SOIL ORGANISMS **91** (3) · December 2019 pp. 107–112

Soil fauna contribution to winter decomposition in subalpine grasslands

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Received 14 October 2019 | **Accepted** 23 November 2019
Published online at www.soil-organisms.de 1 December 2019 | **Printed version** 15 December 2019
DOI 10.25674/so91iss3pp107

Abstract

Cold biomes significantly contribute to the global carbon cycle, and decomposition in these ecosystems is expected to be affected by climatic change. Modifications of snow cover patterns are expected to affect litter decomposition, but the underlying mechanisms remain unclear. In this study, we investigated whether soil meso- and microfauna significantly contribute to wintertime decomposition. Using litterbags with two mesh sizes (68 µm and 1500 µm), we found that small mesh litterbags reduced winter decomposition in the field by 3.4 % for *Patzkea paniculata* litter and by 18.9 % for *Dactylis glomerata* litter, indicating a significant contribution of soil meso- and microfauna to litter decomposition under the snowpack. Whereas previous studies showed that winter decomposition was not related to the soil fauna community, our results suggest that this community, and its possible alteration by climate change, may impact litter decomposition and carbon dynamics in cold biomes.

Keywords detritivorous fauna | *Patzkea paniculata* | *Dactylis glomerata* | litterbags | mesh size

1. Introduction

The dynamics of soil organic matter in cold biomes are receiving increasing attention, since these soils are particularly rich in carbon (Crowther et al. 2019) and will be greatly affected by climatic changes, with potential feedbacks on climate (Aerts 2006, Gavazov 2010, Hobbie et al. 2000). In these ecosystems, the soil is covered during a large part of the year by a snowpack that isolates the ground from extreme temperature (Baptist et al. 2010, Bokhorst et al. 2013). Winter litter dynamic has received recent attention, because substantial decomposition occurs under the snow (Bokhorst et al. 2013, Saccone et al. 2013). For example, litter mass loss during the first winter after litter fall in the French Alps reached up to 59 % in an alpine tundra (Baptist et al. 2010) and 33 % in subalpine meadows (Saccone et al. 2013). This substantial decomposition is facilitated by the thermal resistance of the insulating snow layer (Baptist et al. 2010). However, the mechanisms operating during decomposition under snow and in particular the respective contributions of physical processes, microorganisms and soil fauna are poorly understood. Freeze-thaw events promote litter fragmentation and leaching, in particular during snow melt (Gavazov 2010, Hobbie & Chapin 1996); but the contribution of soil fauna is not well established. To our knowledge, the only studies that explicitly quantified the role of soil fauna during litter decay in alpine and subalpine ecosystems found a limited contribution of animals to decomposition (Schinner 1982, Wall et al. 2008). Liu et al. (2019) found a substantial contribution of soil fauna over 554 days, but decreasing with altitude. None of these studies, however, specifically addressed the contribution of soil fauna to decomposition under the snowpack. In a

ISSN 1864-6417 (print) · **ISSN** 2509-9523 (online)

subarctic heathland, experimental snow depth reduction drastically reduced microarthropod abundance, but did not greatly impact litter decomposition, suggesting a low contribution of soil fauna to decomposition under snow (Bokhorst et al. 2013). An explicit quantification of animal contribution to winter decomposition is of particular importance, because climate-induced changes in the distribution of soil animals have been proposed as a potential driver of cold biome response to climatic change (Aerts 2006, van Geffen et al. 2011). Several studies already highlighted the vulnerability of soil arthropods to climatic changes and extreme events (Bokhorst et al. 2012, Makkonen et al. 2011), but the functional significance of induced community alteration in cold biomes remains unclear.

In this study, we evaluated the role of soil animals during litter decomposition under the snowpack for two co-occurring subalpine grass species, the conservative *Patzkea paniculata* (L.) Schinz & Thell and the exploitative *Dactylis glomerata* (L.). Subalpine meadows are of particular interest because the snowpack may be irregular and deeply affected by future changes in the precipitation pattern (Saccone et al. 2013). To evaluate soil fauna contribution to the winter decomposition of these two grasses, we used litterbags of different mesh size, and compared litter mass loss in natural subalpine grasslands. Following previous studies, we hypothesized that fauna contribution to litter mass loss would be low, which would be reflected by a low difference between large and fine mesh litterbags decomposing in the field. In addition, because differences in mass loss in litter bags with distinct mesh sizes might arise from biological processes, but also from accidental loss of litter through large mesh, we also included a treatment where litterbags, filled with the same litter mixtures, were placed at the surface of pots filled with artificial soils. The field sites and the pots were very close to each other and experienced similar climatic conditions, but the natural soil fauna community was absent from the artificial soils in the pots. This control setup in pots allows assigning any significant difference between mesh size in the field to a contribution of soil fauna, and not to accidental litter loss.

