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Short Communication

Rhizosheaths stimulate short-term root decomposition in a semiarid grassland

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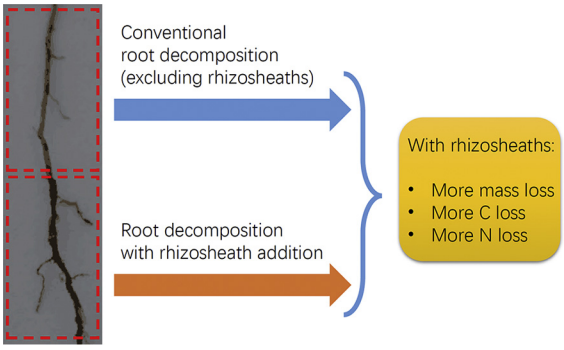
HIGHLIGHTS

- Impact of rhizosheaths on grassland root decomposition was hitherto unknown.
- Rhizosheath addition in litterbag stimulated root mass, carbon and nitrogen loss.
- Ignoring rhizosheaths underrated grassland root decomposition by >20%.

GRAPHICAL ABSTRACT



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ABSTRACT

Rhizosheaths are frequently found in arid and semiarid ecosystems, but their impacts on root decomposition rates and associated carbon (C) and nutrient fluxes remain unclear. We investigated mass, C and nitrogen (N) loss for the roots of *Stipa krylovii* and *Carex korshinskii*; the roots were exposed to rhizosheaths, bulk soil, or no soil in litterbags during a 102-d short-term decomposition experiment. Compared with no soil addition, rhizosheath addition increased the mass loss by 39% for *S. krylovii*, a sheath-forming grass, and by 11% for *C. korshinskii*, a non-sheath-forming grass. Rhizosheath addition also increased root C loss by 39% and N loss by 41% for *S. krylovii* but did not significantly alter root C or N loss for *C. korshinskii*, which may be due to a "home-field advantage" effect. In contrast, bulk soil addition did not alter mass, C, or N loss for either plant species, possibly because bulk soils contained fewer nutrients (C, N, and phosphorus) than rhizosheaths. We demonstrate for the first time that conventional root decomposition studies that do not account for rhizosheaths will underestimate the root mass, C and N loss by >20% in semiarid grasslands. Future studies should emphasize the crucial yet unappreciated role of rhizosheaths in driving soil organic matter cycling.

1. Introduction

Root decomposition is a critical process that influences greenhouse gas emissions, nutrient release, and soil organic matter formation

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(Berg and McClaugherty, 2003). Compared to aboveground litter decomposition, root decomposition may contribute more to soil organic matter formation because compared to leaves, roots usually contain more recalcitrant organic matter (Mambelli et al., 2011; Wang et al., 2015; Xia et al., 2015) and are less likely to decompose in soils (Crow et al., 2009; Kätterer et al., 2011). However, compared with leaf litter decomposition, root decomposition and its influencing factors are less understood and involve more complicated processes because of plant-soil microbe interactions (Iversen et al., 2015; Schmidt et al., 2011; Zhang and Wang, 2015). Root decomposition is a critical process for greenhouse gas emission and nutrient release particularly in dry ecosystems such as semiarid grasslands because large amounts of grass biomass and nutrients are allocated to the roots and because grass roots are more labile than tree roots (Watt et al., 1994; Kong et al., 2013; Silver and Miya, 2001; Yang et al., 2010). Grass root decomposition is likely controlled not only by root litter chemistry but also by rhizosphere properties such as soil moisture, nutrients and soil organic matter composition (Castanha et al., 2015; Solly et al., 2014).

