



The Role of Plant Litter in Driving Plant-Soil Feedbacks

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Most studies focusing on plant-soil feedbacks (PSFs) have considered direct interactions between plants, abiotic conditions (e. g., soil nutrients) and rhizosphere communities (e.g., pathogens, mutualists). However, few studies have addressed the role of indirect interactions mediated by plant litter inputs. This is problematic because it has left a major gap in our understanding of PSFs in natural ecosystems, where plant litter is a key component of feedback effects. Here, we propose a new conceptual framework that integrates rhizosphere- and litter-mediated PSF effects. Our framework provides insights into the relative contribution of direct effects mediated by interactions between plants and soil rhizosphere organisms, and indirect effects between plants and decomposer organisms mediated by plant root and shoot litter. We distinguish between three pathways through which senesced root and shoot litter may influence PSFs. Specifically, we examine: (1) physical effects of litter (layer) traits on seed germination, soil structure, and plant growth; (2) chemical effects of litter on concentrations of soil nutrients and secondary metabolites (e.g., allelopathic chemicals); and (3) biotic effects of saprotrophic soil communities that can perform different functional roles in the soil food web, or that may have specialized interactions with litter types, thereby altering soil nutrient cycling. We assess the role of litter in PSF effects via physical, chemical and biotic pathways to address how litter-mediated feedbacks may play out relative to, and in interaction with, feedbacks mediated through the plant rhizosphere. We also present one of the first experimental studies to show the occurrence and species-specificity of litter-mediated feedbacks and we identify critical research gaps. By formally incorporating the plant-litter feedback pathway into PSF experiments, we will further our understanding of PSFs under natural conditions.

Keywords: decomposition, indirect plant-soil feedback effects, allelopathy, home-field advantage, rhizosphere-mediated feedback, litter-mediated feedback

INTRODUCTION

Plants modify their biotic and abiotic soil environment, which in turn has a major influence on subsequent plant growth, also referred to as plant-soil feedback (PSF) (Bever et al., 1997; Wardle et al., 2004). Plant-soil feedbacks are key drivers of plant physiology, growth and community composition (Kulmatiski et al., 2008; van der Putten et al., 2013; Teste et al., 2017) and thereby underlie ecosystem functioning (Bennett et al., 2017; Mariotte et al., 2018). Therefore, managing

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PSFs can be of importance for improving sustainability in agro-ecosystems (Mariotte et al., 2018), for restoration of natural ecosystems (Kardol and Wardle, 2010 review TREE, Wubs et al., 2016) and for enhancing the resilience of ecosystems under global change and species invasions (van der Putten et al., 2016). For example, exploiting positive PSF effects may allow us to improve yield and reduce the use of artificial fertilizer and pesticides in agricultural fields (Mariotte et al., 2018; Veen et al., 2019). However, to be able to manage PSFs it is crucial to unravel how PSFs operate.

It has been long recognized that PSFs can be mediated via direct interactions between plants and rhizosphere communities, as well as indirect interactions between plants and decomposer communities driven by litter inputs (**Figure 1**) (Wardle et al., 2004; Ehrenfeld et al., 2005; Kardol et al., 2015). However, most studies focusing on PSFs have considered direct interactions (e.g., pathogens, mutualists), while largely neglecting the role of plant litter and decomposer communities (Elgersma et al., 2012; van der Putten et al., 2016). In natural ecosystems, litter may leave physical, chemical and biotic legacies in the soil that have a strong impact on soil functioning and plant growth (Ehrenfeld et al., 2005; Elgersma et al., 2012). In addition, litter-mediated PSFs may modify rhizosphere-mediated PSFs (Kardol et al., 2015; Ke et al., 2015; Zhang et al., 2016), for example, because saprotrophic soil organisms may suppress plant pathogens as a result of competition for space and nutrients (Rodríguez et al., 2016). Therefore, to understand the importance of PSFs under natural conditions, it will be essential to unravel the role of plant litter and decomposer communities in PSFs (Ke et al., 2015; Veen et al., 2018).

