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Short communication

"Afterlife" effects of mycorrhization on the decomposition of plant residues

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ABSTRACT

The symbiosis with arbuscular mycorrhizal fungi is known to affect growth and tissue quality of plants. Therefore, mycorrhization may also have "afterlife" effects on decomposition dynamics. We tested this hypothesis with plant material of mycorrhized and non-mycorrhized plants of seven grassland species. We found that mycorrhization increased the decomposition rate and interpret this result as a consequence of the enhanced nutritive status of the plant tissue with positive effects on decomposer activity. The turnover of organic matter and nutrients in ecosystems may therefore be indirectly influenced by the symbiosis with mycorrhizal fungi.

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The symbiosis with arbuscular mycorrhizal fungi (AMF) is known to enhance plant nutrition, plant growth (Smith and Read, 1997) and the concentration of P, N as well as other elements in plant tissue (e.g. Smith and Read, 1997; Hodge, 2003; Leigh et al., 2009) which are all important determinants of litter decomposition (Swift et al., 1979; Flindt and Lillebø, 2005). Given that the vast majority of terrestrial plants are associated with mycorrhizal fungi (Smith and Read, 1997), mycorrhization may have important effects on nutrient cycling in almost all ecosystems. Langley and Hungate (2003) noted that mycorrhiza can have a multitude of direct effects on the decomposition process belowground. However, we are not aware of any experimental study demonstrating an indirect influence of mycorrhization on decomposition of aboveground plant material.

Mycorrhizal fungi have also been shown to modify the plant's defence system (for review: Hartley and Gange, 2009). This effect may further depend on the induction of defence in response to herbivory (Pozo and Azcon-Aguilar, 2007). Plant defence, however, may also affect decomposition rates negatively (Cornelissen et al., 1999). For the plants used in the here presented experiment, we already showed that mycorrhization increased plant quality for herbivores and that herbivory induced resistance against subsequent herbivores in mycorrhized plants (Kempel et al., in press). From these results we expect that mycorrhization may positively affect decomposition of litter, but that this effect may be cancelled out by the response of plants to the feeding of herbivores.

We made use of a manipulative experiment with seven herbaceous plant species to assess the importance of mycorrhization on the decomposition rate of aboveground plant biomass. We used the grass species *Poa pratensis*, *Festuca rubra*, *Agrostis capillaris* and *Deschampsia flexuosa* and the dicots *Senecio jacobea*, *Plantago lanceolata* and *Artemisia vulgaris*. These species are typical grassland species and known to be frequently associated with AM fungi (Database of "The Ecological Flora of the British Isles at the University of York"; http://www.york.ac.uk/res/ecoflora). The plants were reared in a greenhouse with temperature (15–25 °C, LD 14/12) and additional light supplied by high pressure sodium lamps (Philips Son-T Agro, 400 W). Seeds were surface sterilized and sown in steam-sterilized potting soil. Two weeks after germination, seedlings were planted individually into sterilized pots filled with steam-sterilized soil taken from an old fallow grassland site mixed with sterilized sand (ratio 1:1, v/v). To leach nutrients from the soil pots were irrigated daily with 40 ml of deionised water for 3 days (initial nitrogen availability of 2.9 mg NH_4^+ kg^{-1} soil and 1.2 mg NO_3^- kg^{-1}). Mycorrhizal inoculum was provided by spreading 2 g of clay granules, containing a mixture of root fragments, spores and hyphae of *Glomus intraradices* (AMykor, Greppin, Germany) in a layer 4 cm below the soil surface. The control plants received sterile clay granules. All pots were irrigated every two days with 50–100 ml of water. After further 8 weeks, we allowed larvae of the generalist *Spodoptera littoralis* to feed on half of the plants of each treatment for

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one day to induce possible defence mechanisms (for further details see Kempel et al., in press). All pots were enclosed with nylon gauze (200 μm mesh). All treatments were replicated 10 times and randomly arranged within 5 blocks. Half of the plants were used to assess plant resistance against subsequent herbivory. After 4 weeks shoot biomass of the remaining plants was harvested, dried and weighed. Mycorrhizal colonization of roots was confirmed after staining using the line intersect method (Schmitz et al., 1991).

The dried aboveground plant material (between 0.25 and 1.95 g) was placed into nylon bags (15 cm × 20 cm, mesh size of 20 μm). In June 2007 the litter bags were placed randomly on the bare ground of a freshly ploughed and harrowed grassland site in the Botanical garden of the University of Marburg (Germany). Litter bags were covered with a layer (c. 2 cm) of swath to avoid the establishment of weeds and to prevent drying of samples. The samples were retrieved after 8 weeks, dried and cleaned. Percentage dry weight loss was calculated as a measure of decomposition rate and arcsin√-transformed for analyses. The effects of mycorrhization, induction, plant species, group (grasses or dicots) and block were analysed using a nested ANOVA. For this, mean squares for the factor species and its interactions were used as error term for the factor group and the corresponding interactions. Mycorrhization positively affected plant biomass (Kempel et al., in press). Therefore, biomass of plant material varied between species and mycorrhiza treatment. We therefore re-ran the analysis with initial plant material mass as covariate to remove potentially confounding effects of initial mass of plant material from the analysis.

Decomposition rate varied considerably between plant species (Table 1, Fig. 1) but did not differ between grasses and dicots. Weight loss of plant material from mycorrhizal plants (across all plants 44.0% ± 1.41%, mean ± standard error) was higher than from non-mycorrhizal plants (across all plants 40.0% ± 1.37%, mean ± standard error). The effect of mycorrhization on weight loss was consistent across plant species and species groups (no significant interactions, see Table 1). Previous herbivory had no effect on decomposition. The inclusion of initial plant biomass did not change the effects qualitatively and litter mass did not affect decomposition rates ($F_{1,105} = 0.13$, $P = 0.72$). The effects of mycorrhization can therefore not be explained with changes in biomass of the produced litter.

