

Do Foliar Endophytes Matter in Litter Decomposition?

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Litter decomposition rates are affected by a variety of abiotic and biotic factors, including the presence of fungal endophytes in host plant tissues. This review broadly analyzes the findings of 67 studies on the roles of foliar endophytes in litter decomposition, and their effects on decomposition rates. Aquatic (i.e., in-stream) decomposition studies of endophyte-affected litter were significantly under-represented in the search results ($P < 0.0001$). Indicator species analyses revealed that different groups of fungal endophytes were significantly associated with cool or tropical climates, as well as specific plant host genera ($P < 0.05$). Finally, we argue that host plant and endophyte interactions can significantly influence litter decomposition rates and should be considered when interpreting results from both terrestrial and in-stream litter decomposition experiments.

Litter decomposition is an essential ecosystem process that significantly contributes to the global carbon cycle. Numerous studies have identified several overarching controls on litter decomposition rates, including temperature, dissolved oxygen in aqueous environments, soil moisture, seasonality, quantity of litter pulses, and litter chemistry or quality [1,2,3]. However, litter chemistry is unique among these factors in that it may be mediated by both abiotic—e.g., drought and nutrient availability [4,5]—as well as biotic factors, such as herbivores [6], microbial symbionts [7], and pathogens [8].

Changes in litter chemistry primarily affect decomposition rates by influencing interactions with macroinvertebrate and microbial decomposer communities, which mechanically process litter and break down recalcitrant compounds, respectively. Chomel et al. [9] reviewed the generally recalcitrant properties of alkaloids, phenolic compounds, and terpenes in litter decomposition, but only briefly covered the roles of endophytes—ubiquitous microbes that mostly live asymptotically within host plant tissues—in regulating the production of these secondary metabolites in host plants. Both endophytic fungi and bacteria were isolated from healthy plant tissues, including stems, leaves, and roots [10]; their in planta functions are mostly unknown. Fungal endophytes were most extensively studied in agriculturally significant grass hosts (i.e., Class 1, or clavicopitaceous endophytes; e.g., [11]), where these systemic endophytes were shown to produce toxic alkaloids (e.g., [8,12]), and even alter plant community assembly [13,14]. Furthermore, these systemic endophytes were reported to cause slower rates of litter decomposition in terrestrial systems [15,16]. However, few studies examined the role of foliar endophytes in the decomposition of litter from non-grass hosts (i.e., Class 2 or 3, or non-clavicopitaceous endophytes), and even fewer studies focused on the effects of endophytes on leaf litter decomposition in aquatic systems. Although ubiquitous within plant tissues, endophyte communities can vary spatially and temporally within host plants [17] and represent an important bridge between host plant characteristics that influence decomposition and the decomposer community.

Here, we aimed at distilling the available literature on the effects of foliar endophytes on leaf litter decomposition into an up-to-date review. We used 67 published studies and compiled a report analyzing the contributions of foliar endophytes to litter decomposition rates. We further collected information about the reported taxa of both endophytic and epiphytic fungi recovered from leaf tissue and constructed a comprehensive table for reference.

Do foliar endophytes matter in litter decomposition? Our review of the current literature suggests that it depends, given the complexity of abiotic and biotic factors influencing ecosystem processes. While it is important to point out that there were only 12 studies that directly tested foliar endophyte effects on litter decomposition—half of which focused exclusively on Class 1 grass-endophyte interactions—our synthesis suggests that there is an overarching theme of mismatched focus among studies of litter decomposition. Endophytes are a hyperdiverse group of organisms that includes both bacteria and fungi, colonizing a wide range of host plants and plant tissues from tropical to boreal ecosystems. These microbes exist within the phyllosphere of their host plants and emphasize just one example from the tangled web of plant-microbe interactions. A host plant can represent a patch of occupiable habitat to an endophytic colonizer. Within that patch, there is competition with other endophytes and parasites, but also specific host-endophyte interactions. These specific interactions are, in turn, complicated by variation in the endophyte community composition and the host responses to abiotic factors. However, the resolution of the “patch” unit matters. For example, endophytes can vary spatially within the same host plant, shifting the occupiable patch unit to leaf. Similarly, endophytes within the local litter community can colonize neighboring host plants, shifting the occupiable patch unit to a localized area. Because endophyte-host interactions span more than a single level within the scale of an ecosystem—and ultimately represent just one of many poorly defined mechanisms and interactions between different scales within an ecosystem—endophyte communities present special challenges to predicting and understanding ecosystem processes like litter decomposition.

