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Carex sempervirens tussocks induce spatial heterogeneity in litter decomposition, but not in soil properties, in a subalpine grassland in the Central Alps

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ABSTRACT

Tussocks of graminoids can induce spatial heterogeneity in soil properties in dry areas with discontinuous vegetation cover, but little is known about the situation in areas with continuous vegetation and no study has tested whether tussocks can induce spatial heterogeneity in litter decomposition. In a subalpine grassland in the Central Alps where vegetation cover is continuous, we measured soil properties [concentration of N, C, organic matter (OM) and pH] and monitored litter decomposition traits (dry mass loss, loss of C, N, P and K) inside and outside tussocks of *Carex sempervirens*. Soil C, N, OM concentrations or pH inside tussocks did not differ significantly from those outside tussocks. After 1 year of decomposition, litter dry mass loss, C and K loss were significantly smaller inside than outside tussocks. The slower litter decomposition inside tussocks was likely caused by the elevated tussock base, which made environmental conditions inside tussocks much dryer than those outside in early spring when snow melts. Our results suggest that in areas with continuous vegetation cover tussocks induce spatial heterogeneity in litter decomposition but not in soil properties.

Introduction

Spatial heterogeneity is a pervasive feature of natural habitats and occurs on various spatial scales (Alpert and Mooney, 1996; Jackson and Caldwell, 1993a,b; Kleb and Wilson, 1997). Small-scale spatial heterogeneity can be generated through both biotic and abiotic processes (de Lima Dantas and Batalha, in press; Hook et al., 1991; Jackson and Caldwell, 1993a), and understanding these processes may give insights into the mechanisms on e.g. population maintenance, species interactions and ecosystem functioning (Baer et al., 2004; Fransen et al., 2001; Maestre et al., 2005).

Tussock-forming graminoids are the dominant species in many ecosystems and distributed over a wide range of vegetation and precipitation zones (Briske and Derner, 1998; Fernandez Monteiro et al., in press; Yu et al., 2006, 2008). Due to the compact architecture, tussocks can produce and accumulate a large amount of biomass and litter within a relatively small area and thus may show a large capacity of modifying soil properties beneath them (Briske and Derner, 1998; Hook et al., 1991). Many studies have shown that in dry areas with discontinuous aboveground vegetation cover tussocks of graminoids can accumulate carbon and nutrients in soils beneath them and thus induce small-scale spatial heterogeneity in soil properties (Burke et al., 1995, 1999; Derner and Briske, 2001; Derner et al., 1997; Hook et al., 1991; Jackson and Caldwell, 1993a,b; Schlesinger et al., 1996; Vinton and Burke, 1995). However, little is known about the situation in areas where aboveground vegetation cover is continuous (Burke et al., 1998; Vinton and Burke, 1997).

When aboveground vegetation is continuous, space among tussocks is occupied by non-tussock plants rather than empty areas (Yu et al., 2006, 2008). Although the ability of accumulating carbon and nitrogen may be relatively weak for individuals of non-tussock plants as compared with tussocks (Derner and Briske, 2001), a dense association of non-tussock individuals may also greatly modify soil properties. As a result, the contrast of the ability of accumulating carbon and nitrogen between tussocks and the surrounding dense, non-tussock vegetation may be much weaker than that between tussocks and a surrounding empty space. In areas with continuous vegetation, therefore, tussocks may not induce spatial heterogeneity in soil properties (Burke et al., 1998; Vinton and Burke, 1997). Moreover, because large tussocks are supposed to

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be old and produce more litter, if tussocks can induce spatial heterogeneity in soil properties, then spatial heterogeneity will increase with increasing tussock size. So far, however, no study has explicitly addressed the effects of tussock size on spatial distribution patterns of soil resources.

