	
a) Stabilization: disease transmission increases as a species becomes common.	
Janzen–Connell hypothesis	grasslands [16];forests [7,13,44–45];
Negative plant–soil feedbacks	grasslands [47–50];fields [24,51];forests [52,53];
Density-dependent attack	grasslands [54]; forests [55]
Density-dependent cost of infection	fields [32,56,57]
Disease response to host diversity	grasslands [58,59]; fields [60–62]
b) Destabilization: disease transmission increases as a species becomes rare.	
Pathogen spillover	grasslands [9]; forests [33,63]
Positive plant–soil feedbacks	grasslands [26,34]
B) Density-independent pathogens	
a) Reduced fitness differences: competitively dominant species experience the greatest cost during pathogen infections.	
Equalizing trade-offs	grasslands [37,38,64]; forests [65,66]; fields [67]
Enemy release of invading plants	forests [39]
Agriculture and biocontrol	fields [40,68]
b) Fitness hierarchy reversal/increased fitness differences: susceptible hosts face extreme fitness costs.	
Pathogen-driven succession	deserts [69–71]; forests; fields [72]
Highly virulent epidemics	forests [42]

Note: Modified from Mordecai [6].

To prove the JC effect, ecologists have paid much attention studying the role of pathogens in influencing species diversity. They hypothesized that pathogen accumulation near mother plants can reduce the survival and growth of conspecific seedlings owing to a high seed density, and consequently provide space for plant species with the same resource requirements [13–14]. For example, Augspurger [15] monitored the seed germination and seedling survival of a wind-dispersed tree *Platypodium elegans* on Barro Colorado Island, Panama for one year, and found that both the incidence and the rate of seedling damping-off caused by fungal pathogens were negatively correlated with the distance from the parental tree. Bell et al. [8] in the Chiquibul Forest Reserve near the Las Cuevas Research Station also examined the relationship between the seedling survival rate of tropical forest plant *Sebastiana longicuspis* and the plant population density. Their finding was that seedling survival was three times higher at low density in the non-fungicide-treated plots, whereas it was unaffected by density in the fungicide-treated plots, suggesting that the application of fungicides may kill soil pathogens and increase seedling survival.

Though the JC effect was proposed for tropical forest systems, it has also been applied to other ecosystems such as grassland [16] and ocean systems [17]. For instance, Petermann et al. [16] conducted a controlled greenhouse experiment with 24 species planted in soil from field monocultures, which revealed the JC effect on plant dynamics in the European temperate grasslands. The results showed that the reduction of biomass in monoculture was due to the build-up of soil pathogens, which indicated that the JC effect might play a critical role in driving plant diversity in temperate ecosystems.

3.2. Plant–soil feedbacks

Plants can alter soil properties through the input of organic matter and chemicals, which in turn affect plant performance. This process is referred to as plant–soil feedbacks (PSFs) [18–20]. There is increasing evidence that soil pathogens have an important function in the process