2. Materials and methods

2.1 Decomposition in litterbags

The experiment is part of a wider project also exploring the link between grasshopper herbivory and decomposition (Ibanez et al. 2013), conducted in a subalpine grassland at the Lautaret pass (2100 m) in the central French Alps. Therefore, 48 pots were set up, corresponding to 4 replicates of 3 plant treatments (21 *Dactylis* and 3 *Patzkea* individuals; 3 *Dactylis* and 21 *Patzkea* individuals, 12 *Dactylis* and 12 *Patzkea* individuals), crossed with a grasshopper herbivory treatment, including 4 modalities (see Ibanez et al. 2013 for details on this grasshopper treatment). In each pot, the 24 tillers were planted in June 2010 in large pots (Ø 45 cm, h 50 cm) in a mixture of sand (2/3), vermiculite (1/6) and potting soil (1/6), and fertilized with 3 g of low leaching rate fertilizer (Fertiltopw, 16 – 8 – 10 + 4MgO + oligoelements). On 2 November 2010, senescent leaves were harvested from the plants in each pot and dried for 48 h at 40°C.

5 x 4 cm litterbags with large (1500 µm) and small (68µm, DIATEX, St-Genis-Laval, France) mesh size were filled with 100 mg of *Patzkea* litter, 100 mg of *Dactylis* litter, or a mixture of 50 mg of both litter. On 19 November 2010, half of the litterbags were placed in a grassland located at roughly 50 m from the experimental platform with the pots. In addition, another set of litterbags was placed at the surface of the pots. For this second set, litterbags containing *Patzkea* litter, *Dactylis* litter and mixed litter were placed on the top of the pots dominated by the grasses *Patzkea*, *Dactylis* and with a mixture of both plant species, respectively. These pots, filled with artificial soil and located on a concrete experimental platform, experienced climatic conditions similar to the nearby field site, while the fauna community was expected to be largely reduced. This second set of litterbags was a way to ensure that potential mesh size effects occurring in the field site were not due to accidental litter loss through large mesh during litterbag manipulation, and could therefore be assigned to the activity of soil fauna. The total number of litterbags was therefore 192 (3 litter treatments x 4 grasshopper treatments x 2 mesh sizes x 2 locations x 4 repetitions). The litterbags were harvested on 10 May 2011, dried 24 h at 40°C and weighed.

2.2 Statistical analysis

We evaluated the influence of litterbag location, mesh size and plant litter type on the percentage of mass loss in the litterbags. We also checked if the grasshopper treatment interacted with the above treatments. We included the four factors (litter type, herbivores, location, and mesh size) as well as the interactions in 25 mixed models (Bates et al. 2012) with pot as a random factor, and ranked them by AIC. The 25 models ranged from an intercept model (1 parameter) to the model including all factors and all interactions (24 parameters). The model having the lowest corrected AIC (AICc) value was considered as the model that best explained litter mass loss. For this selected model, the significance of each factor was then tested with an analysis of deviance (type II Wald chi-square test) using the 'Anova' function from the 'car' R package (Fox & Weisberg 2010). Six pairwise post-hoc tests between fine and large mesh sizes, for each combination of litter type and location, were performed with the 'emmeans' R package (Lenth 2019), using the Kenward-Roger approximation for the calculation of the degrees of freedom. Similarly, two pairwise post-hoc tests between fine and large mesh sizes were performed for each location, this time averaging across litter types. We used the R free software (R Development Core Team 2011) for all analyses.

3. Results

The model selected on the base of information criteria (AICc) included all factors, as well as interactions between location, mesh size and litter type on the one hand, and herbivory and litter type on the other hand (Appendix). The impact of the grasshopper treatment, analyzed in Ibanez et al. (2013), is not the focus of the present paper, which is devoted to the soil fauna contribution to winter decomposition. As long as the selected model did not include any interaction between herbivory and mesh size, the presence of grasshoppers in the pots will not be considered any further. The results of the Anova of the selected model for the factors location, mesh size, litter type and their interactions are presented in Table 1.

