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Cryptic Host Relationships of Soil borne Fungal Pathogens

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Abstract: -

Much of what is currently understood about the population biology and ecology of soilborne fungal pathogens comes from studies focused on populations isolated from diseased plants or soil associated with symptomatic vegetation. Many of these pathogens are capable of infecting a wide range of crop species, including key agronomic, horticultural, ornamental, and forest plants. For example, *Verticillium dahliae* is known to infect more than 400 different plant species. Traditionally, plants that do not exhibit disease symptoms have been classified as nonhosts for *V. dahliae*. However, this classification can be misleading, as it does not account for the possibility that the fungus may exist within these plants as an endophyte. In fact, multiple studies have reported the presence of *V. dahliae* in asymptomatic plants, suggesting that these plants should still be considered hosts. This article compiles evidence indicating that, beyond being a significant vascular plant pathogen, *V. dahliae* may also have a cryptic endophytic phase in many asymptomatic plants. Such relationships appear to be more common in nature than previously recognized. Therefore, we propose refining the terminology used to describe host-fungus interactions by distinguishing between “symptomatic hosts,” where fungal infection leads to disease, and “asymptomatic hosts,” which harbor the fungus endophytically without showing symptoms. True nonhosts, on the other hand, should be reserved for plant species that do not interact with the fungus at all. Expanding the definition of a “host plant” to include asymptomatic carriers of the fungus suggests that the host range of some soilborne fungal pathogens is likely broader than previously thought. Ignoring the potential for these pathogens to persist in asymptomatic plants as endophytes leaves critical gaps in our understanding of their population biology, ecology, persistence, and dissemination within agroecosystems.

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Introduction

Endophytes are microorganisms that reside within plant tissues without causing visible symptoms of infection. These organisms, which primarily include bacteria and fungi, often go undetected unless plant tissues are examined microscopically, isolated under sterile conditions, or analyzed through polymerase chain reaction (PCR) techniques to detect microbial DNA from surface-sterilized plant material. Despite their inconspicuous nature, fungal endophytes—our primary focus in this discussion- are widespread among vascular plants, as evidenced by numerous studies documenting their isolation and identification. The diversity of fungal endophytes is substantial, with some plant species hosting hundreds of different fungal species, particularly in tropical environments. Many of these fungi have been explored for their ability to produce biologically active secondary metabolites with potential applications in medicine, agriculture, and other fields.

Fungal endophytes differ from mycorrhizal fungi, which extend beyond plant roots, whereas endophytes are confined to internal plant tissues. Within this broad category, Rodriguez et al. classified fungal endophytes into four groups: *Clavicipitaceous* endophytes, which are highly specialized and primarily found in grasses; non-*Clavicipitaceous* fungi that colonize the entire plant; non-*Clavicipitaceous* hyper-diverse fungi that colonize aerial plant tissues; and dark septate endophytes. Among these, class 1 *Clavicipitaceous* endophytes, particularly those in the genera *Epichloë* and *Neotyphodium*, have been extensively studied. These fungi form a specialized symbiotic relationship with grasses, providing benefits such as drought tolerance, enhanced resistance to pests and pathogens, and improved nutrient uptake, particularly phosphorus. They are also well known for producing alkaloids and other bioactive compounds that protect against herbivory but can be toxic to vertebrates. However, most fungal endophytes are generalists rather than obligate symbionts. Notably, some well-known plant pathogens, such as *Fusarium* and *Rhizoctonia*, as well as plant decay fungi like those in the genus *Xylaria*, have also been identified as endophytes. Since much research has traditionally focused on these fungi as pathogens, our understanding of their ecological roles in agricultural systems remains incomplete.

