REGULAR ARTICLE

Direct and indirect control by snow cover over decomposition in alpine tundra along a snowmelt gradient

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Abstract We assessed direct and indirect effects of snow cover on litter decomposition and litter nitrogen release in alpine tundra. Direct effects are driven by the direct influence of snow cover on edaphoclimatic conditions, whereas indirect effects result from the filtering effect of snow cover on species' abundance and traits. We compared the in situ decomposition of leaf litter from four dominant plant species (two graminoids, two shrubs) at early and late snowmelt locations using a two-year litter-bag experiment. A seasonal experiment was also performed to estimate the relative importance of winter and summer decomposition. We found that growth form (graminoids vs. shrubs) are the main determinants of decomposition rate. Direct effect of snow cover exerted only a secondary influence. Whatever the species, early snowmelt locations showed consistently reduced decomposition rates and delayed final stages of N mineralization. This lower decomposition rate was associated with freezing soil temperatures during winter. The results suggest that a reduced snow cover may have a weak and immediate direct effect on litter decomposition rates and N availability in alpine tundra. A much larger impact on nutrient cycling is likely to be mediated by longer term changes in the relative abundance of lignin-rich dwarf shrubs.

Keywords Growth form · Nitrogen mineralization · Snow cover · Litter decomposition · Alpine tundra

Responsible Editor: Hans Lambers.

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Introduction

Recent climate projections suggest that, associated with higher temperature, snowfall may decline in the coming decades, especially in American, European and Russian mountain ecosystems (Beniston 2005; Serreze et al. 2000). In these systems, the landscape scale distribution of snow is one of the most important variables controlling structure and function of mountain ecosystems (Walker et al. 1999). Variations in the depth and duration of snow cover result in large differences in edaphoclimatic conditions, as well as in plant community composition (Körner 1999; Walker et al. 1993). Changes in snow cover regime

may affect nutrient cycling processes and soil carbon sequestration (Robinson 2002). Assessing the effect of snow distribution on the rate of litter decomposition and associated nitrogen release is a crucial element in predicting the impact of global change on mountain ecosystems.

Snow directly and indirectly controls litter decomposition and nitrogen release (Groffman et al. 2001; Walker et al. 1999). Direct control involves the short term effects of snow cover on winter soil temperature (by insulating soil) and/or on summer soil moisture. Indirect control involves the long term effects of snow cover variations on growing-season length, soil fertility and water availability (Edwards et al. 2007), which drive the ecological sorting of species and plant functional traits (Choler 2005; Kudo 1996). Several recent studies have addressed the impact of variations in snow depth on carbon (C) and nitrogen (N) mineralization (see Campbell et al. 2005 for a review). This was done by manipulating snow cover (Chimner and Welker 2005; Walker et al. 1999), or by correlating Net Ecosystem CO_2 Exchange (NEE) to inter-annual variations in snow depth (Monson et al. 2006). However, these studies mainly focused on the direct effect of snow-depth variations on C mineralization (i.e. variations associated to local edaphoclimatic conditions) and did not address the effect of snow-induced changes in plant community structure and therefore in litter quality on this process. In order to determine the main controls over litter decomposition and associated N released in snow-covered ecosystems, we need to examine the interplay between (1) snow-induced changes in edaphoclimatic conditions in the short-term and (2) snow-induced changes in litter quality and decomposability in the longer-term.

Several approaches have been proposed to address the challenge of studying the long-term effects of climate change on ecosystems (Rustad 2006): (1) monitoring temporal changes (2) mathematical modelling or (3) observations of existing environmental gradients treated as space-for-time proxies. In alpine ecosystems, snow distribution and the timing of snowmelt are closely related to mesotopography (the ecoclines along small to medium-sized hill slopes). Along mesotopographical gradients, strong turn-over in species composition and changes in litter quality have been reported (Choler 2005; Kudo and Ito 1992). Vascular plants from early snowmelt locations exhibit a combination of leaf trait attributes, including high Leaf Dry Matter Content (LDMC) and high C/N ratio (Baptist and Choler 2008; Choler 2005; Kudo 1996; Kudo et al. 2001) which are known to be associated with recalcitrant litter (Cornelissen et al. 1999; Kazakou et al. 2006; Perez Harguindeguy et al. 2000). Conversely, species from late snowmelt locations, exhibit high Specific Leaf Area (SLA) or Leaf Nitrogen Concentration (LNC), which are trait attributes of faster-decomposing litter (Cornelissen et al. 1999; Kazakou et al. 2006; Perez Harguindeguy et al. 2000).

To assess the interplay betwen direct and indirect controls of snow cover on litter decomposition, we compared litter decomposition in two locations situated at the extremes of a mesotopographical gradient: namely an early snowmelt location and a late snowmelt location. We addressed the following questions: (1) how important is the influence of species identity (indirect effect of snow cover) compared to that of edaphoclimatic conditions (direct effect of snow cover) on litter decomposition in alpine tundra, (2) how do seasonal patterns of decomposition relate to snow cover dynamics, and (3) what is the impact of seasonal and annual litter decomposition on N release along this gradient. To address these questions, we established two litter decomposition experiments: (1) a two-year reciprocal transplant litter experiment to disentangle direct from indirect effect of snowcover on decomposition (Experiment I), and (2) a seasonal experiment to identify the relative influence of summer and winter periods on litter decomposition (Experiment II).