In arid and semiarid ecosystems, rhizosheaths that contain both fine soil particles and plant root mucilage as well as high number of soil microbes and tightly coat the root surface widely exist (Bailey and Scholes, 1997; Bergmann et al., 2009; Watt et al., 1994). For example, 107 of 130 South African grass species can form rhizosheaths outside of their roots (Bailey and Scholes, 1997). Rhizosheaths also widely occur for many grasses such as *Leymus chinensis*, *Stipa grandis*, *Cleistogenes squarrosa*, and *Agropyron cristatum* (D.L.K. personal observation), which are dominant on typical steppes in China (Bai et al., 2004; Kong et al., 2011). Rhizosheaths are usually distinct from bulk soil in many critical aspects; e.g., rhizosheaths contain more soil carbon (C) and nitrogen (N) and exhibit higher abundance of soil microbes and greater microbial activity (Bergmann et al., 2009; Hanna et al., 2013). These characters of rhizosheaths can maintain high soil moisture and physically protect roots, eventually beneficial for plant growth in dry ecosystems (Buckley, 1982; North and Nobel, 1997; Price, 1911; Watt et al., 1994). As such, rhizosheath formation represents an important strategy for plants to cope with water limitation, physical damage from coarse sand, and physiological stress due to high temperatures in arid environments (Buckley, 1982; North and Nobel, 1997).

For plant roots that form rhizosheaths, root decomposition for sheath-forming species occurs mostly within rhizosheaths; this phenomenon occurs because rhizosheaths are usually sticky soil mantles that closely adhere to roots and are not easily detached. In semiarid grasslands plant species that do not form rhizosheaths often coexist with those that do form rhizosheaths and can also expose their roots to neighboring rhizosheaths (Chen et al., 2001; Kong et al., 2010). Importantly, factors that affect root decomposition, including soil moisture, nutrient content and microbial activity (Silver and Miya, 2001; Solly et al., 2014), seem more favorable for root decomposition in rhizosheaths than in bulk soil (Bergmann et al., 2009; Hanna et al., 2013). However, in traditional litterbag decomposition studies, root samples are generally prepared by removing rhizosheaths (Parton et al., 2007; Silver and Miya, 2001; Smith et al., 2014). Whether and to what extent this conventional practice underestimates or overestimates root decomposition rates and C and N fluxes for sheath-forming and non-sheath-forming grasses is, however, unknown.

To address these questions, we conducted a 102-d litterbag-based root decomposition study for *Stipa krylovii* (a sheath-forming grass) and *Carex korshinskii* (a non-sheath-forming grass) and analyzed the root mass, C, and N loss in a semiarid temperate grassland in North China. Three treatments were applied to the root-containing litterbags as follows: 1) addition of sieved rhizosheaths, 2) addition of sieved bulk soil, and 3) no soil addition, the last of which represented the conventional approach for root decomposition. We hypothesized that root decomposition in the treatment of rhizosheath addition would be higher than that in bulk soil addition and no soil addition.

2. Materials and methods

2.1. Study site and species selection

The study site was located in a semiarid grassland in North China (42°02′N, 116°17′E) and has been described elsewhere (Liu et al., 2009). The mean annual precipitation at the site is 383 mm, and the majority of the precipitation falls between May and October. The mean annual temperature is 2.1 °C; the minimum and maximum monthly mean temperatures are −17.5 °C in January and 18.9 °C in July, respectively. The soil is a Haplic Calcisol, the mean soil bulk density is 1.31 g cm^{-3}, and the soil pH is approximately 6.84 (Liu et al., 2009). The plant community includes *Leymus chinensis*, *Stipa krylovii*, *Artemisia frigida*, *Potentilla acaulis*, *Allium bidentatum*, *Cleistogenes squarrosa*, *Agropyron cristatum*, and *Carex korshinskii*. We selected two common grass species for the decomposition study: *S. krylovii*, a bunch-type grass that forms rhizosheaths, and *C. korshinskii*, a rhizomatous grass that does not form rhizosheaths probably because of few root hairs or lack of exudation with great adherence to fine soil particles (Holz et al., 2018).

2.2. Root and soil sampling

Roots of these two species were collected to a soil depth of 15 cm with a spade in late June 2014. The roots of *S. krylovii* were excavated at a distance of 15 cm from the center of the bunch. To ensure enough root material, approximately 20 mature bunches of *S. krylovii* and approximately 10 mature clones of *C. korshinskii* were sampled. After they were excavated, the root and soil samples were collected and immediately transported to the laboratory for root and soil separation before the samples had dried. Rhizosheaths were collected by carefully hand-kneading rhizosheath that was present outside of the *S. krylovii* roots. Rhizosheaths obtained were further carefully checked with a magnifying glass, and any observable root hairs were carefully removed. After shaking or hand-kneading, the root samples were gently cleaned to remove any remaining soil and subsequently air-dried. Bulk soil was collected from a nearby grassland location where less dense vegetation was present. Each rhizosheath and bulk soil sample was air-dried and sieved through a 1-mm mesh screen. A subsample of these soils was used for root decomposition experiments, and another soil subsample was ground for soil chemistry analyses (see below).