Redefining the concept of host plant for fungal pathogens

In plant pathology, the term "host" has traditionally been associated with plants that exhibit disease symptoms following fungal infection and colonization, influenced by environmental conditions. However, from an ecological standpoint, a host plant is any plant that harbors a fungus, regardless of whether symptoms are present. If a plant is colonized by a fungal pathogen but remains asymptomatic, it may be more appropriate to classify it as a host rather than a nonhost within an ecological framework. Whetzel addressed this distinction early on by suggesting the term "suscept" for plants vulnerable to disease. Other terms used to describe plants that carry pathogens without showing symptoms include "symptomless carriers" or "tolerant" hosts. In this discussion, we will examine cases where fungi-specifically *Verticillium dahlia*-exist in an endophytic relationship with certain plants while acting as pathogens in others. To clarify, we differentiate between "symptomatic hosts," which display visible disease symptoms due to fungal infection, and "asymptomatic hosts," where infection leads to an endophytic association. This concept differs from "tolerant or resistant" symptomatic hosts, in which fungal colonization can lead to varying symptom severity, ranging from no disease to reduced disease intensity. The variation in symptom expression on symptomatic hosts may result from (i) differences in pathogen virulence, (ii) varying levels of plant resistance, or (iii) specific interactions between plant and pathogen genotypes.

For example, the defoliating pathotype of *V. dahliae* exhibits higher virulence on cotton and olive than the non-defoliating pathotype, regardless of the plant genotype. Similarly, under controlled conditions, isolates of *V. dahliae* from artichokes caused disease in artichokes, cardoons, eggplants, and watermelons, while isolates from watermelon, muskmelon, and eggplant displayed different pathogenic behaviors depending on the host–isolate combination. Symptomatic hosts of *V. dahliae* are generally restricted to dicotyledonous plants, whereas the full range of asymptomatic hosts remains uncertain, though they appear to be primarily associated with cereals and monocot crops.

Symptomatic host plants of *V. dahlia*

The majority of research on *Verticillium dahliae* has been conducted from a plant-pathogenic perspective, with numerous comprehensive reviews addressing this role. *V. dahliae* is an anamorphic Ascomycete primarily recognized as a significant soilborne plant pathogen, capable of persisting in the soil for long periods due to the formation of microsclerotia-clusters of thick-walled, heavily melanized cells that serve as fungal resting structures. The disease occurs when the fungus extensively colonizes a plant's vascular system, leading to wilting and necrosis. Over 400 plant species, all dicotyledonous and including key agricultural, ornamental, and forestry plants, have been identified as hosts in the traditional plant pathology sense or as symptomatic hosts under the classification used here.

Rather than being strictly host-specific, *V. dahliae* isolates are considered host-adapted, meaning they can infect multiple plant species but tend to be more virulent on the host from which they were originally isolated. The population structure of *V. dahliae* has been extensively examined through vegetative compatibility tests, which assess the ability of isolates to undergo hyphal anastomosis and form stable heterokaryons. This research has led to the classification of several vegetative compatibility groups (VCGs). In potato, for instance, VCG 4A is considered adapted to the crop and is also the more virulent of the two primary VCGs (VCG 4A and VCG 4B) found in U.S. potato fields. However, in other regions, different VCGs, such as 2A and 2B, are also associated with potato. These host adaptations are not limited to potatoes. In Israel, for example, VCG 2B isolates originating from cotton were highly virulent on cotton but showed lower virulence on eggplant. Conversely, VCG 2B isolates from other plant sources were more virulent on eggplant than on cotton. Collectively, these findings suggest that specific *V. dahliae* populations-whether defined by VCGs or genotypes—exhibit varying degrees of adaptation to particular plant hosts. However, under controlled conditions, isolates can still cause disease in plant species beyond their original host.