Mean litter mass loss across all treatments averaged 31.6 ± 0.54%, and was significantly higher for *Dactylis* (34.4%) than for *Patzkea* (27.9%, P << 0.0001, table 1). Decomposition was on average significantly faster in the pots than in the field (mean mass loss 34.2 ± 0.70% and 29.0 ± 0.74%, respectively, P << 0.0001, figure 1 and table 1). When both species were considered together, the mesh size did not affect mass loss in the pots (mean mass loss 34.4 ± 1.03 and 34.0 ± 0.96% with small and large mesh size, respectively, figure 1, P = 0.705 for the pairwise tests). Conversely, in field conditions, the pairwise tests indicated that mass loss was higher in large (31.2 ± 0.91%) than small (26.8 ± 1.07%) mesh size litterbags (P < 0.0001). However, as indicated by the significant interaction between mesh size, litter localization and litter specific

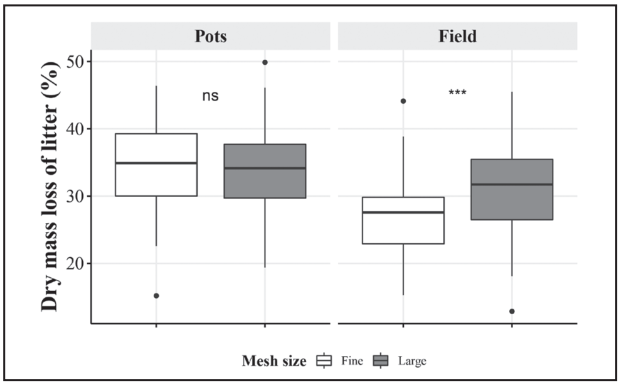

Figure 1. Litter mass loss in small mesh (white bars) and large mesh (grey bars) litterbags, after winter decomposition in the pots and in the field, averaging for litter type. The results of the 2 pairwise tests are shown for each location (ns: p = 0.70, ***: p < 0.001). The thick line corresponds to the median, the box to the first and third quartiles, the whiskers to the minimum and maximum values, and points to outliers.

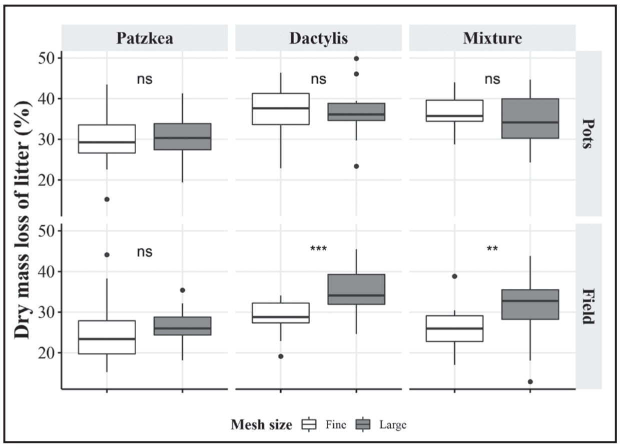

Figure 2. Litter mass loss of *Patzkea paniculata*, *Dactylis glomerata* and the mixture in small mesh (white bars) and large mesh (grey bars) and litterbags, for each location (pots and field), after winter decomposition. The results of the 6 pairwise tests are shown for each location and litter type (ns: p > 0.3, **: p < 0.01, ***: p < 0.001).

Table 1. Anova table (type II tests) of litter mass loss in function of mesh size, litter bag localization and litter types, as well as their interactions.

Source of variance	Chisq	Df	Pr (> Chisq)
Mesh size	10.06	1	0.0015
Localization	62.71	1	<< 0.0001
Litter type	21.81	2	<< 0.0001
Mesh size : Localization	13.69	1	0.0002
Mesh size : litter type	2.19	2	0.335
Localization : litter type	4.57	2	0.10
Localization : Mesh size : litter type	6.21	2	0.045

composition (P = 0.04, figure 2 and table 1), the effect of mesh size in the field differed between litter types. When litter types were considered separately (Fig. 2), the pairwise tests showed that mesh size had a significant effect in the field for *Dactylis* ($p < 0.0001$) and the mixture ($p = 0.0010$), but not for *Patzkea* ($p = 0.320$). In the pots, mesh size did not have any significant effect for either litter type ($p > 0.5$ in all cases).

4. Discussion

The 29.0 ± 0.74 % winter mass loss in our field experiment compares relatively well with the mass loss between 10 and 33 % found in a similar experiment with 2 mm mesh size litterbags (Saccone et al. 2013). Studies on the role of litter quality on decomposition demonstrated that the nutrient-rich litter of exploitative species decomposes more rapidly than nutrient-poor litter produced by conservative species (Fortunel et al. 2009). In contrast, Bokhorst et al. (2013) found that in winter, litter decomposition was not controlled by this gradient between exploitative and conservative plants. The latter results are not corroborated by our study, in which this disconnection between winter decomposition and plant strategy was not observed. In our case, and in line with the general pattern observed in other seasons, the conservative species *F. paniculata,* producing low quality litter (Bernard et al. 2019, Gross et al. 2007, Ibanez et al. 2013), decomposed more slowly in the field in large litterbags than the exploitative *D. glomerata.* Overall, decomposition proceeded more rapidly in the pots than in the field, probably due to the chemical fertilization of the pots.