Several key contributing factors should be considered in litter decomposition studies when designing experiments or interpreting

results (Figure 4). First, host–endophyte interactions are context-dependent, and may be influenced by the host’s genotype or origin and both abiotic and biotic factors that affect leaf chemistry (e.g., drought or herbivores). The presence of secondary compounds—whether produced as host defenses or induced by systemic Class 1 endophyte infection (in grasses)—tend to slow litter decomposition overall in terrestrial habitats. Similarly, symptomatic endophyte infections in litter typically slow decomposition dynamics by inhibiting subsequent colonization or directly breaking down recalcitrant compounds. However, saprotrophic endophytes can both exert priority effects on new colonizers and ameliorate available nutrients on litter; as common members of the foliar endophyte communities, their presence should be considered, especially in studies of microbial decomposer succession or community assembly on litter. Finally, access by detritivores is important in mediating litter decomposition rates, particularly when unpalatable or recalcitrant compounds are present and would otherwise retard microbial decomposition.

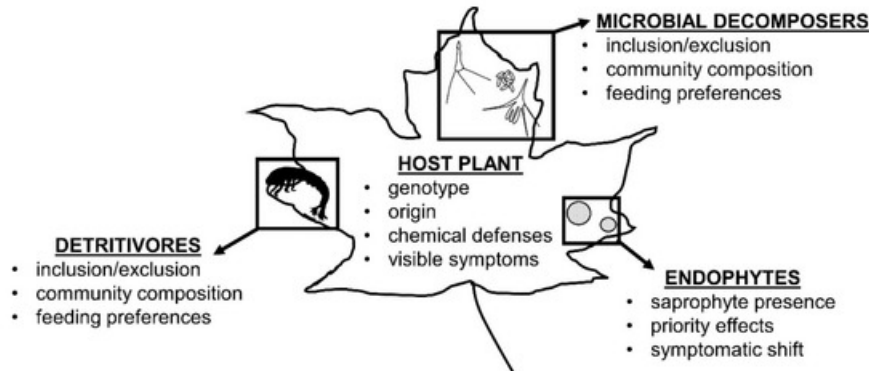


Figure 4. Infographic of factors that influence endophyte-mediated litter decomposition.

Most importantly, affecting all of these contributing factors is the type of ecosystem itself (e.g., riparian versus terrestrial, or grassland versus forest). Decomposition proceeds faster in aquatic environments due to a combination of factors including constant moisture and mechanical breakdown from moving water. Likewise, warm ambient temperatures and high humidity tend to accelerate decomposition in tropical forests. In grass systems, other factors, such as variable precipitation regimes and agricultural land use, must be considered, especially since the presence of toxic alkaloids can harm grazing livestock. Grasses also harbor Class 1 endophytes, which are vertically transmitted, as opposed to the horizontal transmission of Class 2 and 3 endophytes that are more prevalent in non-grasses. We found that climate type—even broadly categorized—resulted in significantly different groups of specialized taxa. Different plant genera also tended to host specialist fungal taxa, in addition to many well-known generalist endophytes (e.g., *Phoma* and *Xylaria*). In summary, host plant and endophyte interactions can be significant factors in both terrestrial and aquatic litter decomposition rates and should be taken into consideration when interpreting results, but more studies specifically exploring foliar endophyte effects on litter decomposition are clearly needed.

Keywords

plant-microbe interactions; ecosystem ecology; microbial ecology; fungal endophytes



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