Plant-soil feedback effects mediated via the biotic community in the rhizosphere are known to be driven by species-specific relationships between plant species and organisms inhabiting the rhizosphere. Sugars and plant signaling compounds excreted from plant roots attract or repel soil biota inhabiting the rhizosphere (Philippot et al., 2013; el Zahar Haichar et al., 2014; Kaiser et al., 2015), thus creating a plant-specific rhizosphere microbiome (Raaijmakers et al., 2009). Depending on the balance between mutualists and pathogens, this community will directly stimulate or inhibit plant growth (Raaijmakers et al., 2009; van der Putten et al., 2016). Importantly, such species-specific PSFs may also be mediated via plant litter pathways (Elgersma et al., 2012; Mazzoleni et al., 2015). For example, we showed in a greenhouse experiment that the biomass of the grass *Festuca rubra* was higher on soils previously incubated with conspecific litter (litter-mediated feedback), while biomass of the tree *Betula pendula* was not affected by litter, but was increased on soils where conspecific plants were grown previously (rhizosphere-mediated feedback) (**Box 1; Figures 2A,B**). Recent work has indicated multiple mechanisms that may explain such specific litter-mediated PSFs. For example, decomposer communities may have a strong affinity for plant litter types from the plant with which they are associated (Austin et al., 2014; Palozzi and Lindo, 2018), resulting in accelerated litter breakdown (Freschet et al., 2012a; Veen et al., 2015) and plant-specific patterns of nutrient release (Perez et al., 2013). In addition, the release of DNA and toxic compounds from decomposing plant litter can inhibit the growth of the plant from which the litter originates

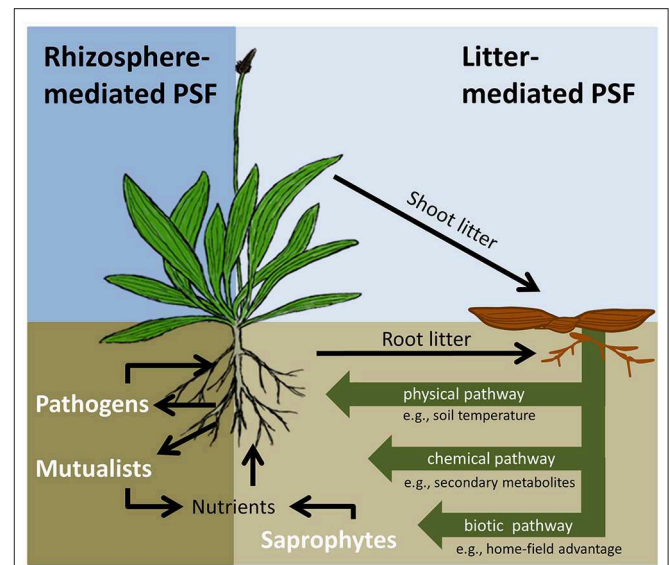


FIGURE 1 | Overview of the plant-soil feedback (PSF) framework integrating rhizosphere- and litter-mediated PSF effects. Rhizosphere-mediated PSFs will be driven by direct interactions between living plant roots and pathogens or mutualists. Litter-mediated PSFs will run via physical (e.g., litter layer thickness; litter physical traits), chemical (e.g., soil nutrient availability; secondary metabolites; allelopathy) or biotic (e.g., soil community composition; biotic interactions; home-field advantage effects) pathways. Litter-mediated PSFs via the physical pathway may be driven by species-specific impacts of e.g., litter layer thickness or light availability underneath litter layers on seedling germination or plant growth (Facelli and Pickett, 1991a). Litter-mediated effects via the chemical pathway may be driven by plant growth responses to the release of primary or secondary chemicals from leaf litter during decomposition (Facelli and Pickett, 1991a). Finally, litter-mediated PSFs via the biotic pathway may be driven by local variation in the composition and activity of decomposer communities and hence the rates at which they control the recycling of plant litter. Rhizosphere-mediated and litter-mediated PSFs interact, for example, through direct competition for space and nutrients between pathogens, mutualists and saprotrophs, the immobilization of nutrients released from litter by biota in the rhizosphere, or responses of pathogens and mutualists to physical and chemical changes in the soil induced by litter. Also, it is important to note that, physical, chemical, and biotic pathways of litter-mediated PSFs interact, for example, because plant-induced changes in the saprotrophic community will affect the rate at which nutrients and chemical compounds from litter are released into the soil. Interactions between the different pathways of litter-mediated PSFs are not specifically depicted in the figure.

(Mazzoleni et al., 2015; Carteni et al., 2016). How the negative feedback of self-DNA works is not fully understood, but it is hypothesized that plants have mechanisms to recognize their own DNA (Mazzoleni et al., 2015; Carteni et al., 2016). Understanding the specificity of litter-mediated PSFs is crucial to elucidate how PSFs control plant growth and coexistence in natural systems (Kardol et al., 2015; van der Putten et al., 2016).

Here, we propose a novel framework that integrates rhizosphere- and litter-mediated PSF effects (**Figure 1**). In this paper we will focus on the role of litter-mediated PSF effects as there are already detailed reviews and meta-analyses focussing on rhizosphere-mediated PSFs (e.g., Kulmatiski et al., 2008; van der Putten et al., 2013). We explore three main pathways via which plant litter can drive PSFs: physical, chemical and biological (Ehrenfeld et al., 2005). For each of these pathways,

BOX 1 | Description of set up and results of greenhouse experiment. The aim of this experiment is to disentangle rhizosphere- and litter-mediated plant-soil feedback effects for the tree *Betula pendula* and the grass *Festuca rubra*.

