

Endophytic phyllosphere fungi and nutrient cycling in terrestrial ecosystems

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The importance of phyllosphere fungi to ecosystem functioning via soil processes has aroused increasing interest during the last decade. Here, we briefly review the current knowledge of how the foliar endophytic fungi and nutrient cycling interact. Recent findings suggest that endophytes may affect plant litter quality, organisms that control litter decomposition and the availability of nutrients in plant communities. However, the results obtained so far are highly variable. We attempt to integrate these observations with the knowledge of ecology and life-history strategies of endophytic fungi, and highlight general rules and gaps in our knowledge. Finally, we suggest testable hypotheses for future studies.

Keywords: Decomposition processes, nutrient cycling, phyllosphere fungi, terrestrial ecosystems.

Introduction

INTERACTIONS within and among trophic levels that are mediated by fungal endophytes have received a great deal of attention since endophytes were proved to be ubiquitous plant associates^{1–6}. During the last decades virtually every plant species has been shown to harbour at least a few species of endophytes and many plants seem to harbour diverse assemblages of them^{7–14}. The endophytes at one trophic level interact with other primary consumers such as plant pathogens and herbivores^{1,5,6,15}, and across trophic levels via interactions with the host plants, herbivore enemies and saprotrophs^{3,5,6,16–20}.

The profound effects of endophytes on primary producers, and aboveground primary consumers and their natural enemies, have been demonstrated in myriad empirical studies and also extensively reviewed in several recent papers^{5,6,15,19,21}. Similar comprehensive work on the effects of endophytes on belowground food webs is lacking. However, endophytes potentially interact with mycorrhizal fungi and nitrogen-fixing bacteria of the shared host plant as well as with root herbivores, detritivores and saprotrophs^{3,22}. A few recent studies reveal

how fungal endophytes can affect litter decomposition rates^{23,24}, stimulate soil carbon sequestration and alter the flux of greenhouse gases (CO₂ and N₂O) from the soil to the atmosphere²⁵. This suggests that research efforts should be extended to explore the endophyte effects on belowground food webs and processes they may control.

In this article, we focus on nutrient cycling and argue that endophytes can be crucial players in modulating belowground processes. We propose that to understand the belowground role of endophytes is to acknowledge the variation in endophytic fungal communities and the related complexity of endophyte-mediated ecological interactions.

Ecology and evolutionary strategies of the fungal symbionts

We argue that the effects of endophytes on nutrient cycling are governed by the same key elements in their ecology and life-history strategies that drive and determine the nature of fungus–plant interactions along the continuum from antagonistic to mutualistic relationships^{2,4}.

By definition, the endophytic fungi live all or at least a significant part of their life cycle internally and asymptotically within their host plant tissues²⁶. Virtually all fungi associated with plant foliage, be it pathogenic or saprotrophic, have at least an imperceptibly short asymptomatic period in their life cycle^{27,28}. Hence, the endophyte–plant interactions should not be treated separately from the parasitic, pathogenic and saprotrophic interactions^{27,28}. Accordingly, to fully understand the evolutionary origin and ecological role of endophyte–plant interactions, endophytes should be viewed as an extended latency period of fungi rather than a biological entity of their own right^{27,28}. The theories of endophyte evolutionary history also support this view: endophytic fungi are thought to have evolved from parasitic or pathogenic fungi in multiple parallel and reverse trajectories ever since the early evolution of terrestrial plants^{2,28}. Indeed, there is evidence of endophytic fungi in land plants in 400 million-year-old fossil records²⁹. In short, one may conclude that the fungal endophytes simply represent diverse examples of the asymptomatic phase of the

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fungus–plant interactions that can vary in time and space according to the growth form and life-history strategy of the fungus, the tissue architecture of the host, the genetic compatibility between the fungus and the host, and the environmental conditions^{2,4–6,12,28,30}.

The most generalized and taxonomically heterogeneous pool of foliar endophytic mycota are the nonsystemic endophytes^{4,9,12,31}. They are horizontally transmitted from plant to plant by sexual and/or asexual spores. The frequency of highly restricted local infections, often originating from single spores among a few epidermal cells, gradually increases until they reach a saturation point^{7,8,12,32}. Because of horizontal transmission and frequent sexual reproduction, the species and genetic diversity of nonsystemic endophytes is high even within a single leaf^{6,7,9,12,14,31–33}. The communities of nonsystemic endophytes can also vary among geographically isolated host plant species and populations¹⁴, among stands of discontinuous forests³⁴, extreme environments such as fire-prone forests³⁰ and along with forest succession³⁵. Equally, they can respond to the micro-climate of the forest stand^{7,8,12,32}. Nonsystemic endophytes have often been misleadingly labelled as non-grass endophytes. However, they can be found in all types of plants, including grasses, and many of them are classified commonly as pathogens or saprotrophs in mycology⁴.