Litter decomposition is a fundamental process of ecosystems (Shaw and Harte, 2001; Swift et al., 1979), which is primarily controlled by climatic factors and litter quality but also strongly affected by micro-site conditions and vegetation types (Aerts, 1997; Köchy and Wilson, 1997; Prescott et al., 2003). Because inside tussocks microclimatic conditions such as light and temperature (Chapin et al., 1979; Fetcher, 1985; Levine, 2000), microbial activity (Burke et al., 1995; Northup et al., 1999; Vinton and Burke, 1995), nutrient availability (Burke et al., 1995, 1999; Derner et al., 1997; Derner and Briske, 2001; Hook et al., 1991; Jackson and Caldwell, 1993a,b; Schlesinger et al., 1996; Vinton and Burke, 1995), vegetation composition (Yu et al., 2006, 2010) and grazing intensity (Levine, 2000; Yu et al., 2006, 2010) can be significantly different from those outside tussocks, it is likely that plant litter decomposition inside tussocks may also differ, i.e. tussocks may induce spatial heterogeneity in litter decomposition. Up to date, however, no study has been conducted to explicitly test this hypothesis.

To explore whether tussocks in areas with continuous vegetation induce small-scale spatial heterogeneity in soil properties (concentrations of C, N and OM and pH) and in litter decomposition traits (dry mass loss, litter C, N, P and K loss), we collected soil samples and monitored litter decomposition inside and outside tussocks of *Carex sempervirens* Vill. in an abandoned subalpine grassland in the Swiss National Park. Specifically, we address the following questions: (1) Do soil C, N and OM concentrations and pH inside the *C. sempervirens* tussocks differ from those outside? (2) Does tussock size play a significant role? (3) Do litter decomposition rate (dry mass loss) and litter C, N, P and K losses change from inside to outside the tussocks?

Materials and methods

Study site

We chose an abandoned subalpine grassland as our study site, located in the Swiss National Park in the Engadine valley of the Central Alps (Schütz et al., 2000; Yu et al., 2006, 2008). This grassland is 10.7 ha in size and faces southwest with a slope of about 6° at an altitude of about 1950 m a.s.l. The mean annual temperature is 0.27 °C and the mean annual precipitation is 926 mm. The mineral soil is coarse silty loam with 67.1% (based on weight) coarse (>2 mm) rock fragments and a bulk density of 1.26 g cm^{-3}. The soil is derived from dolomitic sediments (Schütz et al., 2000), making them calcareous (average pH 7.03).

The study grassland is covered by continuous vegetation, i.e. vegetation cover of all species is nearly 100%. The most common species in this grassland are *Festuca rubra*, *C. sempervirens* and *Sesleria coerulea*. Other common species include *Helictotrichon pubescens*, *Trifolium repens*, *Achillea millefolium*, *Trisetum flavescens*, *Ranunculus montanus*, *Galium pusillum*, *Agrostis tenuis*, *Polygonum viviparum*, *Polygala chamaebuxus*, *Thalictrum alpinum*, *Senecio abrotanifolius*, *Koeleria pyramidata*, *Luzula campestris* and *Polygala alpestris* (Yu et al., 2006). *C. sempervirens* tussocks occupy approximately 25% of the area.

Target species

Carex sempervirens Vill. (evergreen sedge) is a perennial tussock-forming sedge, and 20–60 cm tall. *C. sempervirens* tussocks have a well-defined base that consists of densely packed tiller stems, fine roots and litter (Yu et al., 2006, 2008). In the study site, tussocks of *C. sempervirens* are well delimited and surrounded by dense, grassland vegetation. It is widely distributed in the mountain ranges of Central and Southern Europe and often dominates nutrient-poor grasslands both below and above timberline (cf. Lüth et al., in press).