Methods

Study site

The research area was located in the mountain ranges of Grand Galibier and Grandes Rousses, South-Western French Alps (45°7′N, 6°5′E) above the potential tree line (2300–2400 m a.s.l.). This study was conducted in three sites, located at least 500 m from each other in order to account for spatial variability. Each site corresponds to a mesotopographical gradient with an early and a late snowmelt location (see Fig. S1, for arrangement of study sites and snowmelt locations). Sites A, B and C were located between 2520 and 2550 m. Early snowmelt locations exhibited moderate slopes (<20°) and faced

East (A, B) or North-East (C). Late snowmelt locations corresponded to flat depressions. Within each site, snowmelt locations (late and early) were located at a distance of about 10 to 50 m.

In late snowmelt locations, soils are classified as stagnogley, enriched in clay whereas in early snowmelt locations they are considered as alpine ranker (Duchaufour and Gilot 1966). The bedrock is basic flysh in sites A and B and calcareous in site C. In early snowmelt locations at the three sites (A, B and C), communities were dominated by *Kobresia myosuroides* (Cyperaceae) and *Dryas octopetala* (Rosaceae). In late snowmelt locations, *Carex foetida* (Cyperaceae), *Salix herbacea* (Salicaceae), *Alopecurus gerardi* (Poaceae) and *Alchemilla pentaphyllea* (Rosaceae) were the most abundant species (Table 1). To estimate standing biomass and aboveground net primary productivity, we harvested aboveground biomass in three randomly located 40×40 cm quadrats on 23/07/03 at peak standing biomass in both snowmelt locations of all sites. In the case of shrubs, only leaves were harvested. Aboveground net primary productivity was determined by dividing standing biomass by the time between the date of snowmelt and peak biomass. The relative cover of vascular plant species within an homogeneous area ranging from 25 to 100 m^2 was visually estimated using a six point scale: 1:<5%; 2: 5–10%; 3: 10–25%; 4: 25–50%; 5: 50–75%; 6:>75%. Specific Leaf Area (SLA), Leaf Dry Matter Content (LDMC) and Leaf Nitrogen Concentration (LNC) were measured during the month of July 2004 at peak standing biomass. Following standard protocols (Cornelissen et al. 2003), five fully expanded leaves of each of the five species were collected in each site either in early or late snowmelt locations and maintained in moist paper. After rehydration for 6 h, they were weighed and total leaf area was measured using a leaf area meter (Gatehouse scientific instruments LTD, Norfolk, UK) before drying the leaves for 48 h at 60°C and weighing them for dry mass. Leaves were later ground and analyzed for carbon and nitrogen concentration using a CHN analyzer (CHS NA1500, Carbo Erba Instrument, Milan, Italy).

Climatic recordings

Soil temperature was recorded hourly in each snowmelt location from 2003 to 2006 with Hobo probes (Hobo

PRO series H08-030-08, Onset computer corporation, Bourne, MA, USA) buried at 5 cm depth (one per snowmelt location, six Hobo probes in total). Soil temperatures that remain close to 0°C (usually between −1 and 1°C) throughout the day indicate a deep persistent snow cover in mountainous ecosystems (see Kueppers and Harte 2005 for example). The winter period was calculated as the number of days with a mean soil temperature ≤0°C (Table 1). Five weeks separated snowmelt time in early compared to late snowmelt locations (Table 1). Mean wintertime soil temperature was also determined in each snowmelt location. Finally, volumetric soil water content in each snowmelt location was measured at a depth of 5 cm during the 2005 and 2006 growing seasons using an Echo Probe (Decagon Devices, Pullman, WA).

Litter decomposition experiments

Experiment I

For experiment I, we chose two graminoids, one from late snowmelt locations (*Carex foetida*) and one form early snowmelt locations (*Kobresia myosuroides*), as well as two shrubs, one from late snowmelt locations (*Salix herbacea*) and one from early snowmelt locations (*Dryas octopetala*). At the end of the growing season, we collected fresh litter from each of these species and oven dried it at 60°C for 48 h. Three hundred eighty four 10×10 cm polyethylene litter-bags (2 mm mesh size) were filled with 1 g of litter from each species. This corresponds to an litter input of 100 g m^{-2} which is realistic in late snowmelt locations but slightly too elevated in early snowmelt locations as larger amounts of persistent, standing necromass have been observed (personal observation) and litter is more likely to be wind-blown.

In order to evaluate direct vs. indirect effect of snowcover, we performed reciprocal transplants of litter between early and late snowmelt locations. We incubated litter samples in both their original snowmelt location and the other location. A first reciprocal experiment was performed with the two selected graminoids during 2003–2005, and a second reciprocal experiment with the two selected shrubs during 2004–2006 (see Fig. S1). To allow for comparison between the two experiments, a "standard" litter common to both experiments was included (SLI, for the graminoid experiment 2003–2005 and SLII for the

Table 1 (a) Winter duration, soil temperature and soil moisture records are an average of three years records from the three sites A, B and C within each snowmelt location (from the end of 2003 to the end of 2006). (b) Aboveground productivity (calculated from snowmelt until peak standing biomass), aboveground biomass and relative abundance of *Alopecurus gerardi*, *Carex foetida*, *Salix herbacea*, *Kobresia myosuroides* and *Dryas octopetala* in late and early snowmelt locations

Characteristics	Late snowmelt location	Early snowmelt location
(a) Edaphoclimatic conditions		
Winter duration (d)	240 (12)	206 (15)
Mean winter soil temperature (°C)	−0.15 (0.01)	−3.05 (0.45)
Mean summer soil temperature (°C)	7.7 (1.55)	7.6 (1.62)
Gravimetric summer soil moisture (gH_2O g^{-1} soil)	0.35 (0.03)	0.42 (0.03)
(b) Plant features		
Aboveground Productivity (g m^{-2} d^{-1})	7.23 (0.45)	2.18 (0.14)
Total aboveground biomass (g m^{-2})	325.7 (22.0)	185.9 (11.7)
Relative abundance (%)		
Alopecurus gerardi	11.1 (5.9)	0
Carex foetida	16.7 (1.9)	0
Salix herbacea	15.6 (9.7)	0
Kobresia myosuroides	0	24.6 (4.1)
Dryas octopetala	0	33.2 (1.8)