2.3. Litterbag experiment

We established a litterbag experiment and exposed root samples to one of the following treatments (five replicates each): 1) addition of sieved rhizosheaths, 2) addition of sieved bulk soil, and 3) no soil addition (control). Initially, 8 g of air-dried root material was evenly placed into nylon litterbags (18 cm × 18 cm, 0.15 mm mesh). The amount of soil applied to each litterbag for the soil addition treatments was 24 g, which corresponded to the amount of rhizosheaths naturally adhering to 8 g of roots. For each species, the litterbags were assigned to five 0.6-m × 0.6-m blocks that were spaced approximately 20 cm apart. The litterbags were buried at a depth of 10 cm on 3 July 2014 and were collected after 102 d. After being collected, the root samples were cleaned and oven-dried at 60 °C for 48 h, after which they were weighed.

2.4. Root and soil chemicals

Root C and N concentrations in the samples were measured before and after decomposition using an element analyzer (Vario MAX CN, Elementar Analysensysteme GmbH, Germany). The water soluble carbohydrate in root extract was determined, and root lignin content was determined as the Klason lignin after carbohydrate components were removed by hydrolysis with 72% (v/v) sulfuric acid (Hättenschwiler and Jørgensen, 2010). Subsamples of bulk soil and rhizosheaths were

finely ground and subsequently analyzed for C and N concentrations using the same elemental analyzer. In addition, we measured the dissolved organic C (DOC), hydrolyzed N and total phosphorus (P) contents in these soil samples. The DOC content was determined using a total organic carbon (TOC) analyzer (Vario TOC Select, Analysensysteme GmbH, Germany) after the soils were extracted with a 0.5 mol L^{-1} K_2SO_4 solution (Jones and Willett, 2006). The hydrolyzed N content was measured using the alkali-hydrolyzed diffusing method (Fan and Cai, 2000). The total soil P content was determined using the Mo—Sb colorimetrical method after the soil samples were digested with HNO_3-$HClO_4$ (Kong et al., 2011). In addition, although we missed the chance to measure microbial biomass of the bulk soils and rhizosheaths that we used for litter decomposition, we made supplementary measurements of soil microbial carbon and nitrogen for bulk soil and rhizosheaths that were collected from the same sources in mid-May 2018 (see the Appendix).

2.5. Data analysis

Root mass, C, and N loss were calculated as the percent loss during decomposition, i.e., ((value-before − value-after) / (value-before)) × 100%. The root mass loss was adjusted by accounting for the ash content of the root samples. Differences in root chemicals between the two species before decomposition were analyzed using one-way ANOVA. Two-way ANOVA was used to explore the effects of plant species, soil addition treatment, and their interaction on root mass loss as well as C and N loss. For each species, differences in root mass, C, and N loss between different soil addition treatments were evaluated by one-way ANOVA and least significant difference (LSD) post hoc tests. Similar analyses were also used to evaluate differences in chemical properties between rhizosheaths and bulk soil. All analyses were performed using SPSS 16.0 (SPSS Inc., Chicago, USA). Differences were considered significant at $P < 0.05$.

3. Results

The Two-way ANOVA revealed that soil addition treatments significantly affected root mass, C, and N loss. In addition, the effects of soil addition differed between *C. korshinskii* and *S. krylovii* (Table 1). Compared with no soil addition (the control), rhizosheaths addition increased the root mass loss by 11% for *C. korshinskii* ($P = 0.037$) and by 39% for *S. krylovii* ($P < 0.001$; Fig. 1a). Compared with no soil addition, rhizosheaths addition to the roots of *S. krylovii* significantly increased root C and N loss by 39% and 41%, respectively (both $P < 0.001$; Fig. 1b, c). Compared with bulk soil addition, rhizosheaths addition consistently resulted in significantly higher root mass loss, C loss, and N loss for *S. krylovii* (all $P < 0.05$). For *C. korshinskii*, compared with bulk soil addition, rhizosheath addition also caused higher average root mass loss, C loss, and N, but none of these differences were statistically significant (all $P > 0.05$; Fig. 1).