Soil sampling and chemical analysis

On 29–30 June 2004, we haphazardly selected 52 *C. sempervirens* tussocks of five size classes (tussock basal diameter <5, 5–10, 10–20, 20–30 and >30 cm) within the study area. There were ten tussocks (replicates) for each of the two smallest size classes (<5 and 5–10 cm), six for the largest size class (>30 cm), and 13 for the other two classes (10–20 and 20–30 cm). For each selected tussock, we removed the surface organic layer (including the fresh, un-decomposed litter and the more decomposed litter) so that the mineral soil was exposed. We collected a soil sample 5 cm deep beneath the tussock base and a companion sample at the same depth collected 20 cm away from the edge of the tussock base. The position of the companion sample was located in the east side of the tussock except that there was another tussock nearby. In this case, we moved the sampling location clockwise (i.e. east-south-west-north) until a proper position was found. Sampling deeper into the mineral soil profile was not possible because of the rocky substrate. Soil samples were oven-dried at 65 °C for 48 h and passed through a 2 mm mesh sieve. The sieved soils were then ground to pass a 0.5 mm screen, split and homogenized. Because the mineral soil in this area is calcareous, the soil were treated with a 50% HCl solution to remove carbonates, rinsed with deionized water, and dried for 1–2 h before analysis. Mineral soil samples were analyzed for C and N concentration on a LECO induction furnace at 1000 °C (LECO Corp., St. Joseph, MI). Soil OM concentration was determined by loss-on-ignition at 430 °C (Davies, 1974). Mineral soil pH was measured on a 2:1, water:soil paste.

Litter decomposition experiment and chemical analysis

Fresh green leaves of *C. sempervirens* were collected from the same grassland and dried at 60 °C for 72 h. Litter is defined as the dry leaves of *C. sempervirens*, although their chemical status may be quite different from that of fresh litter; dry material was used to standardize the moisture content of the substrate. On average 4 g (range 3.80–4.07 g) dry leaves were put into 10 cm × 10 cm polyester bags (2 mm mesh size). We selected 40 tussocks with basal diameter of 15–20 cm (16.0 ± 0.1, mean ± SE). Each of these tussocks was at least 50 cm away from any other tussocks. For each tussock, we placed one litter bag within its canopy on top of its base, and another one on the soil surface 20 cm away from the edge of the tussock base on the east side of the tussock. The litter bags were put into position on 5 July 2003. After about 3 months of decomposition (on 16 October 2003), we randomly selected 50% of the litter bags (20 from within the tussocks and 20 from outside for a total of 40 bags). After about 1 year (on 20 June 2004), the remaining 40 litter bags were collected.

Upon retrieval from the field, the bags were dried at 60 °C for 72 h, and then opened and the litter weighed. We ground the litter to pass a 0.5-mm screen for analyses of C, N, P and K concentration. Litter C concentration was determined by wet combustion method, N concentration by semi-micro Kjeldahl method, and P concentration by molybdenum blue colorimetric method (Bao, 1999). K was extracted from the litter with HF and HCl_4 and K concentration determined by flame emission (Bao, 1999).

We also measured initial the C, N, P and K concentration of the leaf litter placed into the litter bag using the same methods on six randomly selected samples.

Summer soil moisture measurements

We selected 20 *C. sempervirens* tussocks for soil temperature and moisture measurements. On 5, 13, 18 and 31 August 2005, soil moisture (0–10 cm depth) was measured inside and outside the tussocks with a fieldscout TDR-100 (time domain reflectometer; Spectrum Technologies, Plainfield, IL, USA). These data were used to represent soil moisture in summer. Because of logistical problems, soil moisture was not measured in other seasons.

Data analysis

We calculated C, N, P and K loss in the litter at time *i*, respectively, as [(initial concentration × initial dry weight of the litter) − (concentration at time *i* × dry weight of the litter at time *i*)]/(initial concentration × initial dry weight of the litter). Initial C, N, P and K concentration of leaf litter were the average values of those across the six samples, respectively.

We used ANOVA with repeated measures (rm ANOVA) to test the effects of sample location (inside *vs.* outside tussocks) and tussock size on soil C, N, OM and pH, with location as the repeated variable (von Ende, 2001). Paired *t*-tests were used to compare the differences in means of litter decomposition traits (dry mass loss, N, C, P and K loss) and soil moisture measured within and outside tussocks (Sokal and Rohlf, 1981).

Results

Soil chemical traits

Concentrations of total C, N and OM and pH in mineral soil inside the tussocks of *C. sempervirens* did not differ significantly from those outside the tussocks (Table 1, Fig. 1). There was no significant effect of tussock size × location on any of the four traits measured, suggesting that tussock size did not influence the potential tussock-mediated effects on these traits (Table 1, Fig. 1).