The more specialized group of *Epichloë* endophytes³⁶, which belong to the family Clavicipitaceae, grows systemically throughout the aboveground tissues of the host plant. In contrast to the nonsystemic endophytes, these endophytes have been detected only in grasses^{4,21}. This perennial symbiosis is highly integrated and the survival and distribution of the fungus largely depend on the host, particularly in fungi that have entirely lost their ability for contagious spreading by spores^{21,28}. The associated loss of recombination potential through sexual reproduction by sexual spores largely determines the nature of the symbiosis along the continuum from asymptomatic to pathogenic interactions. Three distinct life-history strategies of systemic endophytes are commonly recognized between the extremes of sexuality and asexuality: (1) strictly sexually reproducing and pathogenic fungi causing ‘choke’ disease, which castrates all host inflorescence; (2) fungi producing both ‘choke diseased’ inflorescences and symptomless endophyte-infected seeds, and (3) strictly asexual and asymptomatic fungi^{21,28}.

In the case of the strictly asexual endophytes, the vertical transmission is commonly assumed to have evolved toward mutualism because the fitness of the fungus entirely depends on the fitness of its host²⁸. The fungus unquestionably subsists entirely on the resources of the host plant, and numerous empirical studies have demonstrated that it can confer diverse benefits to the host, such as increased growth, reproduction, stress tolerance, and most commonly, defensive mutualism against herbivores and pathogens^{5,6,37,38}. The endophyte–grass symbioses

are, however, variable and the benefits of systemic endophytes to the host grass depend on the genetic variation of the host and the endophyte as well as on the availability of soil resources and other environmental factors such as the intensity of herbivory^{4–6,31,37–40}.

Endophytes and nutrient cycling

Endophytes are likely to affect the decomposition of plant litter and soil nutrient transformations at least in three ways: (1) by acting as saprotrophs in abscised plant parts and aiding in their decay; (2) by affecting the amount and/or quality of the plant litter, and (3) by affecting the abundance, richness and composition of decomposer organisms (Figure 1). We explore each of these pathways and link them to the ecology and life-history strategies of the endophytic fungi. We also try to guide the future research by formulating testable hypotheses on the effects of endophytes on litter decomposition and nutrient cycling in terrestrial ecosystems.

The understanding of how aboveground plant–herbivore interactions control belowground processes in terrestrial ecosystems has rapidly accumulated over the last decades. Herbivores control plant species composition in many ecosystems⁴¹, and plant defoliation can modify plant carbon allocation⁴² and carbon release from plant roots to the soil⁴³. These effects can have significant consequences on the abundance and activity of soil organisms in the plant rhizosphere, soil nutrient availability and plant growth^{44,45}. Herbivores can also induce the production of defence compounds in plant leaves and these compounds can remain through leaf senescence and later affect leaf litter decomposition^{46,47}. We suggest here that the endophytes may have a similar key role as the herbivores in controlling species composition, primary production and nutrient cycling in plant communities.

Endophytes as latent saprotrophs

Fungi that are isolated as nonsystemic endophytes from the healthy leaves of grasses and other plants also survive in decomposing plant litter as saprotrophs (Figure 1) and endophytes, as they can play a role in leaf senescence and leaf abscission^{14,24,27,30,48}. Some of these fungi spread from litter by producing sexual spores and infect intact leaves to become endophytes^{24,27,48}. The endophytic life-style, which enables the fungi to be the first to capitalize the host resources, may provide competitive advantage for space and soluble nutrients over the saprotrophic fungi, which later colonize the plant litter^{27,48}. In support of this argument, several studies have shown that endophytes can act as early successional saprophytes, and also as gatekeepers for other saprophytes to the newly abscised leaves^{27,48}. A recent study shows that the environmental conditions prevailing in an ecosystem select those