Values are the mean ± standard error (se) except for edapho-climatic conditions where it is standard deviation (sd)

shrub experiment 2004–2006). This standard litter was harvested from a Swedish grassland and used for a similar purpose in an cross-European comparison (Quétier et al. 2007). All samples were retrieved after one and two years of incubation, on the 24/09/04 for *K. myosuroides*, *C. foetida* and SLI (first year), on the 10/10/05 for *K. myosuroides*, *C. foetida*, SLI (second year) and *D. octopetala*, *S. herbacea*, SLII (first year), and on the 02/10/06 for *D. octopetala*, *S. herbacea* and SLII (second year). The litter-bags were deployed giving eight replicates for two retrievals of four species (*C. foetida*, *S. herbacea*, *K. myosuroides* and *D. octopetala*) in the three sites A, B and C in both snowmelt locations.

Experiment II

For seasonal experiment, litter from *C. foetida*, *S. herbacea*, *K. myosuroides*, and *D. octopetala* was harvested at the end of September 2005, together with litter from a fifth species, *Alopecurus gerardi* which is also very abundant in late snowmelt locations (see Table 1). This species was harvested still green because it senesced later in season under snow. Litter bag construction and filling followed the same procedure as in Experiment I.

Experiment II was set up on 10/10/05. Individual species litterbags filled with litter from the late snowmelt (*C. foetida*, *S. herbacea*, *A. gerardi*) and early snowmelt locations (*K. myosuroides* and *D. octopetala*) were deployed in each species' original snowmelt location. In total, 225 litter-bags were deployed giving five replicates for three retrievals of five species (*C. foetida*, *S. herbacea*, *A. gerardi*, *K. myosuroides* and *D. octopetala*) in the three sites in late or in early snowmelt locations. The design was therefore not orthogonal with respect to snowmelt locations (see Fig. S1). Three retrievals were performed: at the end of the first winter just after snowmelt (between 03/05/06 and 20/06/06 in early and late snowmelt locations, refered as Winter 1) at the end of the growing season (02/10/06, refered as Summer), and after the second winter (between 18/05/07 and 25/06/07 in early and late snowmelt locations, refered as Winter 2).

Litter processing

For each experiment I and II, the remaining litter was carefully sorted and weighed after drying at 60°C during 48 h. Three sub-samples of each litter were analysed for initial C and N litter concentra-

tion using an elemental analyser (CHS NA1500, Carbo Erba Instrument, Milan, Italy) and for lignin concentration using the H_2SO_4 (72%) digestion method (Ellis et al. 1946). Content of N was determined by multiplying concentration of N by mass. It is expressed as the percentage of the initial content remaining.

To estimate litter decomposition, we calculate mass loss (%) over the different periods as follows:

$$\text{Mass loss}_{\Delta t} = \frac{\left(\text{mass}_t - \text{mass}_{(t-1)}\right)}{\text{mass}_{(t-1)}} * 100$$

Statistical procedures

Experiment I followed a split-plot design. We used Linear Mixed Models (Pinheiro and Bates 2000) to assess effects of snowmelt location and litter species on mass loss. Sites were considered as random factor while retrieval time, snowmelt location, litter species and their interactions were fixed factors. Data for graminoids and shrubs were analysed separately. An ANCOVA was applied to test the regression between (1) yearly mass loss of each litter species against mean winter soil temperature and (2) litter N (proportion of initial N content) of each litter species against mass loss, for each retrieval in each snowmelt location. Litter species was considered as a categorical factor while mean winter soil temperature (1) and mass loss (2) were considered continuous.

In Experiment II, we estimated decomposition rate for each period, each litter species and for each snowmelt location using:

Decomposition rate(mg/d)

$$= \frac{1}{T} \cdot \left[\text{remaining mass}_{t+T} - \overline{\text{remaining mass}_t}\,\right],$$

where T is the period between the two measurements (in days). We used a linear model (ANOVA) to compare period and site effects for each litter species separately and to test for differences in litter N dynamic for each species (proportion of initial N content) after the first winter, summer and second winter. Statistical analyses were performed using the R software (Pinheiro et al. 2007; R Development Core Team 2007).

Results

Standing biomass in late snowmelt communities was twice as large as in early snowmelt communities (Table 1). Late snowmelt communities produced more aboveground biomass in a shorter period, which explains the four-fold difference in productivity between early and late snowmelt locations when expressed on a daily basis (Table 1). In late snowmelt location, the cumulated relative abundance of the three species selected for the decomposition experiments (A. gerardi, C. foetida and S. herbacea) represented up to 40% whereas the relative abundance of K. myosuroides and D. octopetala corresponded to more than 50% in early snowmelt community (Table 1). Species had contrasting leaf trait values as well as different litter chemistry (Table 2). Green tissue from late snowmelt locations species (C. foetida, A. gerardi and S. herbacea) characteristically had higher SLA, lower LDMC, lower green leaf C/N, and litter C/N because of higher leaf N concentration. Species from early snowmelt locations (K. myosuroides and D. octopetala) had opposite attributes. In contrast, lignin concentration correlates with growth form: shrubs showed higher lignin concentration than graminoids.