To test the role of plant litter inputs in driving plant-soil feedback effects, we set up a reciprocal litter transplant experiment in the greenhouse with soils and leaf litters from two plant species, i.e., the tree *Betula pendula* and the grass *Festuca rubra*. Soils and litters were collected from six replicate ex-arable grasslands and adjacent forests along a well-established chronosequence, in the nature reserve “the Veluwe” in the Netherlands; located between Ede (52°04'20"N, 5°44'12"E) and Wolfheze (52°00'77"N, 5°48'58"E) (Kardol et al., 2006; Morriën et al., 2017; Veen et al., 2018). At each site, soil samples and associated plant litter were collected in October 2014 underneath *Betula* and *Festuca* plants (see Veen et al., 2018 for details on sample collection). For each site, soil samples were sieved over 10 mm to remove large roots and stones. Litter subsamples were also homogenized per site, air-dried, cut into 1-cm fragments and sterilized using gamma-irradiation (25 K Gray). We used the soils and litters to set up a two-phase experiment, with a litter incubation phase where we created “litter-specific soils” and a feedback phase where we tested the biomass response of *Betula* and *Festuca* seedlings to the incubated soils.

For the litter incubation phase, we used the soils to fill two 0.5-L pots per site, with each pot receiving 160 g of soil on a dry weight basis. Then, 2.0 g of litter was added to each pot following a full-factorial design. This resulted in two soil sources (*Betula*, *Festuca*) × 2 litter types (*Betula*, *Festuca*) × 6 replicates = 24 pots (Figure 2C, incubation phase). After 3 and 6 months of litter incubation, we added an additional 2.0 g of fresh litter to each of the pots, resulting in a 9-month litter incubation period in total. The amount of litter used was representative of the amount of natural litter fall in temperate grasslands (Penuelas et al., 2007). During incubation, pots were kept at 18°C and 65% water holding capacity (WHC). For the feedback phase, we collected two 32-g subsamples of soil (dry weight basis) from each pot, which we inoculated into two pots with 128 g of sterilized soil (dry weight basis) to test the biomass response of *Betula* and *Festuca*, respectively, resulting in 48 pots (Figure 2C, feedback phase). Soil for sterilization was collected from one of the ex-arable fields (van der Putten et al., 2000). We used this approach, which is common in plant-soil feedback research, to reduce the effect of abiotic differences between soil sources on plant growth in the feedback phase (Brinkman et al., 2010). During the feedback phase pots received 2.0 g of the same litter type as what they had received during the incubation phase and were put in the greenhouse for 5 months before growing *Betula* and *Festuca* seedlings. Seedlings were grown for 6 weeks according to a full-factorial design with each plant species growing on each combination of soil and litter sources. During the feedback phase pots were kept at day/night temperatures of 21/16°C, relative humidity of 60% and a day length of 16 h and 70% soil WHC. At the end of the experiment, we determined plant shoot and root biomass. Data were analyzed in R Core Team (2013) using general linear mixed models (Bates and Maechler, 2009) with soil source, litter source and plant species as fixed factors and replicate site as a random factor, followed by Tukey HSD tests. We have checked for a normal distribution of the residuals and homogeneity of variances before proceeding with our analyses.

Both shoot ($F_{1,39} = 75.70, P < 0.001$) and root ($F_{1,39} = 183.03, P < 0.001$) biomass were higher for *Festuca* than for *Betula* seedlings (Figures 2A,B). In addition, there was a main effect of soil source, indicating that shoot ($F_{1,39} = 11.03, P = 0.002$) and root ($F_{1,39} = 16.65, P < 0.001$) biomass were higher in *Betula* soils than in *Festuca* soils (Figures 2A,B). Finally, the interaction between litter source and plant species affected root biomass ($F_{1,39} = 13.04, P < 0.001$) and tended to affect shoot biomass ($F_{1,39} = 3.64, P = 0.064$), indicating that *Festuca* plants had more root biomass on soils incubated with *Festuca* litter, while there was no effect of litter incubation treatment on *Betula* (Figures 2A,B). Our findings show that litter inputs can have species-specific feedback effects to plant growth. As a result, litter feedbacks have the potential to contribute to or modify rhizosphere-mediated feedbacks. From this experiment we cannot disentangle to what extent feedback effects were mediated via litter-induced changes in soil chemistry or via changes in the composition and functioning of the saprotrophic community. However, our findings indicate that we need to integrate litter-feedback effects into the framework of plant-soil feedbacks.

we describe how they may contribute to explain PSF effects. It is important to note that even though we separate the litter-mediated PSFs via the three different pathways, under natural conditions, effects are often hard to disentangle as PSF effects will be mediated by interactions between the pathways. In addition, we identify ways forward in PSF research to increasing our understanding of interactions between litter-mediated and rhizosphere-mediated PSFs, which will advance our knowledge of PSFs in natural ecosystems.