Litter decomposition traits

Litter dry mass loss did not differ between the two locations after about 3 months of decomposition (Fig. 2A), but was signifi-

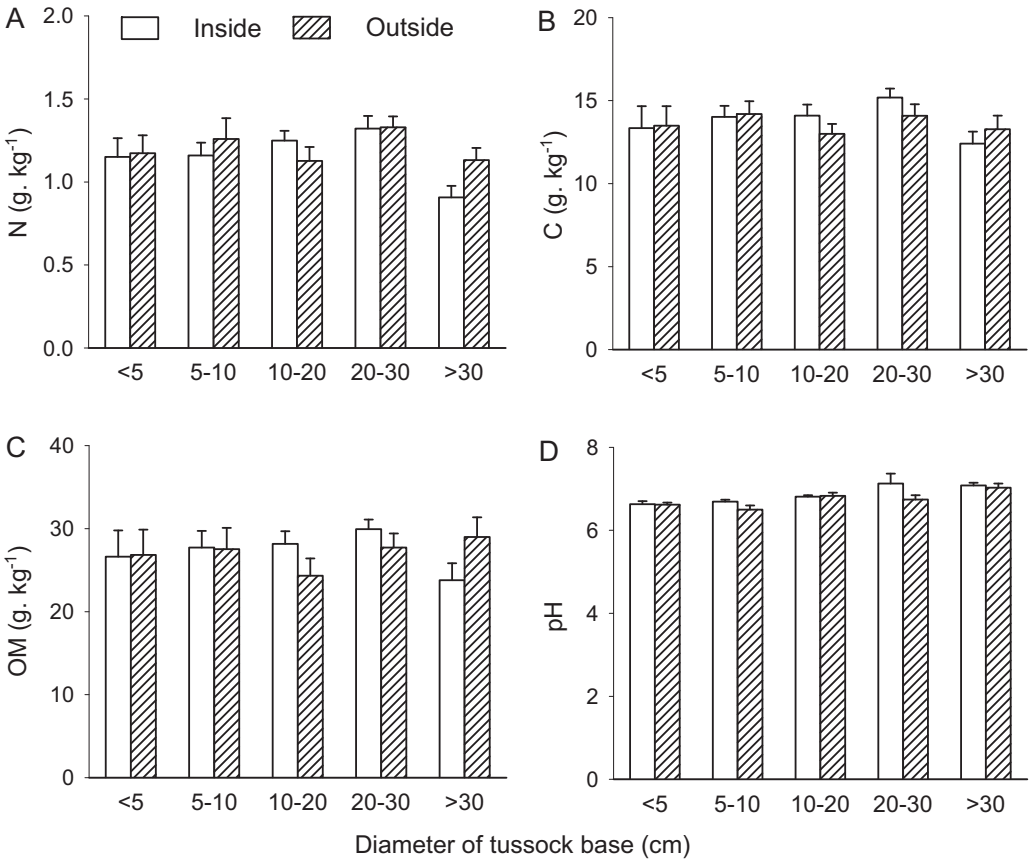

Fig. 1. Concentration of total nitrogen (A), carbon (B), organic matter (C) and pH (D) in mineral soil inside and outside *Carex sempervirens* tussocks of different sizes in an abandoned subalpine grassland. Mean ± SE are given.

Table 1
Effects of tussock size and sample location (inside *vs.* outside tussocks) on soil total nitrogen (N), carbon (C), organic matter (OM) and pH.

	N		C		OM		pH	
Effect	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Size	1.62	0.185	0.82	0.518	0.33	0.855	3.59	0.012
Location	1.50	0.227	0.33	0.570	0.04	0.844	3.42	0.071
Size × Location	2.08	0.098	1.15	0.343	2.53	0.053	1.52	0.213

F and *P* values based on rm ANOVA are given; degree of freedom are (4, 47) for the effects of size and size × location and (1, 47) for the location effect.