Annual litter mass loss: Experiment I

Decomposition of standard litter (SLI and SLII) indicated that decomposition was higher during 2004–2006 (graminoid experiment) than during 2003–2005 (shrub experiment) (see Fig. S2). This difference ranged from 0.62% to 4.67% of total mass loss. Compared to the magnitude of the differences observed for mass loss between graminoids and shrubs (more than 20%, see Fig. 1), this difference was very small and allows for direct comparisons of litter decomposition between both graminoids and shrubs. Statistical analyses underlined large species specific differences in total litter mass loss (especially when grouped per life form) whereas the effect of snowmelt locations was not significant (Table 3, Fig. 1 and Fig. S3). Graminoids exhibited the largest mass loss and decay constant (k) compared to shrubs which experienced almost two-fold-less mass loss (Fig. 1, Table S1).

Although the effect of snowmelt location was not significant (Table 3), we found a trend toward higher

Table 2 Habitat, growth form, and functional traits of green leaves (Specific Leaf Area, Leaf Dry Matter Content, C/N), litter (lignin concentration, C/N, C and N concentration) of *Carex foetida, Kobresia myosuroides, Alopecurus gerardi, Salix herbacea, Dryas octopetala* and standard litter (Standard). In case of C/N litter characteristics and lignin concentration, n=3, in the case of green leaf traits, n=10

| Species	Snowmelt location	Growth form	SLA (m²/kg)	LDMC (mg/g)	C/N	Lignin concentration (mg/g)	Experiment I			Experiment II		
							C/N litter	Leaf N (mg/g)	leaf C (mg/g)	C/N litter	Leaf N (mg/g)	leaf C (mg/g)
C. foetida	Late	Graminoid	19.4 (0.7)	261.5 (6.4)	11.2 (0.5)	61.0 (3.1)	20.6 (0.3)	23.2 (0.4)	471.0 (0.1)	37.7 (2.1)	12.2 (0.7)	451.0 (5.0)
K. myosuroides	Early	Graminoid	12.4 (0.2)	322.1 (5.4)	19.2 (0.7)	74.0 (5.1)	44.8 (2.3)	10.6 (0.5)	471.0 (0.0)	37.9 (4.2)	11.6 (0.7)	431.0 (25.0)
A. gerardi	Late	Graminoid	19.1 (0.4)	245.8 (4.3)	13.1 (0.6)	38.3 (3.2)	–	–	–	25.6 (0.9)	17.6 (0.9)	446.0 (10.0)
S. herbacea	Late	Shrub	19.8 (0.6)	318.0 (10.1)	14.7 (0.7)	335.3 (8.1)	23.0 (0.7)	22.0 (0.7)	506.0 (0.3)	21.7 (0.6)	22.7 (0.6)	489.0 (8.0)
D. octopetala	Early	Shrub	11.6 (0.5)	387.1 (6.2)	20.3 (0.7)	361.0 (1.7)	50.2 (0.7)	10.2 (0.1)	510.0 (1.0)	35.6 (2.4)	14.3 (0.8)	504.0 (3.0)
Standard	–	Graminoid	–	–	–	–	37.3 (1.9)	12.6 (0.6)	462.0 (3.0)	–	–	–

Values are the mean (se)

decomposition rates in late snowmelt location. Indeed, differences between mass loss in the late snowmelt locations and mass loss in early snowmelt locations for each site and each year produced always the same trend (Fig. 1). The probability that no negative value be obtained with 12 replicates, as shown on Fig. 2, is equal to 0.0002 (binomial test). We conclude that litter degradation was consistently higher in late snowmelt compared to early snowmelt locations, but that the amplitude of this indirect effect was weak.

As no summer soil temperature and soil moisture differences could be detected between the late and the early snowmelt locations (Table 1), we focused on winter conditions to explain the snowmelt location effect. The reduced thickness of the snowpack in early snowmelt locations lead to low soil temperatures associated with large temperature fluctuations during winter (Table 1). A regression analysis of mass loss of each litter species after one year in each snowmelt location against the location's mean winter soil temperatures (Fig. 3) showed a clear effect of winter soil temperature on mass loss ($F_{1,8}=23.2$, $P=0.001$, $F_{1,8}=8.4$, $P=0.02$ for graminoids and shrubs respectively). The effect of litter species was not significant ($F_{1,8}=0.64$, $P=0.44$, $F_{1,8}=4.2$, $P=0.07$ for graminoids and shrubs respectively). The temperature × litter species interaction was never significant ($F_{1,8}<0.1$, $P=0.99$, $F_{1,8}=1.30$, $P=0.28$ for graminoids and shrubs respectively).

Seasonal litter mass loss: Experiment II

Experiment II revealed large and significant effects of litter species on seasonal mass loss and decomposition rate (mass loss per day) (Fig. 4). After 1.5 year, the three graminoid species (*C. foetida*, *A. gerardi*, *K. myosuroides*) lost respectively 45.8%, 72.5%, and 49.3%, whereas *D. octopetala* lost 20.6% and *S. herbacea* 23.4% of their initial litter mass. Mass loss in Winter 1 was high in comparison to total litter mass loss, ranging from 46.2% for *S. herbacea* to 80.7% for *A. gerardi*. In contrast, it ranged from 10% to 40% during Summer and from 7% to 27% during Winter 2. Only the decomposition of *S. herbacea* followed a different pattern, with similar mass loss observed during Winter 1 and Summer. Estimated decomposition rates were higher during the first winter for most species, except *S. herbacea* (Fig. 4, Table 4). During

