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Legume presence reduces the decomposition rate of non-legume roots

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ABSTRACT

Living plants can enhance litter decomposition rates via a priming effect by releasing root exudates which provide energy to saprotrophic microbes and thereby enable them to degrade litter faster. The strength of this effect, however, is expected to be dependent on the litter properties. To test whether the presence of a growing plant affects the decomposition rate of dead roots with different traits, we used dead roots of seven species (3 grasses, 3 legumes, 1 forb) as litter and quantified litter mass loss after eight weeks of incubation in soil with or without a growing white clover (*Trifolium repens*) plant. We expected root decomposition to be faster in the presence of *T. repens*, especially for roots with high C:N ratio. We found that the presence of *T. repens* slowed down the decomposition of grass and forb roots (negative priming), while it did not significantly affect the decomposition of legume roots. Our results show that root decomposition can be slowed down in the presence of a living plant and that this effect depends on the properties of the decomposing roots, with a pronounced reduction in root litter poor in N and P, but not in the relatively nutrient-rich legume root litters. Negative priming effect of legume plants on non-legume litter decomposition may have resulted from preferential substrate utilisation by soil microbes.

1. Introduction

Litter decomposition and mineralisation are key processes in sustaining primary productivity. Input of litter to soil is derived both from aboveground as well as from belowground plant parts. In temperate grasslands, litter input is larger belowground than aboveground, comprising both root exudates and dead plant roots (Rasse et al., 2005; De Deyn et al., 2008; Freschet et al., 2013). Despite its great relevance, considerably less is known about the decomposition of roots as compared to decomposition of aboveground plant parts. In general, studies of leaf litter decomposition show that environmental conditions (temperature, moisture) and litter quality (concentrations of nutrients, carbon:nitrogen ratio C:N and lignin:N ratios) are most important in determining the speed of litter decomposition (Silver and Miya, 2001; Vivanco and Austin, 2006; Fornara et al., 2009; Freschet et al., 2012a). Leaf litter decomposes fastest in warm and moderately moist conditions and when it is rich in nutrients (i.e. having low C:N ratio) and poor in recalcitrant (i.e. structurally complex) carbon compounds like lignin (Taylor et al., 1991). The rate of root litter decomposition and mineralisation can be expected to be driven by the same parameters as leaf litter upon entering the soil. Recent studies focusing on root decomposition found no consistent relationships between root litter decomposition rate and litter N and P concentrations, while a negative relation with lignin concentration and with root C:N was apparent (Silver and Miya, 2001; Freschet et al., 2012a,b; Smith et al., 2014). While direct comparative studies are still scarce, leaf and root decomposition rates have been found to show similar patterns and it seems that chemical composition, including C:N ratio, plays a central role in the process of litter decomposition, irrespective of whether the litter is derived from aboveground or belowground plant parts (Birouste et al., 2012; Freschet et al., 2013).

One reason why root decomposition remains poorly studied compared with leaf litter decomposition is that direct quantification of root decomposition as the rate of mass loss represents an inherent challenge as it cannot be performed without disturbing the soil and roots (Silver and Miya, 2001). Most root decomposition studies have used a litter bag approach (Silver and Miya, 2001; Freschet et al., 2012a,b; Smith et al., 2014) which enables comparison of treatment effects between species in a standardised way and gives an indication of potential differential responses though does not mimic in situ decomposition rates. However, this method

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does not reflect in situ decomposition rates as root washing and drying, which is required for accurate estimation of litter mass at the start of decomposition, disrupts the natural rhizosphere community at the soil-root interface. It has been shown that the absolute root decomposition rates are likely to be underestimated when using litterbags and nutrient mobilisation may be affected, especially when working with ectomycorrhizal tree species (Dornbush et al., 2002; Li et al., 2015). However, an alternative method to litter bags such as using intact soil cores remains difficult as the initial mass of roots within cores is unknown and homogenous distribution of roots in the soil is assumed (Dornbush et al., 2002; Li et al., 2015).

Living plants can significantly affect the decomposition of soil organic matter and roots through rhizosphere effects, leading to faster or slower decomposition rates (Kuzyakov, 2002, 2010; Fornara et al., 2009; Guenet et al., 2010). The induction of faster decomposition, called positive priming effect, is thought to be governed by root exudates which function as an easily available energy source for soil microbes and enable them to degrade more recalcitrant litter (Kuzyakov, 2002, 2010). Moreover root exudates not only contain C-rich compounds but also N, and both exudate quantity and composition affect microbial activity. Especially root exudates of leguminous plant species tend to be N-rich (Fustec et al., 2011), and can thereby promote growth and activity of soil microorganisms and litter decomposition (Sugiyama and Yazaki, 2012). However, it has also been shown that soil microbes may respond to increased N availability in the soil by reducing the production of enzymes used to mine N from recalcitrant organic matter, thereby slowing down its decomposition (Craine et al., 2007). Also, living plants can slow down litter decomposition, called negative priming (reviewed in Dormaar, 1990), by competing with decomposers for nutrients or by exuding chemical compounds that suppress the decomposers (Van der Krift et al., 2002; Guenet et al., 2010; Kuzyakov, 2010; Coq et al., 2011). Another hypothesis to explain negative priming is the preferential substrate utilization hypothesis (Sparling et al., 1982; Kuzyakov, 2002 for a review). This hypothesis states that the microorganisms actively shift their use of substrates and will use the most easily accessible fresh organic matter as a C source instead of degrading more recalcitrant dead organic matter, which is energetically more costly.