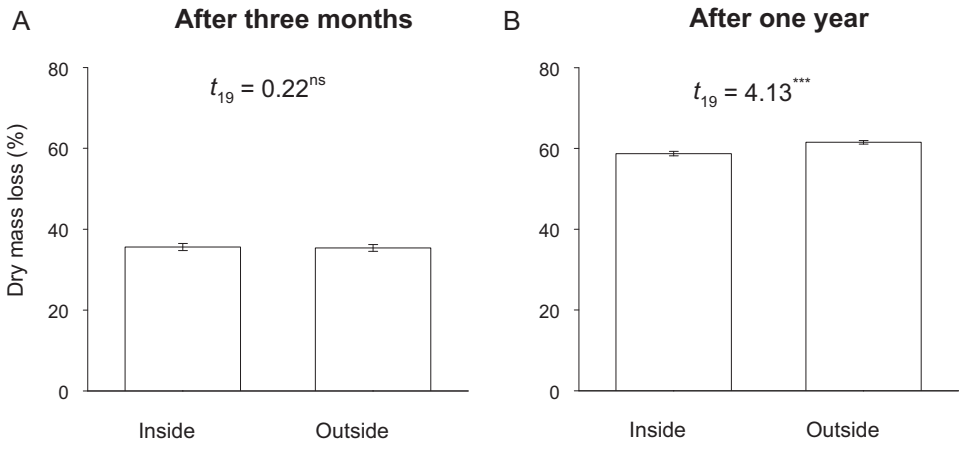

Fig. 2. Dry mass loss (mean ± SE, $n = 20$) of *Carex sempervirens* leaf litter after placed inside and outside tussocks of *C. sempervirens* for about 3 months (A) or 1 year (B) in an abandoned subalpine grassland. Results of paired *t*-tests are also given ($^{***}P < 0.001$ and $^{ns}P \geq 0.05$).