Fig. 1 Mean and 95% confidence intervals of litter mass loss after the first and second year of decomposition **a** in late snowmelt and early snowmelt locations (all species), **b** for each species (both snowmelt locations) and **c** for each species within each snowmelt location (Experiment I)
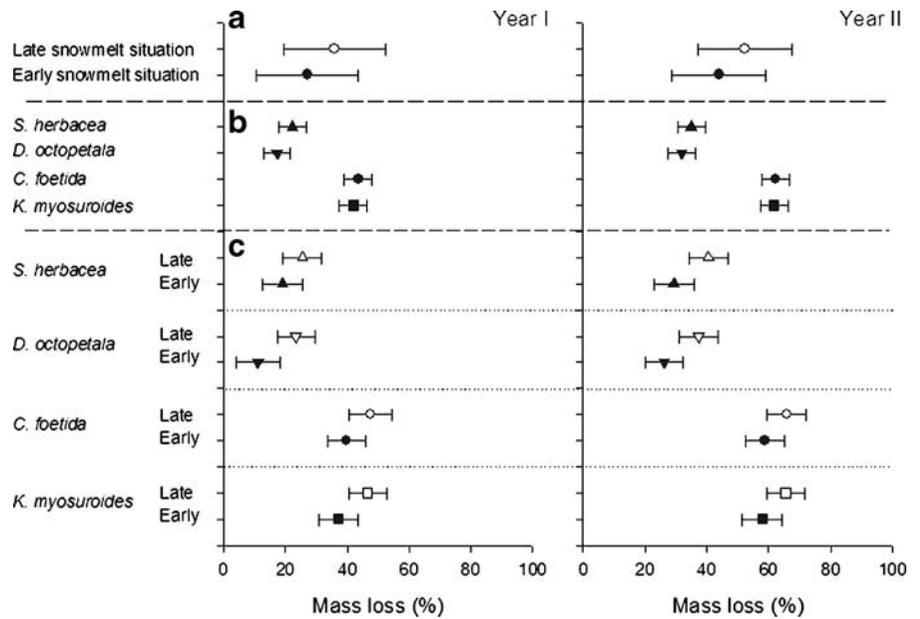
Winter 2, decomposition rates were in general lower than in Summer and Winter 1. The period × site interaction was significant for all species. This was related to variable patterns of decomposition among sites between Summer and Winter 2. However, the higher decomposition rates recorded during Winter 1 compared to others seasons was consistent throughout the sites. Finally, the large variation in winter decomposition rate between species highlighted the importance of growth forms and litter quality on decomposition, with shrubs having lower decomposition rates compared to graminoids, as found in Experiment I.

Litter nitrogen dynamics

After two years of decomposition, all species, except *D. octopetala* exhibited net N release (Fig. 5). Graminoids began releasing earlier than shrubs, so that 40% and 70% of the initial N remained after two years for *K. myosuroides* and *C. foetida* respectively. We found a significant regression between N release or immobilization and mass loss (mass loss effect: $F_{1,20}=74.3$, $P<0.0001$, $F_{1,20}=14.8$, $P<0.001$ for graminoids and shrubs respectively). However, within each species, there were no consistent differences in the patterns of N dynamic between snowmelt locations. These results meant that for each species, the percentage of released or immobilized N at a given

mass loss was the same, irrespective of the snowmelt location. Species differed significantly in litter N dynamic ($F_{1,20}=210.6$, $P<0.0001$, $F_{1,20}=67.8$, $P<0.0001$ for graminoids and shrubs respectively) with higher N release for *K. myosuroides* and *S. herbacea* compared to *C. foetida* and *D. octopetala* respectively after two years of decomposition. However, species-

Table 3 Mixed linear model results for mass loss, comparing species, snowmelt location and year effects for the graminoids and the shrubs (Experiment I)

| Source	F value$_{(df)}$	P
Graminoids		
Years	$559.1_{(1,172)}$	<0.0001
Species	$1.9_{(1,172)}$	0.17
Snowmelt location	$6.5_{(1,2)}$	0.12
Years × Species	$0.45_{(1,172)}$	0.50
Years × Snowmelt location	$0.53_{(1,172)}$	0.47
Species × Snowmelt location	$0.53_{(1,172)}$	0.47
Shrubs		
Years	$294.5_{(1,172)}$	<0.0001
Species	$21.6_{(1,172)}$	<0.0001
Snowmelt location	$8.8_{(1,2)}$	0.097
Years × Species	$1.6_{(1,172)}$	0.20
Years × Snowmelt location	$0.39_{(1,172)}$	0.53
Species × Snowmelt location	$2.3_{(1,172)}$	0.13
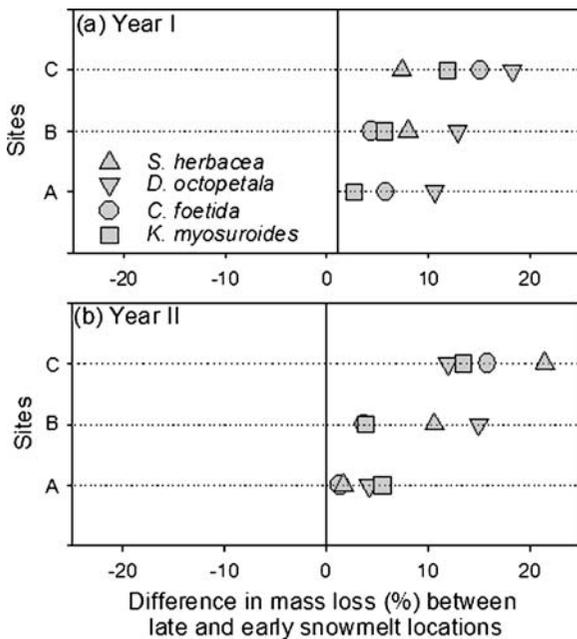
Fig. 2 Mass loss difference (%): late snowmelt locations minus early snowmelt locations mass loss for each species, each site (A, B and C) for a year I and b year II (Experiment I)

induced changes of N dynamic pattern were only detected in the case of the graminoids (mass loss × species effect : $F_{1,20}=9.3$, $P=0.006$, $P>=0.58$ for graminoids and shrubs respectively). On a seasonal basis, all species except *S. herbacea* exhibited patterns of N release (Fig. 6, Table 5). In early snowmelt locations, *D. octopetala* and *K. myosuroides* experienced N release during the first winter followed by a weak N re-immobilization during Summer and Winter 2.