We already showed for the plants used in this decomposition experiment that mycorrhization enhanced the growth of plants and also improved the nutritional quality for herbivores (Kempel et al., in press). Here, we show that mycorrhization also increases the decomposition rate of plant residues. Therefore, in addition to their direct contribution to the decay of organic matter (e.g. Hodge et al., 2001; Aristizabal et al., 2004), AMF has indirect effects on decomposition. Several studies showed that feeding by herbivores and decomposition rate are determined in a similar way by tissue quality (Cornelissen et al., 1999; Schädler et al., 2003). This study suggests that also mycorrhization affects both processes in a similar direction. A short period of herbivore feeding on the plant, however, did not decrease decomposition rates. Nevertheless, the plant species used in this study showed an increased resistance against subsequent herbivore feeding especially if they were colonized by mycorrhizal fungi. We explained this finding by the induction of defence mechanisms (Kempel et al., in press). Obviously, this effect did not translate into changed decomposition dynamics. There are several possible explanations for these contrasting effects. First, for aquatic systems it has been shown that secondary compounds rapidly leach from litter and are less important for decomposition processes (Ardon and Pringle, 2008). This was also suggested for terrestrial systems (see Throop and Archer, 2007). Second, the mesh size of litter bags used in our experiment excluded the macro- and mesofauna. As previously shown, the relationship between litter quality and decomposition rate is stronger in the presence of soil fauna (Schädler and Brandl, 2005). Some changes in plant tissue chemistry following insect herbivory may be toxic or deterrent for arthropods but not necessarily for the microflora. Therefore, the effects of induction and mycorrhiza induced changes of litter quality on decomposition may be more pronounced in the presence of soil fauna. Third, living aboveground parts of plants may not necessarily reflect the decomposition dynamics of senescent litter. However, the return of plant material as green litter may outweigh the importance of senescent litter in managed grasslands with consequences for nutrient cycling due to changes in tissue quality during the senescence process (Sanaullah et al., in press). Green leaves are usually considered as more nutrient rich than the senescent litter of the

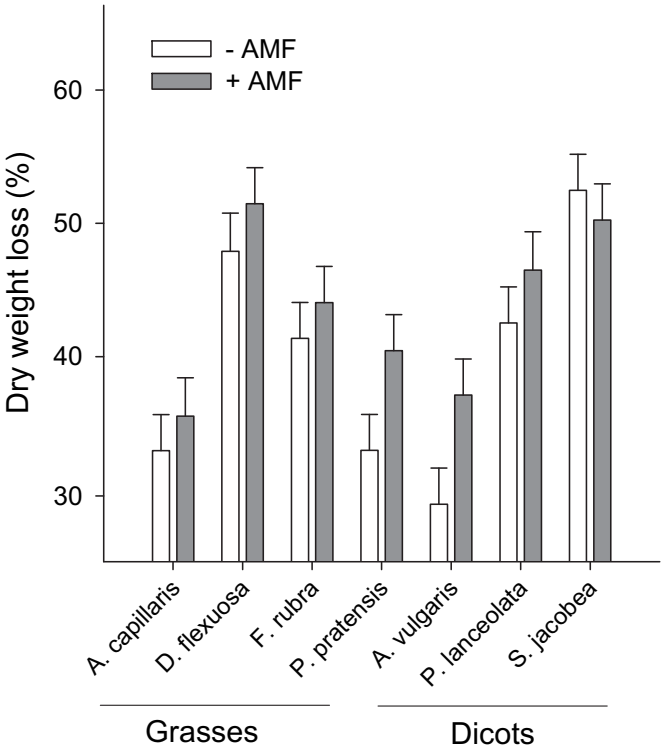

Fig. 1. Effects of mycorrhization by *Glomus intraradices* (−AMF = without, +AMF = with) of herbaceous plant species on the dry weight loss of plant material in the litter bag experiment (means ± standard error).

Table 1
Results of the nested ANOVA of the effects of block, mycorrhization, herbivory, plant group (grasses vs. dicots) and plant species on the decomposition rate of plant residues. Plant species was nested in plant group. Terms indicated by upper case letters (A–D) were tested against the term with the accordant lower case letter (a–d), all other terms were tested against the residual mean squares. Significance levels are indicated with ** for $P < 0.01$ and *** for $P < 0.001$.

Source of variation	df	MS	F
Block	4	0.11	1.42
Mycorrhization (M)	1	0.53	7.10**
Herbivory (H)	1	0.03	0.35
M × H	1	0.02	0.28
Plant group (G)^{A}	1	0.14	0.11
G × M^{B}	1	0.01	0.20
G × H^{C}	1	0.01	0.07
G × M × H^{D}	1	<0.01	<0.01
Plant species (S)^{a}	5	1.25	16.96***
S × M^{b}	5	0.07	0.97
S × H^{c}	5	0.02	2.15
S × M × H^{d}	5	0.07	0.92
Residual	105	0.007	

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same species (e.g. Fonte and Schowalter, 2004) and therefore the fresh material is rapidly decomposed despite variations of secondary compounds. However, nutrient reabsorption during senescence greatly differs between grassland species and faster decomposition of green material is not always the case (Bloemhof and Berendse, 1995). Thus, the differential effects of mycorrhization on decomposition of green versus senescent plant material depending on plant species identity needs further experimental consideration.

Overall, our experiment indicates that mycorrhization is a hitherto overlooked determinant of decomposition of plant residues. We therefore conclude that mycorrhized plants may increase the quantity and quality of the produced plant material with important consequences for the cycling of organic matter and nutrients.

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