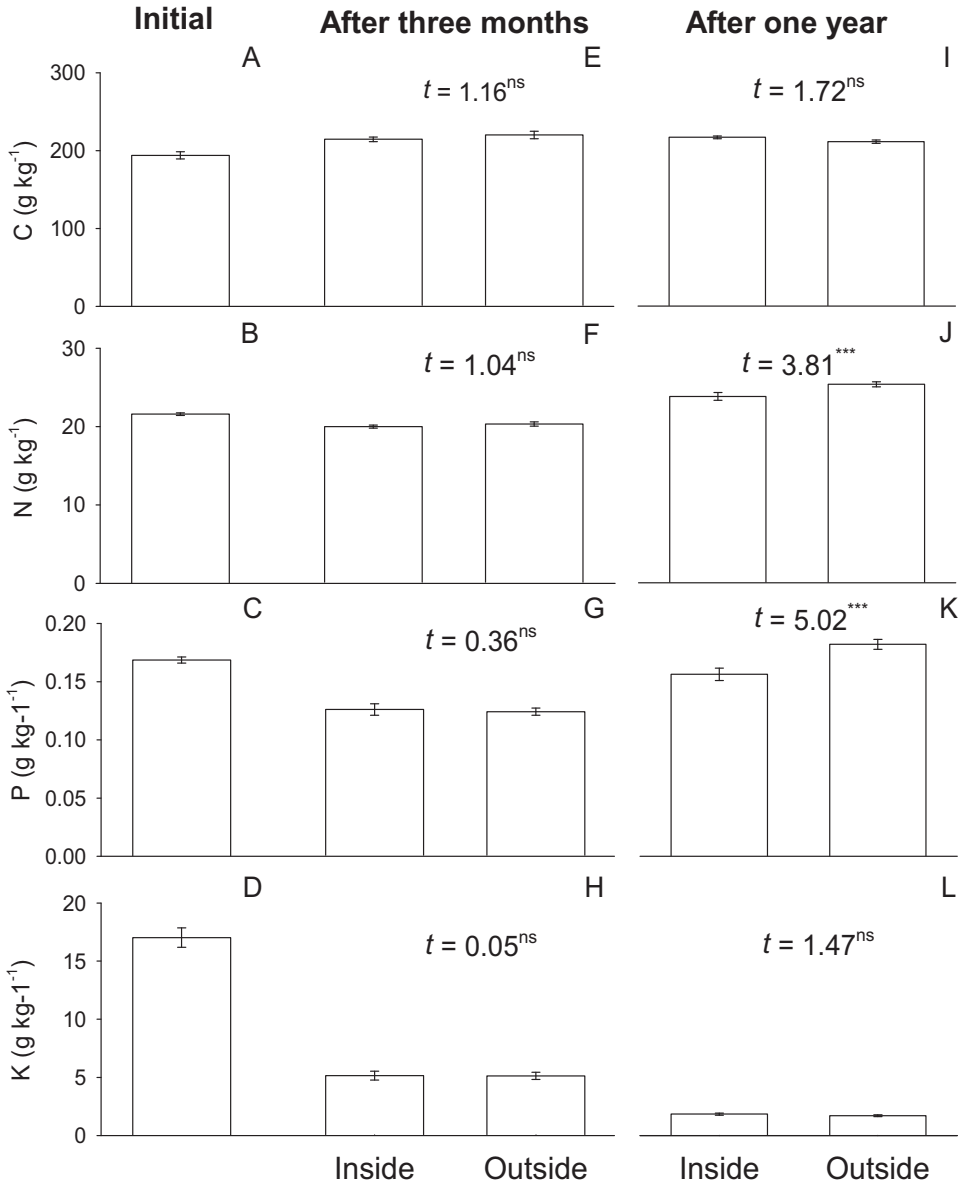

Fig. 3. (A–D) Chemical concentration in fresh leaf litter of *Carex sempervirens* (initial, $n = 6$) or after the litter was placed inside and outside tussocks of *C. sempervirens* ($n = 20$) for about 3 months (E–H) or 1 year (I–L) in an abandoned subalpine grassland. Mean ± SE and results of paired *t*-tests are given ($^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$ and $^{ns}P \geq 0.05$).