Compared with those of *S. krylovii*, the roots of *C. korshinskii* had a higher root N concentration, a higher water soluble carbohydrate content, and a lower C/N ratio (Table 2), and there was no difference in lignin content between the roots of both species (Table 2). Compared with rhizosheaths, the bulk soil consistently had a lower total C content (equivalent to 52% of that of rhizosheaths), DOC content (equivalent to 39% of that of rhizosheaths), total N content (58%), hydrolyzed N content (58%), soil C/N ratio, and total P content (64%) (Table 3). In addition, bulk soil had lower soil microbial carbon and nitrogen as well as lower soil water content than rhizosheaths (Table 1 in the Appendix).

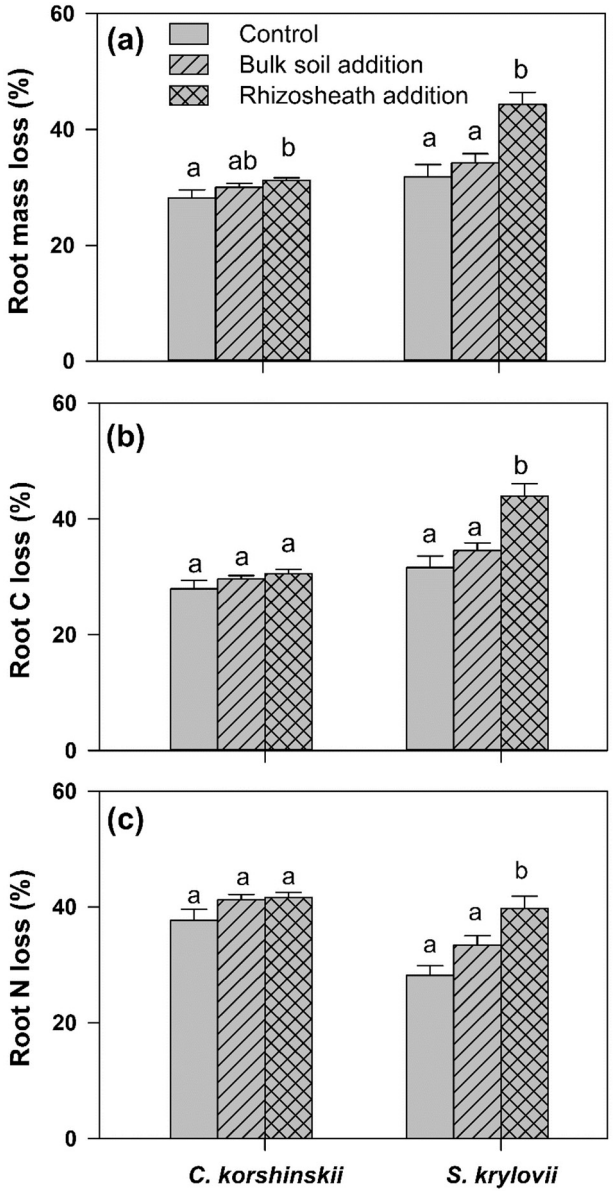

Fig. 1. Effects of the addition of bulk soil and the *S. krylovii* rhizosheaths on root decomposition (% mass loss) (a), root C loss (%) (b) and root N loss (%) (c). The different letters above the bars indicate significant differences between treatments at $P < 0.05$. The error bars refer to the standard errors from five replicates.

4. Discussion

We showed for the first time a phenomenon supporting our hypothesis that exposure of roots to rhizosheaths can facilitate root

Table 1
Two-way ANOVA for the effects of species, soil addition and their interaction on root mass loss, C loss and N loss during root decomposition.