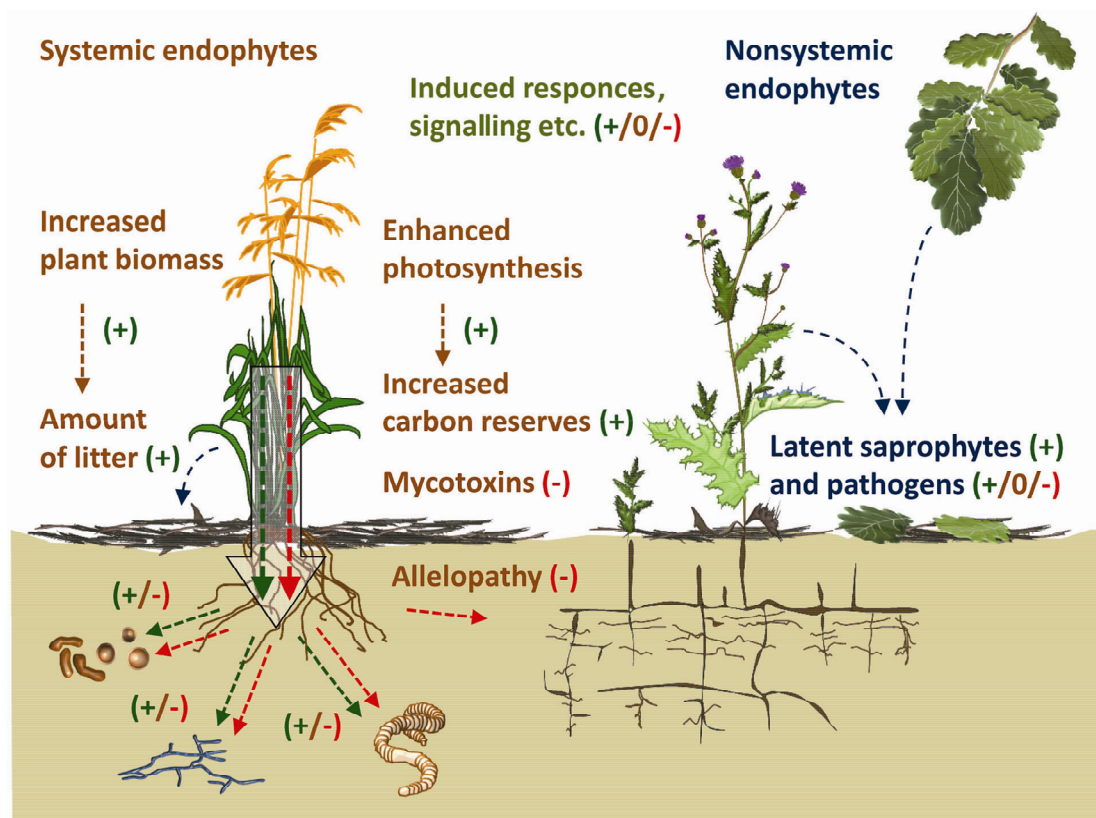


Figure 1. Pathways of endophyte-mediated nutrient cycling.

endophyte species which could also survive as saprotrophs in leaf litter³⁰. However, more research and particularly well-designed long-term experiments are needed to discern the extent to which the nonsystemic endophytic fungi affect litter decomposition, nutrient release and soil organic matter accumulation in forest and grassland ecosystems.

Amount and quality of organic matter

Systemic grass endophytes can increase the growth, reproduction and stress resistance of their host plant^{2,19,37,49,50} and thereby increase the amount of litter produced by the host (Figure 1). However, this may well be compensated by the effect of endophyte-mediated resource competition on biomass production by other plants in the community^{50,51}. A number of studies suggest that the systemic endophytes can, by enhancing the competitive dominance of their host species, prevent species invasions⁵¹ and reduce plant species richness in successional grasslands⁵⁰. As high species richness typically enhances the productivity of plant communities⁵², the total productivity of the plant community might remain unchanged, or even decrease, despite the productivity of the endophyte-colonized host species increasing over time^{50,51}. The information that is currently available is, however, too few

to draw general conclusions about effects of systemic endophyte colonization on plant community productivity and litter accumulation. These effects are also likely to be complicated by interactions with herbivores which can create a significant shortcut of nutrients from green plant material to soil in excreta^{41,53}. However, this shortcut could be reduced in endophyte-colonized plant communities which deter herbivores due to their endophyte associates.

In contrast to the systemic grass endophytes, variability appears to be the nature in interactions between the non-systemic endophytes and their host plants^{4,6}. Empirical evidence suggests that nonsystemic endophytes play a less important role in host plant growth, reproduction or the defensive mutualism against herbivores and pathogens than that observed in the systemic grass–endophyte symbiosis^{4,6,12}.