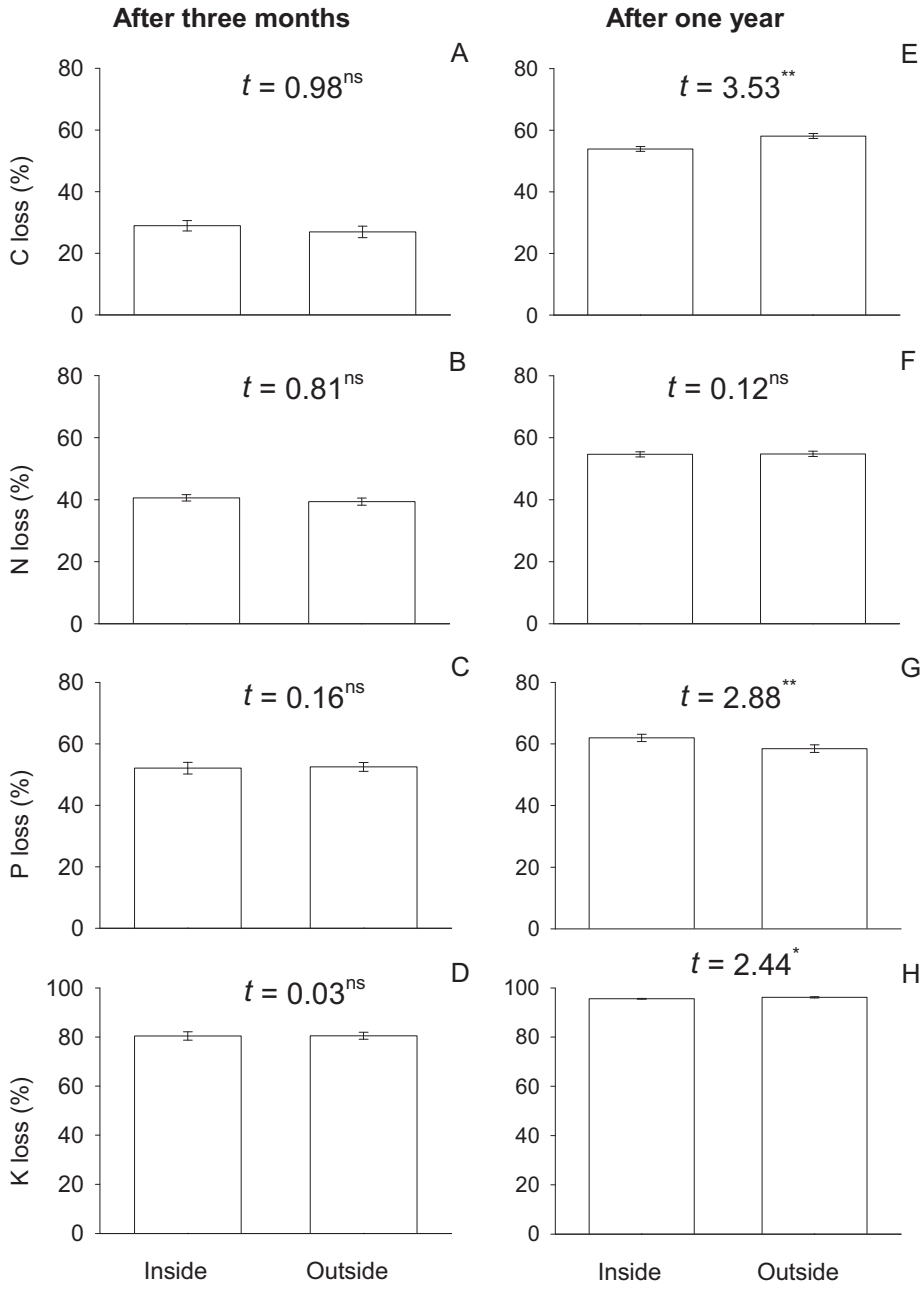

Fig. 4. Litter chemical loss after the litter was placed inside and outside *C. sempervirens* tussocks for about 3 months (A–D) or 1 year (E–H) in an abandoned subalpine grassland. Mean ± SE ($n = 20$) and results of paired *t*-tests are given ($^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$ and $^{ns}P \geq 0.05$).

cantly smaller inside than outside the tussocks after about 1 year of decomposition (Fig. 2B).

Initial C, N, P and K concentrations in the leaf litter were 193.9 ± 4.7 (mean ± SE), 21.6 ± 0.2, 0.169 ± 0.002 and 17.0 ± 0.8 g kg^{-1}, respectively (Fig. 3A–D). After about 3 months litter C, N, P and K concentrations were not significantly affected by the location of litter bag placement (Fig. 3E–H), but after about 1 year litter N and P concentrations were significantly smaller inside than outside the tussocks (Fig. 3J and K).

After about 3 months of decomposition, litter C, N, P and K losses were not significantly affected by the location of litter bag placement (Fig. 4A–D). After 1 year of decomposition, C loss and K loss were lower inside than outside the tussocks (Fig. 4E and H), whereas P loss was higher (Fig. 4G). Litter N loss did not differ with regard to litter bag placement (Fig. 4F).

Soil moisture

Soil water content inside the tussocks of *C. sempervirens* did not differ from that outside the tussocks on 5, 13 or 31 August 2005, but it was higher within tussocks on August 18 (Table 2).

Table 2
Soil water content (%, mean ± SE, $n = 20$) inside and outside *C. sempervirens* tussocks in an abandoned subalpine grassland.

Measuring date	Inside	Outside	*t*
August 5, 2005	7.79 ± 0.52	7.95 ± 0.65	0.20^{ns}
August 13, 2005	8.21 ± 0.53	7.89 ± 0.68	0.43^{ns}
August 18, 2005	8.05 ± 0.52	6.75 ± 0.56	2.29^{*}
August 31, 2005	14.65 ± 0.95	14.05 ± 0.38	0.45^{ns}

Degree of freedom is 19; results of paired *t*-tests are given ($^{*}P < 0.05$, $^{ns}P \geq 0.05$).