	Mass loss		Root C loss		Root N loss	
	F	*P*	*F*	*P*	*F*	*P*
Species	43.98	<0.001	49.15	<0.001	40.89	<0.001
Soil addition	12.38	<0.001	12.35	<0.001	7.55	0.001
Species × Soil addition	4.72	0.008	4.92	0.006	2.74	0.06

Table 2
Differences in root chemical properties (mean ± standard error; $n = 5$) between *C. korshinskii* and *S. krylovii* before root decomposition. Significant differences at $P < 0.05$ are indicated in different letters.

Soil properties	*C. korshinskii*	*S. krylovii*
Root N (g kg^{-1})	12.83 ± 0.11^b	10.96 ± 0.19^a
Root C/N	33.85 ± 0.30^b	37.87 ± 0.76^a
Root lignin (g kg^{-1})	18.28 ± 1.44^a	17.49 ± 0.38^a
Water soluble carbohydrates (g kg^{-1})	3.23 ± 0.04^b	1.52 ± 0.024^a

Table 3
Soil properties (mean ± standard error; n = 5) of the bulk soil and rhizosheath of *S. krylovii*. Different letters show significant differences in soil properties between different soils at $P < 0.05$.

Soil properties	Bulk soil	Rhizosheath
Total C (g kg^{-1})	11.74 ± 0.16^{a}	22.64 ± 0.30^{b}
DOC (mg kg^{-1})	102.15 ± 1.27^{a}	264.25 ± 2.22^{b}
Total N (g kg^{-1})	1.45 ± 0.02^{a}	2.51 ± 0.03^{b}
Hydrolyzed N (mg kg^{-1})	102.67 ± 2.46^{a}	176.50 ± 5.02^{b}
Soil C/N	8.09 ± 0.10^{a}	9.02 ± 0.05^{b}
Total P (g kg^{-1})	0.29 ± 0.01^{a}	0.45 ± 0.004^{b}

decomposition for a sheath-forming species and that exposure of its roots to bulk soils does not result in such an effect. As such, our results are consistent with the hypothesis that the presence of rhizosheaths can accelerate root decomposition. In root decomposition assessments, rhizosheaths are usually excluded when root samples are prepared for decomposition. Our results indicate that this conventional approach (i.e., rhizosheath exclusion) could dramatically underestimate the rates of both decomposition and C and N release, at least for the species we examined here. This finding could also be particularly important for rhizosheath-forming plant species, whose mass, C and N loss estimates were approximately 28%, 28%, and 29% lower, respectively, in the presence of rhizosheaths than in the absence of soil (the conventional approach) even after only several months of decomposition. Given the widespread occurrence of rhizosheaths for *L. chinensis* and bunch-type grasses such as *S. krylovii* (field observation by D.L.K.), which account for >80% of the aboveground primary productivity on typical steppes in China (Bai et al., 2004; Kong et al., 2011), the underestimations of root mass, C and N loss by the conventional approach may be >22%, 22% and 23%, respectively, when all else being equal across these species. Note that rhizosheath addition treatment in our study neither involved full exposure of the roots to rhizosheaths nor simulated the same moisture conditions as those in a real rhizosheath environment in the field. However, if we did not separate rhizosheaths from the roots, we would be unable to quantify the initial root mass in the litterbags or to guarantee similar root mass in the litterbag replicates for the root decomposition experiment. Therefore, although rhizosheaths separation and re-addition is not a perfect method, this is probably the best approach so far for simulating the exposure of roots to rhizosheaths and accurately recording the amount of the root and soil mass added. If these conditions were also considered, the difference in root decomposition between the presence and absence of rhizosheaths might be even larger. Such large differences should not simply be considered a small "error" but a "mistake". Therefore, the integration of rhizosheath soil into empirical and modeling studies of root decomposition is urgently needed to understand and predict ecosystem processes in semiarid grasslands. Additionally, to gain a deep and comprehensive understanding of the above role of rhizosheaths, it may be promising to characterize the fine structures of rhizosheaths and bulk soil using technique such as Cryo-scanning electron microscopy (McCully et al., 2010). Moreover, developing new in situ methods for exploring rhizosheath effects is desirable, as the sieved rhizosheath additions can simulate but not represent the true effects of rhizosheaths on root decomposition.