PHYSICAL PATHWAYS

Physical pathways have received little attention in research on litter-mediated PSFs, but it has long been known that plant litter has strong effects on the physical soil environment (Facelli and Pickett, 1991a), both in natural (Facelli and Pickett, 1991b) and agricultural ecosystems, i.e., via crop residues (Teasdale et al., 1991; Walia and Dick, 2018). The effects of plant litter on the physical soil environment have strong potential to feed back to plant performance through effects on seed germination, seedling establishment, and initial plant growth (Olson and Wallander, 2002; Asplund et al., 2018).

A layer of leaf litter may improve the microclimatic conditions for seed germination through moisture retention and buffering against temperature extremes. In laboratory studies, it has been

shown that under conditions of strong desiccation, acorns covered by a layer of leaves suffered lower water losses and, therefore, had higher rates of germination (García et al., 2002). However, under field conditions the evidence for improved germination rates in the presence of a litter layer is mixed (e.g., Barrett, 1931; Shaw, 1968; García et al., 2002; Kremer et al., 2019), probably because the extent to which the litter layer improves germination depends on ambient moisture conditions. Further, soil temperature is generally higher under a layer of plant litter (Sharratt, 2002), because the build-up of litter on the ground surface affects the transfer of heat between the soil and the atmosphere, which in turn can lead to increased seed germination rates (Paul et al., 2004). In addition, plant litter may physically protect seeds against predation (García et al., 2002). In contrast, the litter layer can also have negative impacts on seed germination and plant growth, because it can reduce the amount of light reaching the soil surface (Facelli and Pickett, 1991a) and it may act as a physical barrier to seedling emergence (Barrett, 1931). Finally, incorporation of litter into the soil matrix may modify soil structure, which may modify plant growth responses. Although most evidence for physical effects of litter on plant performance comes from studies on leaf litter, there may also be important effects mediated via root litter (Bardgett et al., 2014), but these remain to be tested. As root litter is already incorporated into the soil matrix, it may not form a litter

layer and therefore may have different physical PSF effects than leaf litter.

Litter-mediated PSFs via the physical pathway have not been studied extensively, but may be plant species-specific. The retention of soil moisture underneath leaf litter layers is strongly related to the traits of the plant litter species, for example specific leaf area (SLA), three-dimensionality of the litter, or tensile strength (Swift et al., 1979; Makkonen et al., 2013). Also, plant litter may have species-specific effects on soil water repellency, depending on the presence of organic hydrophobic compounds (Cesarano et al., 2016). Similarly, light extinction curves in litter layers differ between litter species (Facelli and Pickett, 1991b). The empirical support is scarce, but these litter-specific effects on environmental conditions strongly suggest that litter-mediated PSFs via the physical pathway have species-specific effects on seed germination and seedling growth.

Plant responses to litter-induced changes in environmental conditions via the physical pathway may also be species-specific (e.g., Olson and Wallander, 2002). In many empirical experiments it remains hard to untangle physical litter PSF effects, from chemical or biological effects. However, measurements on e.g., light penetration or mechanical barriers by litter in pot and field experiments indicate that physical litter-mediated PSF effects may play a role in driving species-specific plant responses. For example, using a controlled pot experiment testing effects of litter on seedling emergence, Donath and Eckstein (2008) found significant interactions between litter type and plant species origin at least partly driven through mechanical effects. Woodland species produced more biomass in presence of oak litter than in presence of grass litter, indicating a positive litter-mediated PSF effect which was explained by oak litter consisting of individual leaves, while grass litter typically forms dense interwoven mats which might be difficult to penetrate and could inhibit shoot emergence. For mechanical inhibition, seed size and seed position can be important in determining the strength of physical litter feedbacks (Donath and Eckstein, 2010). Zhang et al. (2017) found that a moderate amount of litter was beneficial for seedling emergence of small-seeded species, while large-seeded species were more tolerant to high amounts of litter input than small-seeded species. Also, litter accumulation by an exotic plant species *Avena fatua* reduced the germination of small-sized seeds of native species via increased litter depth and light reduction, thereby facilitating invasion of *A. fatua* in Californian grasslands (Mariotte et al., 2017). The impact of light reduction suggests that at least physical pathways may play role, but to what extent other pathways also play a role remains to be tested.