Systemic endophytes can affect the quality of plant litter by modulating the foliage quality of the host plant. Most of the literature about the chemical ecology of the systemic endophyte–plant symbiosis is focused on the endophyte-produced bioactive alkaloids (Figure 1), such as pyrrolizidines (lolines), ergot alkaloids, indole diterpenoids (including lolitrem), and the pyrrolopyrazine alkaloid (peramine)^{2,6,54,55}. The chemical ecology of the endophyte–grass symbiosis is far more complex¹⁹ since, in addition to alkaloid production, endophytes can (1)

alter the concentration of nutrients, sugars, water and other compounds in grass leaves^{56–58}, and (2) affect the physiological condition of the host plant tissues by modulating their oxidative balance, phytohormone signalling and other metabolic pathways (Figure 1)^{19,20,59}. In general, the induced responses to various attackers and invaders are regulated in plants by two evolutionarily conserved phytohormone signalling pathways, i.e. by the salicylic acid (SA) and the jasmonic acid (JA) pathways^{19,60,61}. Plant responses to biotrophic pathogens (including many endophytes) are mediated by the SA pathway⁶². Recently, Saikkonen *et al.*¹⁹ suggested that the strictly asexual *Epichloë* endophytes, which are presumably derived from the biotrophic pathogens, can be expected to induce the SA pathway. Continuing this argument, since the nonsystemic endophytes produce biologically active compounds and alter various signalling and metabolic pathways in their host plant, they are also likely to affect the quality of plant litter (Figure 1). Plant responses to herbivore attack, and particularly the induced production of secondary metabolites, have been shown to affect plant litter quality and litter decomposition^{46,47}. We predict that similar effects will emerge when the role of these endophytes is further examined.

Endophytes and decomposer organisms

Endophytes have both positive and negative effects on decomposer organisms (Figure 1)^{63,64}. The positive effects can arise by the facilitation of microbial invasion (including the latent saprotrophs and potential pathogens) of the plant as the immune system, signalling system and induced defence responses of the host plant are attenuated. For example, endophytes can probably positively affect saprotrophs through the JA and SA phytohormone signalling pathways. Saikkonen *et al.*¹⁹ proposed that endophytes like the biotrophic parasites likely induce the SA pathway, thus suppressing the mutually antagonistic JA pathway, which is mainly involved in the defence against necrotrophic pathogens and chewing herbivores. Accordingly, the endophytes could positively affect the necrotrophs, which are facultative saprotrophs that first actively kill the host plant and then engage in decomposition. Endophytes could also affect litter quality by increasing host photosynthesis and regulating host carbohydrate metabolism and utilization, thus potentially increasing carbon reserves in the host plant^{19,27,28,56,58}. This might, however, not have significant effects on litter decomposition as the decomposition rate usually depends more on nitrogen concentration⁶⁵. Alternatively, the negative effects can arise prior to colonization of the leaf litter and competitive exclusion of the saprophytic fungi. Production of allelochemicals by the colonizing endophytes, which can be toxic to both microbial and invertebrate decomposers, would also lead to negative effects.

Hypotheses on endophyte effects on decomposition processes

Current endophyte literature provides conclusive evidence that endophytes are important agents in plant communities and the associated food webs. The literature also provides insights into the potential mechanisms through which the endophytes could affect nutrient cycling. Yet, we are only beginning to understand how the endophyte-mediated aboveground and belowground processes link with each other³. Therefore, experimental studies that will integrate the knowledge of ecology and life-history strategies of endophytic fungi with the understanding of the role of endophytes in the aboveground food webs and nutrient cycling are very much in need. As a brief concluding summary, we offer a few general hypotheses to be tested in future studies:

1. Endophytes have a significant role in determining plant litter decomposition and soil nutrient availability.
2. The nonsystemic endophytes, during the saprotrophic phase of their life cycle, enhance litter breakdown, and release of nutrients thereby influencing plant nutrient availability and plant growth.
3. In contrast, the systemic grass endophytes decelerate nutrient cycling by negatively affecting the quality of plant litter and soil decomposer organisms.
4. The nonsystemic and systemic endophytes interact indirectly. The positive effects conferred by the systemic endophytes on their grass hosts depend on soil nutrient availability, which in turn is affected by the nonsystemic endophytes that participate in litter decomposition.

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