Despite root decomposition stimulation by rhizosheaths in both species, such stimulation of root mass, C and N loss by rhizosheaths was much weaker for *C. korshinskii* than for *S. krylovii* (Fig. 1, Table 1). This finding contradicts the root chemical results, as the roots of *C. korshinskii* had a higher root N concentration and water soluble carbohydrate content but a lower C/N ratio than did those of *S. krylovii* (Table 2), which would result in a greater root decomposition rate for *C. korshinskii* than for *S. krylovii* (Hättenschwiler and Jørgensen, 2010; Silver and Miya, 2001). In addition, the similar root lignin content between *C. korshinskii* and *S. krylovii* cannot explain the different responses of root decomposition to rhizosheath addition between *C. korshinskii* and *S. krylovii* (Silver and Miya, 2001; Xia et al., 2015). A likely explanation for the relatively lower stimulation of root decomposition of *C. korshinskii* by the *S. krylovii* rhizosheath may be the "home-field advantage" effect described for soil microbial communities that often decompose litter faster at home sites than at away sites (Freschet et al., 2012; Veen et al., 2015). Given the widespread occurrence of the "home-field advantage" effect, it is likely that the greater stimulation of root decomposition of *S. krylovii* by rhizosheaths may result from the induction of rhizosheath microbes that are specialized for sheath-forming species but not for non-rhizosheath-forming species (Ayres et al., 2009; McGuire et al., 2010; Veen et al., 2015). This idea can be tested by future detailed work on soil microbiome during root decomposition of the two species as well as many other species under rhizosheaths addition.

Based on the analyses of soil chemicals and microbes for the bulk soils and rhizosheaths, the stimulation of root decomposition by rhizosheath can be due to the following mechanisms. First, high microbial biomass and activity (Table 1 in the Appendix) which result from greater resource contents (e.g., C, N and P) in rhizosheaths than in bulk soil (Holz et al., 2018; Mau et al., 2015) (also see Table 3) can accelerate root decomposition. Second, root decomposition can also be stimulated by widely reported "priming effects", i.e., increased decomposition of old and recalcitrant C by the addition of new and labile C (Bird et al., 2011; Cheng et al., 2014; Pausch et al., 2013; Wang et al., 2017). This mechanism seems possible because of the greater DOC content in rhizosheaths than in bulk soil reported here (Table 3) and elsewhere (Holz et al., 2018; Luo and Zhou, 2006; Nguyen, 2003). Third, a favorable abiotic environment, e.g., a higher water holding capacity in rhizosheaths than in bulk soil (see Table 1 in the Appendix), may also facilitate root decomposition in rhizosheaths. This phenomenon may be due to relatively low water potentials caused by increased concentrations of organic compounds (Table 3) from root mucilage, which reduces water loss from rhizosheaths and facilitates water transfer to rhizosheaths from the surrounding soil. Additionally, the higher soil water content could also strengthen the positive effects of rhizosheaths on root decomposition via the first two mechanisms. As we aimed to report this interesting finding in a timely manner, the detailed mechanisms have not been addressed in the present study. Future investigations of the molecular composition (e.g. Wang et al., 2015), physical properties of rhizosheaths (e.g., McCully et al., 2010) and especially the microbial properties such as diversity, species composition (Bakker et al., 2015; Bergmann et al., 2009; Koranda et al., 2011; Singh et al., 2007; Smalla et al., 2001) between the bulk soil and rhizosheaths will help elucidate these detailed mechanisms.

In summary, we found for the first time the phenomenon of stimulation of root decomposition by a rhizosheaths-forming species in a semiarid grassland. Given the great abundance of rhizosheath-forming species and the disproportionately high root biomass allocation in semiarid grasslands, previous reports of both root decomposition and its associated C and nutrient cycling may be underestimated by >20%. Future studies are desirable for developing new in situ methods combined with techniques in chemistry and soil microbiomics to explore the effects of rhizosheaths on root decomposition for more plant species as well for revealing the mechanisms behind these phenomena.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.05.398.

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