Discussion

Soil C, N, OM concentrations and pH inside the *C. sempervirens* tussocks did not differ from those outside (Table 1, Fig. 1), suggesting that in the study grassland where vegetation cover is continuous *C. sempervirens* tussocks do not induce small-scale heterogeneity in soil properties. In contrast, higher soil OM, C and/or N concentration inside than outside tussocks of several different plant species were detected in dry areas with discontinuous vegetation cover (Burke et al., 1995; Hook et al., 1991; Jackson and Caldwell, 1993a,b; Schlesinger et al., 1996; Vinton and Burke, 1995). Burke et al. (1998) proposed that plant-induced spatial variation in soil C and N concentration may be less significant in areas where aboveground plant cover is continuous because the biological (accumulation of above- and below-ground litter) and physical (erosion and redistribution of resources) concentration effects are stronger when vegetation surrounding the tussocks is absent. In the present study, aboveground vegetation cover of the study grassland is continuous, and thus it is likely that the biological concentration effects of *C. sempervirens* tussocks were less pronounced and did not induce a significant difference in mineral soil C, N or OM concentration inside and outside tussocks (Burke et al., 1998; Vinton and Burke, 1997). An alternative explanation is that, because vegetation cover is continuous, the effects of the surrounding dense vegetation of non-tussock species on soil properties were equally significant as those of the *C. sempervirens* tussocks so that we could not find a significant difference in soil properties between areas inside and outside the *C. sempervirens* tussocks.

After about 1 year of decomposition litter dry mass loss, C loss and K loss were lower and P loss higher within than outside the tussocks of *C. sempervirens* (Figs. 2 and 3), suggesting that tussocks of *C. sempervirens* can induce spatial heterogeneity in litter decomposition. Litter decomposition can be influenced by various factors, and high soil moisture and N concentration, for instance, can accelerate litter decomposition rate (Aerts, 1997; Köchy and Wilson, 1997; Moore et al., 2005; Prescott et al., 2003). In this study, the micro-site effects on litter decomposition were unlikely caused by differences in soil N and C concentration or pH because these factors did not differ significantly between the two locations (Table 1, Fig. 1). Also differences in litter decomposition cannot be attributed to differences in *summer* soil moisture because we did not find significantly higher soil moisture within than outside tussocks in August (Table 2).

However, differences in litter decomposition could be explained by differences in soil moisture in early spring. In the subalpine grassland, the average basal height of *C. sempervirens* tussocks with basal diameters of 15–20 diameter is 5.9 cm (SE = 0.22, $n = 78$, F.-H. Yu, unpublished data). Therefore, the slower litter decomposition inside the tussocks was most likely because during the early spring when the snow melted, the elevated tussock base of *C. sempervirens* (Yu et al., 2006) made the environmental conditions inside tussocks much dryer than those in the surrounding lower area outside the tussocks. This should have resulted in a much slower decomposition rate inside tussocks than outside during early spring, which may have contributed substantially to the smaller decomposition rate inside tussocks during the whole year. Further experimental studies are needed to test this hypothesis.

The slower litter decomposition within tussocks may help to explain the large amount of litter accumulated within tussocks (Briske and Derner, 1998). Previous studies have shown that many other plant species can root and grow within tussocks of *C. sempervirens* (Yu et al., 2006, 2008). Thus, besides the litter of the tussock species itself, there will be also a large amount of litter produced by other species that grow within the tussocks of *C. sempervirens*. The slower decomposition rate and the increased production of dry matter from other species within tussocks thus may account for the accumulation of the litter within the tussocks (Briske and Derner, 1998).

Conclusions

We conclude that in the subalpine grassland with continuous vegetation tussocks of *C. sempervirens* do not induce spatial heterogeneity in soil C and N, in contrast to situations with tussock species in dry areas with discontinuous vegetation. However, with time mineralization rates inside and outside *C. sempervirens* tussocks can be quite different, leading to spatial heterogeneity in litter decomposition. The slow decomposition rate and the accumulation of large amount of litter inside tussocks may be important for the litter production of subalpine and alpine grasslands that are dominated by tussock plants.

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