Discussion

Only a few studies have addressed the relative importance of species vs. climatic effects on decomposition in alpine or arctic tundra. Hobbie (1996) compared the effects of increased temperature and litter from different Alaskan tundra on carbon and nitrogen mineralization in microcosms. These authors also tried to disentangle the influence of plant community composition from that of the soil environment at a moist acidic and a moist non-acidic site (Hobbie and Gough 2004). In alpine environments, Bryant et al. (1998) considered that the variation in decomposition rates along a snowmelt gradient was a

function of temperature and moisture. However snow was not assessed as a potential determinant of litter decomposition. O'Lear and Seastedt (1994) reported higher decomposition in a late compared to an early snowmelt location, but this study examined the litter decomposition of a single species, *Acomastylis rossi*. Thus, despite numerous studies in snow-covered ecosystem highlighting the major role played by snow in nutrient cycling (Campbell et al. 2005), our study addresses for the first time the direct and indirect effects of snow on litter decomposition in alpine tundra.

Direct controls over decomposition

All the species studied here experienced lower litter decomposition rates in early snowmelt com-
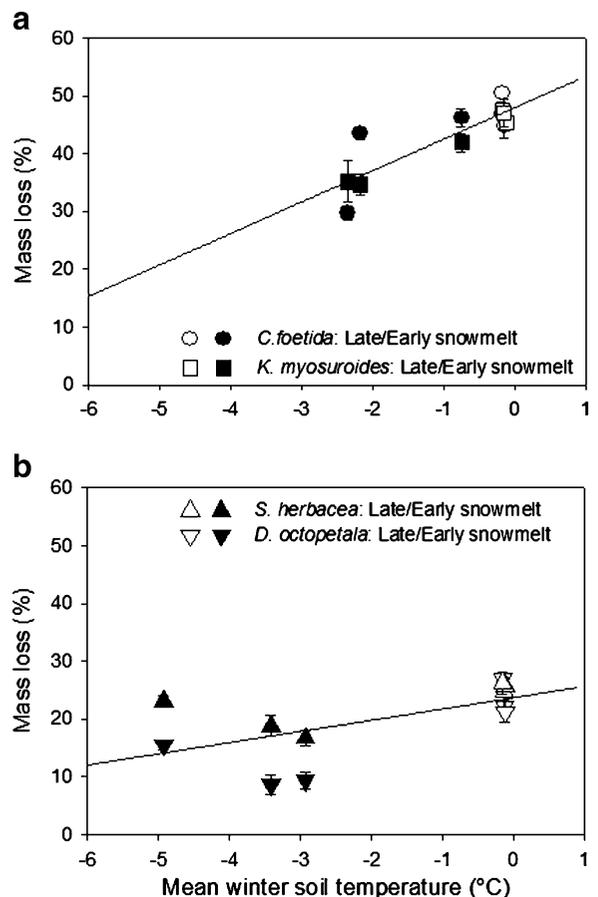

Fig. 3 One year mass loss by species in relation to mean wintertime soil temperature for graminoids (a) and shrubs (b) (Experiment I). Each point corresponds to first year mass loss in each snowmelt location
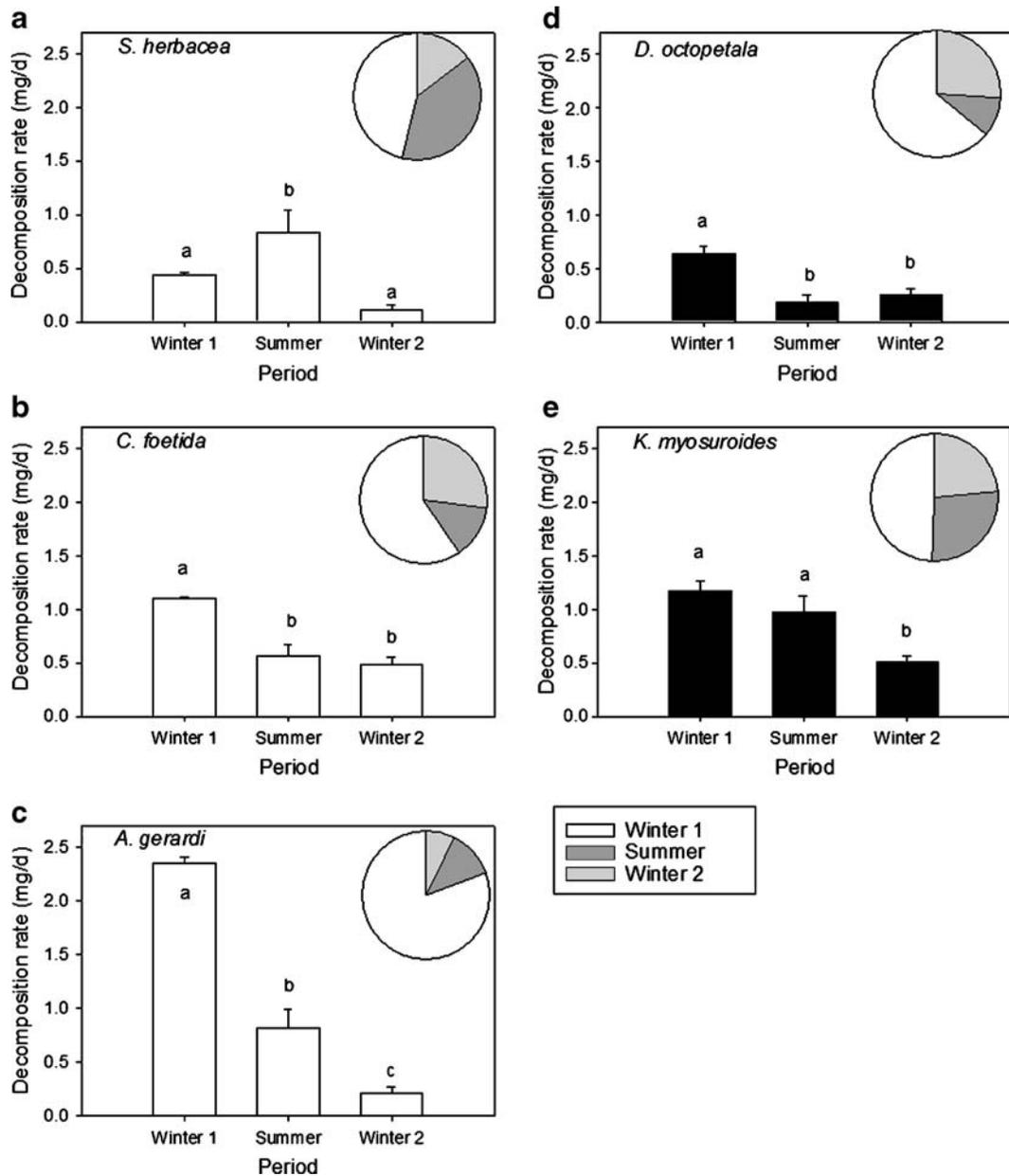
Fig. 4 Decomposition rates by species for each period (mg/d) (Experiment II). *Circle graphs* depict mass loss (in % of total mass loss from fall 2005 to spring 2007) and correspond to each period within species. See Table 4 and text for statistical analysis