Together, these plant-specific impacts on and responses to the litter layer show that the creation of physical barriers and alteration of the abiotic environment by plant litter may play a key role in PSF in natural ecosystems. Understanding how shoot and root litter traits drive such physical litter-mediated PSFs may offer a promising avenue for further exploring the role of litter in PSF (Bardgett et al., 2014; Cortois et al., 2016). However, only few empirical studies have specifically focused on the role of physical effects in driving PSF. This is experimentally

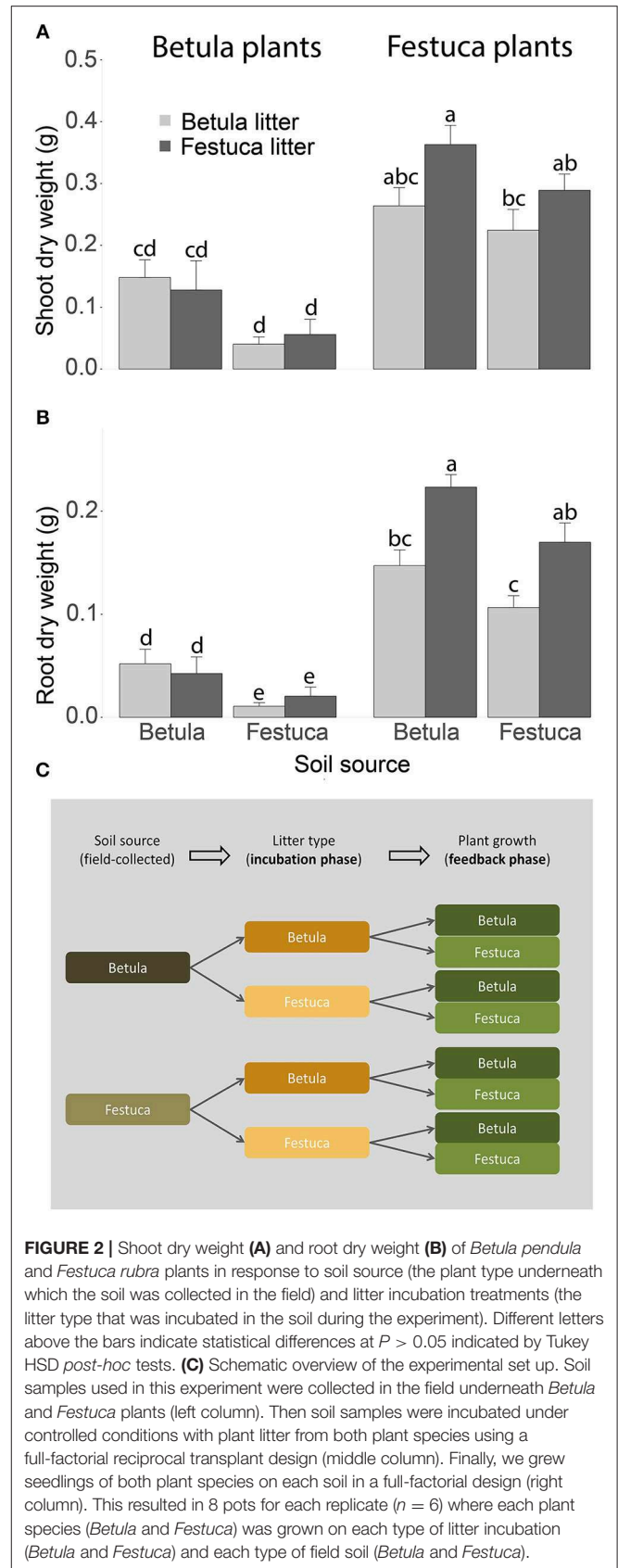


FIGURE 2 | Shoot dry weight (A) and root dry weight (B) of *Betula pendula* and *Festuca rubra* plants in response to soil source (the plant type underneath which the soil was collected in the field) and litter incubation treatments (the litter type that was incubated in the soil during the experiment). Different letters above the bars indicate statistical differences at $P > 0.05$ indicated by Tukey HSD *post-hoc* tests. (C) Schematic overview of the experimental set up. Soil samples used in this experiment were collected in the field underneath *Betula* and *Festuca* plants (left column). Then soil samples were incubated under controlled conditions with plant litter from both plant species using a full-factorial reciprocal transplant design (middle column). Finally, we grew seedlings of both plant species on each soil in a full-factorial design (right column). This resulted in 8 pots for each replicate ($n = 6$) where each plant species (*Betula* and *Festuca*) was grown on each type of litter incubation (*Betula* and *Festuca*) and each type of field soil (*Betula* and *Festuca*).

challenging, but may provide insights in plant growth responses to litter inputs. It is important to mention that the level of specificity of physical litter-mediated PSF may be lower than for rhizosphere-mediated PSF, because the strength and direction of physical litter feedbacks may be largely determined by generic leaf and seeds traits; however, this warrants further investigation.