To date, the majority of studies have reported positive priming effects of organic matter decomposition by living plants (Cheng et al., 2014) and root exudates have been considered to be a crucial factor in this (Kuzyakov, 2010). However, it is still unclear which traits, both of the living plants and of the litter, cause the wide variation in rhizosphere priming effects. In a large-scale grassland biodiversity experiment, root litter decomposition rate was negatively related to the root biomass but was not affected by the functional group of the plants growing in the soil in which the root litter was decomposing (Fornara et al., 2009). In contrast in another grassland biodiversity experiment, the presence of legumes in the community strongly enhanced the decomposition rate of litter and standard substrates (wooden sticks and cotton strips), indicating positive priming effects on litter decomposition (Scherer-Lorenzen, 2008). These results indicate that the presence of leguminous plant species may generally create positive rhizosphere priming effects of root litter decomposition, but not always, and the underlying mechanisms require further elucidation.

Recently it has been proposed that the occurrence of rhizosphere priming effects may strongly depend on whether plants are N- or P-limited, with positive priming effects arising when plants are N-limited and no priming effects when plants are P-limited (Dijkstra et al., 2013). According to this view, one would expect legume species not to have strong priming effects because they are supposedly more limited by P than N as a result of endosymbiosis with N_2-fixing bacteria. In contrast, Cheng et al. (2003) found that both soybeans (a legume) and spring wheat (a grass) consistently generated positive priming effects, also when ample fertiliser was applied, suggesting that priming effects by plants may not, or not solely, depend on their nutrient status and that also in agricultural systems positive priming effects occur.

Root decomposition rates may not only depend on the properties of the root litter or the presence of a living plant, but also on interactive effects between the living plant and the root litter. Van der Krift et al. (2002) showed that the presence of the same focal grass species (*Festuca ovina*) had differential effects on root litter from different plant species as it accelerated the decomposition of root litter from its own species, but slowed down the decomposition of root litter from another grass species (*Anthoxanthum odoratum*). The exact underlying mechanisms are still unknown but may be due to different root litter properties that differentially stimulate decomposer organisms. Here we investigated the impact of a growing legume plant on the decomposition rate of different root species and tested the hypotheses that the presence of a growing white clover plant will: 1) increase the decomposition rate of root litter across litter species; 2) the magnitude of the priming effect of the growing plant on root litter decomposition will depend on the initial C:N ratio of the dead roots. We used a litterbag approach to accurately assess decomposition rates. Although being used in most studies of this kind, it has to be noted that overall decomposition rates are likely underestimated and natural rhizosphere communities disturbed compared to *in situ* situation (Dornbush et al., 2002; Li et al., 2015).

2. Material and methods

2.1. Root litter preparation

In preparation of the experiment, seven grassland species comprising three grasses (*Lolium perenne, Festuca rubra, Arrhenaterum elatius*), three legumes (*Trifolium repens, Trifolium pratense, Vicia cracca)* and a forb (*Cichorium intybus*) common in European grasslands were grown on sandy soil at 60% water holding capacity (WHC). The seeds were purchased from specialised companies in The Netherlands: *T. pratense* and *C. intybus* from Cruydt-Hoeck (Groningen), *L. perenne* and *T. repens* from Agrifirm (Apeldoorn) and in the UK: *V. cracca*, *F. rubra* and *A. elatius* from Emorsegate (Norfolk). The soil was collected from a grassland in the Netherlands, in spring 2013 ('Clue' site, Mosselse Veld, 52°04′N, 5°45′E). The soil is sandy-loam, with particle size distribution: <2 μm, 3.4%; 2–63 μm, 17.3%; >63 μm, 79.7%, pH H_2O 6.4 and %OM 4.5 (Van der Putten et al., 2000; Bezemer et al., 2010). Prior to filling the pots part of the soil was sterilised by gamma irradiation (25 kGray). The unsterilized soil was stored at 4 °C for two weeks until the soil sterilisation was completed. With the sterilised and living soil a soil mixture was prepared consisting of 85% sterilised soil and 15% living soil from which the plants could develop their own soil community. We sterilised part of the soil in order to avoid weed pressure and insect root herbivores but inoculated with living soil to provide a natural pool of soil microbes. Plants were surface sterilised by dipping them in diluted household chloride bleach (10% bleach solution for 30s), and afterwards rinsed several times with tap water. The seeds were subsequently germinated on autoclaved sand and two-week old seedlings were transplanted individually to 2 L pots filled with the soil mixture and grown in the greenhouse for 12 weeks (with day:night regime of 16:8 h light:-dark, 21:16 °C).

At harvest, the shoots were separated from the roots. The roots were washed carefully and dried at 40 °C for one week. The roots were weighed and a subsample of fine roots (diameter < 2 mm) was