pared to late snowmelt locations. During summer, soil temperature and soil moisture were similar in late snowmelt and early snowmelt locations, which is contrary to previous studies of mesotopographical gradients (Bryant et al. 1998; Fisk et al. 1998; O'Lear and Seastedt 1994). Thus, summertime conditions cannot explain the effect of snowmelt location on yearly mass loss. In contrast, the positive

relationship between mass loss and mean winter soil temperature clearly shows that snowmelt location effects are related to soil temperature and therefore to snow depth during winter. In late snowmelt locations, deep snow cover, which acts as an insulating layer, maintains soil temperature at 0°C, whereas the shallow and variable snow cover of early snowmelt locations leads to very low soil

Table 4 Two-way ANOVA results for decomposition rates comparing period (seasons) and site effects (Experiment II)

Source	F value$_{(df)}$	P
C. foetida		
Periods	39.6 $_{(2, 36)}$	<0.001
Sites	0.95 $_{(2, 36)}$	0.40
Periods × Sites	10.9 $_{(4, 36)}$	<0.001
K. myosuroides		
Periods	11.2 $_{(2, 36)}$	<0.001
Sites	0.59 $_{(2, 36)}$	0.56
Periods × Sites	3.5 $_{(4, 36)}$	0.01
A. gerardi		
Periods	154.4 $_{(2, 36)}$	<0.001
Sites	1.4 $_{(2, 36)}$	0.25
Periods × Sites	6.2 $_{(4, 36)}$	<0.001
S. herbacea		
Periods	13.7 $_{(2, 36)}$	<0.001
Sites	5.3 $_{(2, 36)}$	0.01
Periods × Sites	4.8 $_{(4, 36)}$	0.003
D. octopetala		
Periods	18.3 $_{(2, 36)}$	<0.001
Sites	0.42 $_{(2, 36)}$	0.66
Periods × Sites	4.9 $_{(4, 36)}$	0.003

temperatures during winter and tends to limit microbial activity. Snow cover, through soil temperature, may therefore impact decomposition in a significant way particularly during winter.

Results from Experiment II confirmed these findings. On average, 50 to 80% of the two-year mass losses occurred during the winter following litter fall. Previous studies had also demonstrated that significant litter mass loss occurred during winter (Bleak 1970; Hobbie and Chapin 1996; O'Lear and Seastedt 1994; Uchida et al. 2005). The observed mass loss during winter is consistent with reports of surprisingly high soil respiration under snowpack (Brooks et al. 2004; Brooks et al. 1997; Fahnestock et al. 1999; Oechel et al. 1997; Welker et al. 2000; Zimov et al. 1999) and large microbial biomass (Lipson et al. 1999; Schmidt and Lipson 2004) suggesting that cold-adapted microorganisms play an active role in litter degradation under the snow. The only exception to this timing was found for *S. herbacea* which exhibited higher litter decomposition during summer. These results may be

explained by the high concentration of polyphenols observed generally in *Salix sp.* leaves (Nyman and Julkunen Tiitto 2005). Enzymatic degradation of these recalcitrant compounds is hindered by very high activation energy and low temperatures may restrict their catabolisation (Bosatta and Agren 1999; but see Schmidt and Lipson 2004).