CHEMICAL PATHWAYS

During decomposition a wide range of chemical compounds is released from plant litter which can be beneficial or detrimental to subsequent generations of plants (Facelli and Pickett, 1991a). Litter-mediated PSFs via the chemical pathway can be driven by the liberation of plant nutrients, secondary metabolites or DNA from decomposing litter (Facelli and Pickett, 1991a; Mazzoleni et al., 2015). Soil nutrients can be made available through rapid decomposition of nutrient-rich litter. This will increase plant nutrient availability in the next generation. In contrast, litter with a high concentration of structural carbohydrates, such as cellulose, decomposes slower and may produce less positive or even negative PSFs (Vahdat et al., 2011). Although litter-mediated PSF via nutrients may be less species-specific than PSFs mediated via other chemicals, plant species responses to litter-mediated changes in soil nutrient cycling often differ between plant growth strategies. Generally, fast-growing, exploitative plant species will benefit most from positive litter-mediated PSFs via nutrient availability, while plant species with conservative resource-use strategies may be less hampered by slow recycling of nutrients (Wardle et al., 2004). Also, positive litter-mediated PSFs may favor the invasion of exotic plants, that are often better competitors for nutrients released from plant litter (Eppinga et al., 2011). However, generalizing litter-mediated PSFs through nutrients may be complicated because of confounding effects of other chemical compounds or biotic interactions, which may result in unexpected effects on future generations of plants (Hobbie, 2015).

Plant litter also contains a range of secondary metabolites, including alkaloids, phenolic compounds and terpenes, which are often used as a defense mechanism against herbivores and pathogens and therefore play a key role in plant-microbe and plant-herbivore interactions (Chomel et al., 2016). These secondary metabolites are important for determining decomposition rates. For example, tannins may slow rates of litter decomposition (Hättenschwiler and Vitousek, 2000) and phenolic compounds can delay the colonization of litter by decomposer organisms (Ormeno et al., 2006; Chomel et al., 2014). Yet, it is now increasingly acknowledged that some complex compounds, such as lignin, can be degraded more quickly than previously assumed (Lehmann and Kleber, 2015), but that this may depend on the presence of specialized microbial communities, such as certain lignin-degrading fungi (van der Wal et al., 2015). As a result, secondary metabolites can contribute to litter-mediated PSFs via impeding nutrient cycling (Wardle et al., 2012). Secondary metabolites can also have direct impacts on plant growth when released into the soil, and their impact may strongly depend on the residence time in

the soil (Chomel et al., 2016). Many chemical compounds that are present in the living plant, such as alkaloids, are quickly metabolized in litter and are thought to have limited effects on soil processes and plant responses (Siegrist et al., 2010). However, other chemicals liberated from plant litter can persist in the soil after senescence and may inhibit the growth or germination of neighboring and next-generation plants (Bonanomi et al., 2011), a phenomenon referred to as allelopathy (Muller, 1966). For example, the growth of tree seedlings may be inhibited by phenol-rich litter (Hättenschwiler and Vitousek, 2000). Also, flavonoids, which are known to play a role in attracting beneficial microbes, such as *Rhizobia*, may remain in plant tissue after senescence and affect plant growth by scavenging free radicals and improving stress tolerance (Barazani and Friedman, 2001). In addition to secondary metabolites, DNA released from decomposing material may also hamper plant growth of next generations of plants, and this negative feedback is specifically targeted toward congeneric plant species (Mazzoleni et al., 2015).

Litter-mediated PSFs via chemical compounds may strongly differ between above- and belowground plant organs. Although decomposition rates of shoots, stems and roots broadly correlate across large-scale fertility gradients, at the level of sites or individual plant species decomposition rates may differ between plant organs (Hobbie et al., 2010). This means that above- and belowground plant organs, as well as different types of roots, may play a different role in ecosystem processes (Freschet et al., 2012b). For example, leaf litter decomposes often more rapidly than root litter (Freschet et al., 2013), and finer roots, often richer in nitrogen (Pregitzer et al., 1997), faster than coarser roots. Although this may affect litter-mediated PSF, only a few studies have focused on the impacts of root litter on PSF (e.g., Mazzoleni et al., 2015; Zhang et al., 2016), and none of them compare how PSFs induced by root and shoot litter differ. Yet, root decomposition is likely to play a key role in subsurface soil layers and in ecosystems, such as tundra and grasslands, where half to three quarters of plant biomass is produced belowground as roots (Poorter et al., 2012). Therefore, it is essential to start disentangling the role of root and shoot litter driving chemical litter-mediated PSF effects.