The major aim of our design was to assess the contribution of soil fauna to winter decomposition. Animal exclusion in the field resulted in a mean 14.1 % reduction of mass loss. This difference was not observed when the litter bags were placed in the pots, where the natural fauna community is expected to be absent or strongly reduced. Since both large and small mesh litterbags were placed in both conditions (field and pots filled with artificial soil), we can rule out the possibility that the effect of mesh size measured in the field would result from accidental litter loss through the large mesh. Our results therefore demonstrate a contribution of soil animals to decomposition under the snowpack.

In contrast, in a one-year experiment with subalpine and alpine litter, Schinner et al. (1982) could not detect any difference in litter mass loss between 25 µm and 1 mm mesh litterbags. In a recent meta-analysis, García-Palacios et al. (2013) estimated that fauna activity contributed to 18 % of annual litter decomposition in cold and dry biomes. Compared to the 14.1 % fauna contribution to winter mass loss in our study, it suggests that animal activity may not be strongly reduced under the snowpack compared to the other parts of the year. Moreover, the soil fauna contribution to litter winter decomposition was larger for *Dactylis* than for *Patzkea*. This could reflect feeding preferences of animals towards the relatively N-rich and fiber-poor litter (Loranger-Merciris et al. 2008, Quadros et al. 2014, Coq et al. 2018) of the exploitative *Dactylis*.

Our exclusion study does not provide any insights into the animal community involved in litter decomposition. Earthworms and soil macroarthropods, such as millipedes, can be found in similar ecosystems (Seeber et al. 2005), but were excluded by both mesh sizes in our study. Acari and Collembola, two micro-arthropod groups excluded from small mesh but not in large mesh litterbags, are reported as the main actors of decomposition in cold biomes (Makkonen et al. 2011), and can be active under the snow layer (Hågvar & Hågvar 2011). Bokhorst et al. (2013) observed that snow depth reduction drastically decreased micro-arthropod abundance, but not winter decomposition, and concluded that their activity under the snowpack was low. Our study provides opposite evidence that in subalpine grasslands the activity of soil micro-arthropods is maintained during wintertime.

Our study suggests that micro-arthropods can significantly contribute to litter decomposition under the snowpack. This finding demonstrates that alteration of the micro-arthropod community due to climatic modification of the snow depth patterns or in freeze-thaw events may have important impacts on the carbon cycle of cold ecosystems. These insights are particularly relevant as alpine habitats as well as boreal and tundra regions may be particularly vulnerable to climate change (IPCC 2013). Additional mechanistic insights on the relationships between the snow layer variability and the biogeochemical cycles are required to improve our understanding of the impact of climatic change on cold biomes carbon and nutrient cycling.

5. Acknowledgements

We thank Marjorie Bison, Quentin Duparc, Marco Moretti and Amanda Grand-Veyre for their help during the experiments and Johanne Nahmani for her advices on earlier versions of this manuscript. This research was conducted at the Station Alpine Joseph Fourier (UMS CNRS 3370, France) and on the long-term research site Zone Atelier Alpes (ZAA), a member of the ILTER-Europe network (ZAA publication no. 26).

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Appendix: Model selection among 25 mixed models with mesocosms as a random factor. The 25 models ranged from an intercept model (1 parameter) to the model including all factors and all interactions (24 parameters). The model having the lowest corrected AIC (AICc) value was considered as the best model. *with interaction; + without interaction.

Model	Number of parameters	DELTA_AIC
mesh size * location * plant + herbivory * plant	15	0
mesh size * location + herbivory * plant	9	1.2
mesh size * location + herbivory * location + plant * herbivory	10	2.9
mesh size * location * herbivory + herbivory * plant	12	3.3
mesh size * location * herbivory * plant	24	5.1
mesh size * location * plant + herbivory	13	7.9
mesh size * location + herbivory + plant	7	9.1
mesh size * location + herbivory * location + plant	8	10.8
mesh size * location * herbivory + plant	10	11.2
mesh size + location + herbivory * plant	8	11.8
mesh size * location * plant	12	13.9
mesh size * location + herbivory	5	21.2
mesh size * location	4	24.4
plant + location	4	32.5
mesh size + location	3	35
herbivory + location	3	38.4
location	2	41.7
herbivory * plant	6	60.9
herbivory + plant	4	68.7
plant + mesh size	4	70.4
plant	3	74.8
herbivory + mesh size	3	76.2
mesh size	2	79.5
herbivory	2	80.6
intercept model	1	84