Asymptomatic host plants of *V. dahlia*

Scientific literature has documented *Verticillium dahliae* acting as an endophyte in asymptomatic plant species. Many of these plants are cereal crops, commonly included in crop rotations to manage *Verticillium* wilts, as well as weeds that coexist with cultivated crops in agricultural fields. Although associations between *V. dahliae* and monocot plants have been reported, they are primarily based on inoculation studies rather than field sampling. In controlled experiments, Mol (55) inoculated various plant species using a *V. dahliae* isolate from potato and observed no disease symptoms in barley or wheat. However, a significant accumulation of microsclerotia was found in barley roots, whereas only a limited amount was detected in wheat roots. Similarly, Krikun and Bernier conducted greenhouse experiments with two *V. dahliae* isolates (one from potato and another from pea), inoculating several plant species, including the monocots wheat, barley, and oat. The fungus was recovered from aboveground tissues in an asymptomatic state, but its presence depended on the specific plant species–fungus isolate combination. For instance, the potato isolate was detected in oat but not in barley, while the pea isolate was found in barley but not in oat. Interestingly, even within a single plant species, interactions varied by genotype, as *V. dahliae* was recovered from the wheat cultivar 'Glenlea' but not from 'HY-320.' These findings suggest that *V. dahliae* forms highly specialized endophytic relationships with monocots. This raises the question of whether these associations represent an early stage of adaptation toward pathogenicity in monocots or if they are stable endophytic interactions. While a barley disease caused by *V. dahliae* was reported in 1986 no further cases of *Verticillium* wilt in monocots have been documented since, suggesting that *V. dahliae* isolates capable of infecting monocots are rare. Overall, these studies indicate that (i) *V. dahliae* can colonize monocot species as an endophyte, and (ii) the nature of this interaction appears highly specialized, likely influenced by specific plant genotype–fungus genotype dynamics.

Implications and research needs

Expanding our understanding of *Verticillium dahliae's* ability to colonize plants—ranging from asymptomatic to symptomatic hosts—will provide a more comprehensive perspective on this pathogen. From a practical standpoint, gaining deeper insights into the interactions between *V. dahliae* and cereal crops could help optimize crop rotation strategies to reduce soil inoculum levels, making it a more effective management tool. Certain cereal crops, or even specific cultivars, may be less susceptible to *V. dahliae* colonization or may support lower levels of inoculum and microsclerotia compared to symptomatic hosts or other asymptomatic plant species. Additionally, understanding the role of weeds as reservoirs of *V. dahliae* is particularly relevant for sustainable and organic farming systems, where weed populations are often more prevalent than in conventional agriculture. Some weed species may be of greater concern than others as potential inoculum sources for *V. dahliae*.

To date, few studies have explored the population structure of *V. dahliae* in asymptomatic hosts, with research mainly focusing on vegetative compatibility group (VCG) typing of isolates from weed species. Several critical questions remain unanswered. Is there a distinct population of *V. dahliae* that primarily colonizes asymptomatic hosts as an endophyte, separate from the population that infects symptomatic hosts as a pathogen, Or does the entire species possess the flexibility to function as both an endophyte and a pathogen depending on the host species and environmental conditions in a given location? Limited research suggests that *V. dahliae* isolates obtained from asymptomatic plants can still infect and cause disease in symptomatic hosts under controlled conditions. While this implies that *V. dahliae* can alternate between an endophytic and pathogenic lifestyle, further studies—especially field-based research—are necessary to confirm these findings. Another crucial question is whether asymptomatic hosts serve as long-term reservoirs for *V. dahliae* in the absence of symptomatic hosts. Do asymptomatic plants generate similar quantities of microsclerotia compared to symptomatic plants? In other words, can *V. dahliae* survive as effectively in asymptomatic hosts as it does in diseased plants? Inoculation studies involving potato and various cereal crops have shown that cereals produce significantly fewer microsclerotia in their aerial parts and roots than infected potato plants. This suggests that while asymptomatic hosts may not be as conducive to *V. dahliae* survival in the short term, they could still contribute to maintaining fungal populations in the environment over time. However, these findings are based on a limited number of studies conducted on a small set of asymptomatic hosts under laboratory conditions. Given these constraints, broader research efforts are essential to draw more definitive conclusions. As with many soilborne fungal pathogens, new cases of *Verticillium* wilt are emerging in crops that were previously considered nonhosts or only minor symptomatic hosts of *V. dahliae*, including cauliflower, horseradish, lettuce, and pepper. Alongside earlier reports of *V. dahliae* causing disease in barley, these instances suggest that the species may possess greater biological diversity than traditionally recognized. The conventional focus on its role as a plant pathogen may have overlooked significant aspects of its ecology and evolution, leaving much to be discovered.

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