BIOTIC PATHWAYS

Local variation in decomposer community composition and activity drives variation in decomposition rates (Hättenschwiler and Gasser, 2005; Vos et al., 2011; Bradford et al., 2014, 2017). Variation in decomposer composition may be tightly linked to plant composition (Bezemer et al., 2010), indicating that decomposer composition and activity may have an important role in driving litter-mediated PSFs. The litter-fragmenting community (or detritivores), including earthworms, millipedes, myriapods, diplopods, and various insect larvae, transforms a large part of plant litter into feces, thereby increasing the surface area for microbial decomposition, which often results in accelerated litter breakdown (Hättenschwiler and Gasser, 2005; David, 2014; Joly et al., 2018). The impact of litter shredders on decomposition may be strongly affected by decomposers

actively selecting certain litter types or compounds. For example, earthworms often prefer palatable residues, such as litter with low carbon:nitrogen ratios and tend to avoid ingestion of root litter (Curry and Schmidt, 2007; Vidal et al., 2017). In addition, the functioning of the gut microbiome of litter shredders, which is likely to be picked up from the soil (Hannula et al., 2019), may affect decomposition processes. Saprotrophic fungi and bacteria in the soil are involved in the mineralization of nutrients into inorganic forms that can be taken up by plants. How this affects plant species may be strongly determined by the stoichiometric constraints of both plants and the microorganisms involved in soil nutrient cycling (Capek et al., 2018). Depending on how plants drive shifts in the composition and activity of detritivores, saprotrophs, and gut microbes, variation in the soil community will contribute to litter-mediated PSFs by altering soil nutrient availability (Joly et al., 2018) and liberating secondary metabolites from plant litter. Also, interactions between decomposers and other soil organisms (e.g., predators in the soil) may have a large impact on litter-mediated PSFs. For example, consumption of detritivores and microbial decomposers by predators in the soil could inhibit decomposition (Liu et al., 2014) and thereby short-circuit litter-mediated PSFs.

Litter-mediated PSFs may also operate via home-field advantage effects, which is the process that litter decomposition is accelerated near the plant where the litter originates from relative to litter decomposition further away from that plant (see Gholz et al., 2000; Ayres et al., 2009; Veen et al., 2015; Palozzi and Lindo, 2018). The hypothesis is that home-field advantage effects are driven by species-specific associations between plants and decomposer communities (Freschet et al., 2012a; Austin et al., 2014). Recent experimental work showed that different litter types can indeed harbor specific litter microbiomes (Keiser et al., 2011; Lin et al., 2019) and that variation in abundant litter fungal groups can contribute to home-field advantage effects (Veen et al., 2019). This results in plant-specific patterns in nutrient release (Perez et al., 2013) and, hence, may contribute to litter-mediated PSFs. In general, home-field advantage effects may be expected to favor the plants where the litter originated from (Zhang et al., 2016), but nutrients released from litter may also be taken up by neighboring plant species (Hood et al., 2000; Collins et al., 2007). Therefore, the extent of plant specificity in litter-induced feedbacks via home-field advantage remains to be tested (van der Putten et al., 2016; Zhang et al., 2016).

Most studies focus on shoot litter decomposition, but decomposition of root litter may be equally or more important in driving biotic litter-mediated PSFs (Li et al., 2015; Zhang et al., 2016), because it takes place in or near the rhizosphere of plants. As a result, saprotrophic communities involved in root litter breakdown closely interact with mutualists- and pathogens located in the rhizosphere, via competition for carbon and nutrients (Rousk and Bååth, 2011; Boddy, 2016; Money, 2016; Sokol and Bradford, 2019). The extent of these interactions depends on the availability of easily available sugars (Rousk and Bååth, 2011; Ballhausen and de Boer, 2016), the stoichiometry of plant litter (e.g., how much nitrogen is available) (Zhang and Elser, 2017), the chemical composition of the litter (Gartner et al., 2012) and accessibility of other soil organic material to

saprotrophs (Rillig and Mummey, 2006). In turn, the mutualistic, pathogenic, and saprotrophic components of the microbial community are consumed by organisms, such as collembola that graze on fungal mycelium (Scheu and Schulz, 1996) or protists that feed on unicellular bacteria and fungi (Radosa et al., 2019). In addition, saprotrophs can compete for root exudates with plant parasites or ectomycorrhiza in the rhizosphere. As a result, both rhizosphere- and litter-mediated PSFs can be controlled by similar trophic top-down and bottom-up factors (De Long et al., 2019). It is therefore important not to regard them as separate units, but as intertwined operating pathways imbedded in the same food-web context.

