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Letter to the Editor

Hidden Host Plant Associations of Soilborne Fungal Pathogens: An Ecological Perspective

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ABSTRACT

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Much of the current knowledge on population biology and ecology of soilborne fungal pathogens has been derived from research based on populations recovered from plants displaying disease symptoms or soil associated with symptomatic plants. Many soilborne fungal pathogens are known to cause disease on a large number of crop plants, including a variety of important agronomical, horticultural, ornamental, and forest plants species. For instance, the fungus *Verticillium dahliae* causes disease on >400 host plants. From a phytopathological perspective, plants on which disease symptoms have not been yet observed are considered to be nonhosts for *V. dahliae*. This term may be misleading because it does not provide information regarding the nature of the plant–fungus association; that is, a nonhost plant may harbor the fungus as an endophyte. Yet, there are numerous instances in the literature where *V. dahliae* has been isolated from asymptomatic plants; thus, these plants should be considered hosts. In this article, we synthesize scattered research that indicates that *V. dahliae*, aside from being a successful and significant vascular plant pathogen, may have a cryptic biology on numerous asymptomatic plants as an endophyte. Thus, we suggest here that these endophytic associations among *V. dahliae* and asymptomatic plants are not unusual relationships in nature. We propose to embrace the broader ecology of many fungi by differentiating between "symptomatic hosts" as those plants in which the infection and colonization by a fungus results in disease, and "asymptomatic hosts" as those plants that harbor the fungus endophytically and are different than true nonhosts that should be used for plant species that do not interact with the given fungus. In fact, if we broaden our definition of "host plant" to include asymptomatic plants that harbor the fungus as an endophyte, it is likely that the host ranges for some soilborne fungal pathogens are much larger than previously envisioned. By ignoring the potential for soilborne fungal pathogens to display endophytic relationships, we leave gaps in our knowledge about the population biology and ecology, persistence, and spread of these fungi in agroecosystems.

Endophytes are defined as organisms living inside plants that exhibit no visible symptoms as a result of this colonization (60) and generally include bacterial and fungal organisms. Endophytic relationships often go unnoticed due to the lack of symptomatology in the plant and are usually only discovered by examining internal tissues under a microscope, by aseptic isolation from plants, or from polymerase chain reaction (PCR) detection of microorganisms in DNA extracted from surface-disinfested plant tissues (67). Yet fungal endophytes, our focus in this article, are nearly ubiquitous across all groups of vascular plants, as documented by the extensive literature describing isolation and identification of these organisms (2,61). There is also a significant biological diversity among fungal endophytes, and it is not rare for some plant species to host hundreds of different fungal endophytic species (30,51,63), at least under tropical environments. Many of these endophytic fungi have been sought and characterized for their ability to produce biologically active secondary metabolites with potential uses in medicine, agriculture, and other areas (73).

Fungal endophytes are distinct from mycorrhizal fungi, which grow both inside and beyond the plant root system, whereas the growth of endophytes is limited to internal tissues of the plant. Defined in this way, endophytic fungi comprise a highly diverse group of species. Rodriguez et al. (63) categorized endophytic fungi into four classes: class 1, Clavicipitaceous; class 2, non-Clavicipitaceous fungi colonizing the entire plant; class 3, non-Clavicipitaceous hyper-diverse fungi colonizing aerial plant tissues; and class 4, dark septate endophytes. The Clavicipitaceous endophytes of grasses (class 1) are the best-studied group of fungal endophytes, and fungi in this group belong to *Epichloë/Neotyphodium* and related genera. These latter fungi exist in a highly specialized, co-evolved symbiosis as obligate endophytes of grasses, and confer a number of benefits on their hosts, including drought tolerance, pest and pathogen resistance, and alleviation of phosphorous deficiency (50,65). These endophytes are best known for providing defense against herbivory associated with synthesis of various biologically active metabolites, such as alkaloids, which are also toxic to vertebrate herbivores (11,13,34,43,65,78). It appears, however, that most fungal endophytes are more generalists and not obligate symbionts in their growth (63). Importantly, many of these endophytes, such as those in the genera *Fusarium* and *Rhizoctonia*, for example, are mainly known as plant pathogens; or, in genus *Xylaria*, as decay organisms of plants (2,44,61). However, with much of the research focused on these organisms as plant pathogens, our comprehensive understanding of the role of these fungi in agroecosystems is incomplete.

Regarding plant disease in agricultural ecosystems, research on plant–fungus interactions has been essentially focused on plant pathogenicity, and studies on fungal endophytes have been largely limited to the development of biocontrol agents (1,3,27), which sometimes target fungi traditionally considered pathogens (66). An alternative that has been poorly addressed is that these organisms may have a dual role: a pathogenic lifestyle on certain plants and an endophytic one on others. The fact that plant pathogens can be endophytes on other plants has important implica-

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