THE WAY FORWARD

Here, we demonstrated how root and shoot litter can affect PSFs through physical, chemical and biotic pathways. Although an emerging body of literature supports the potential importance of litter-mediated PSFs, many critical knowledge gaps remain which require further investigation. Here we identify five important avenues for further research into the role of litter-mediated PSFs:

- (1) Disentangle the interactions between litter-mediated vs. rhizosphere-mediated PSFs. We already know that rhizosphere pathogens or symbionts play a strong role in mediating PSFs (Bennett et al., 2017; Semchenko et al., 2018) and litter-mediated PSFs are gaining more attention (Freschet et al., 2013; Hobbie, 2015; Zhang et al., 2016; Manrubia et al., 2019), but interactions and their relative hierarchy of importance needs to be elucidated. For example, modeling work showed that rhizosphere-mediated PSFs may modify or override litter-mediated PSFs (Ke et al., 2015). Also, microbes in the rhizosphere can immobilize the nutrients liberated from plant litter, thereby buffering litter-mediated PSFs via nutrient cycling (Miki et al., 2010). These findings indicate the need to study rhizosphere- and litter-mediated PSFs in combination (see **Box 1** for an example) to disentangle their interactions and relative importance. This will require full-factorial experiments where rhizosphere- and litter-mediated PSFs are manipulated. Within such studies it will be important to carefully consider spatial and temporal scales at which litter- and rhizosphere-mediated PSF effects occur, as these are not necessarily the same. In addition (stage-structured), models could be powerful to further explore how litter-mediated PSFs could operate (Ke et al., 2015; Campbell et al., 2016).
- (2) Gain a better understanding of interactions between physical, chemical and biotic pathways of litter-mediated PSFs. For example, litter cover (i.e., physical) may enhance seedling establishment by creating favorable microclimatic conditions (Facelli et al., 1999), but it may have negative impacts on seedling survival due to allelopathy (i.e., chemical) (Wardle et al., 1998) or damage by litter fungal pathogens (i.e., biotic) (Beckstead et al., 2012). Integrating research across all three pathways will help us to untangle the key mechanisms driving litter-mediated PSFs. This will require experiments that specifically manipulate the physical,

chemical or biotic pathway, for example by using sterilized litter to rule out biotic effects or fake (e.g., plastic) litter to identify physical effects. Alternatively, experiments using a more “holistic” approach including physical, chemical and biotic effects of litter without specifically disentangling them, may provide a better understanding of the overall impact of plant litter on PSFs. For example, plant roots from the first generation of plants can be left in the soil intact to allow for physical, chemical and biotic legacy effects of root litter on next generations of plants.

- (3) Elucidate the species-specificity of litter-mediated PSF effects. Evidence is accumulating that plant litters build up unique decomposer communities (Lin et al., 2019; Veen et al., 2019), which may drive litter-mediated PSF via the biotic plant pathway. This may however generate relatively unspecific feedback effects, because different plant species may all profit from nutrients liberated from litter by specialized decomposer communities, however this is not tested. Future work should disentangle to what extent litter-mediated PSFs via the physical, chemical or biotic pathways result in species-specific effects on the growth and performance of next-generation plants.
- (4) More emphasis is needed on the role of root litter decomposition in driving PSFs. So far, most work has focused on aboveground litter pathways, but root decomposition may be key in driving litter-mediated PSFs and, importantly, in modifying rhizosphere-mediated PSFs. Future studies should build on established concepts originating from work on shoot litter decomposition (Wardle et al., 2004; Austin et al., 2014), but they should also focus on the fundamental differences between root and shoot litter, such as impacts of continuous vs. seasonal litter inputs, or the depth of the roots in the soil.
- (5) Litter-mediated PSFs need to be investigated under natural conditions, with a particular emphasis on the contexts under which such effects are most important. As PSF research moves out of the glasshouse and into the field (Kulmatiski and Kardol, 2008; De Long et al., 2019), it will be imperative to include litter-mediated PSFs alongside the more traditional rhizosphere-mediated PSFs when

designing and executing experiments. Only via inclusion of litter-mediated PSFs will we be able to generate a more comprehensive understanding of PSFs and the ecological processes they control under natural conditions. Also, field PSF experiments allow for testing litter- and rhizosphere-mediated PSFs across larger spatial (i.e., at the level of plant communities) and temporal scales (i.e., multiple plant generations).

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author and will be stored in the data archive of NIOO-KNAW.

AUTHOR CONTRIBUTIONS

All authors have contributed to develop the ideas presented in this manuscript. GV and FH designed and performed the experiment (**Box 1**). GV has led the writing of the manuscript and all authors have contributed to individual sections. All authors have read and approved the final version of this manuscript.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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