Although microbial activity seems to be the most important process for winter decomposition, we cannot exclude the possibility that physical processes, such as fragmentation, may affect mass loss (Hobbie and Chapin 1996). However, the freeze thaw cycles which can contribute to litter fragmentation are less frequent in late snowmelt locations, so one could reasonably expect a lower litter mass loss in these areas, which is in contradiction to what was observed in this study. We thus conclude that microbial activity largely predominates
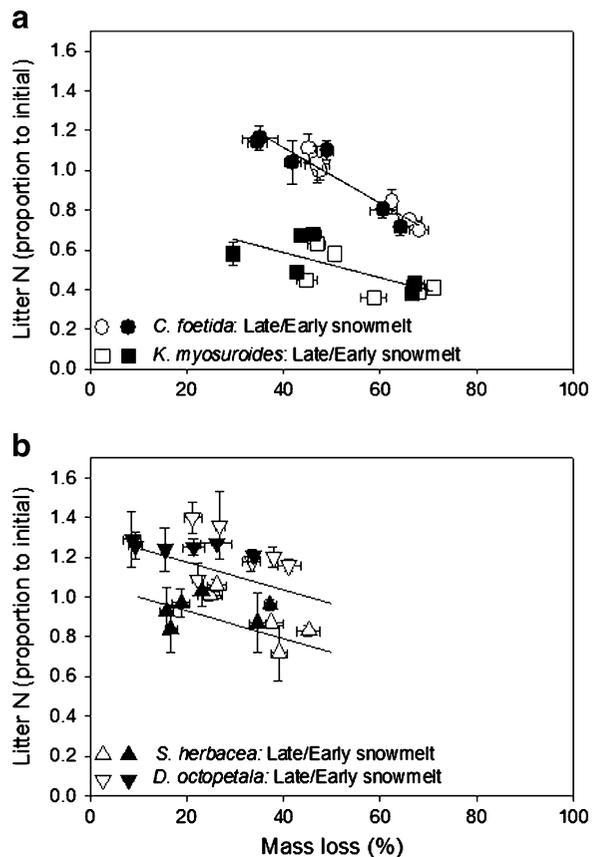
Fig. 5 Litter N content (proportion of initial N) by species in relation to mass loss for graminoids (**a**) and shrubs (**b**) (Experiment I)
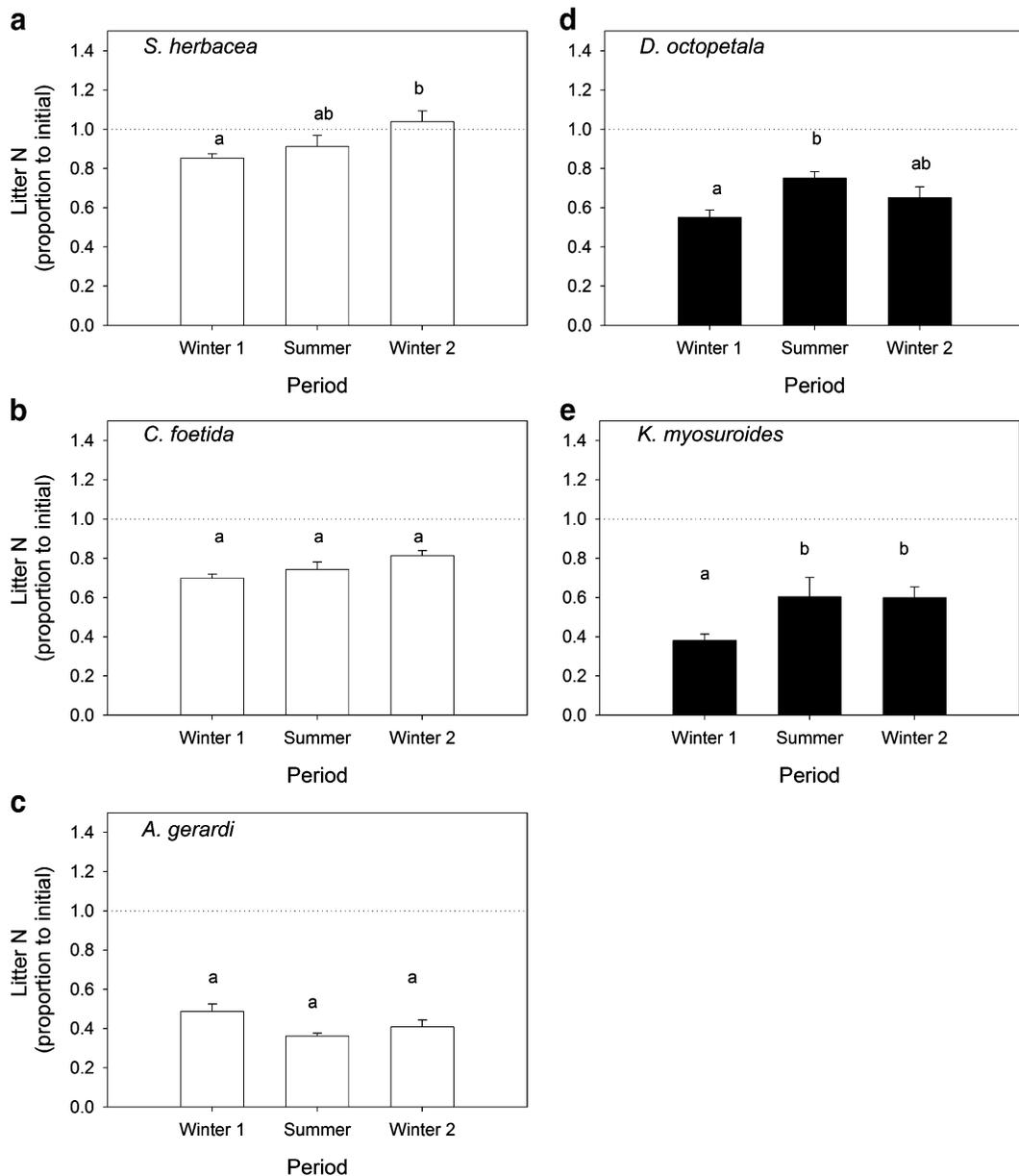
Fig. 6 Litter N content (proportion of initial N) by species for each period (Experiment II)

over physical fragmentation to explain higher mass loss during winter.

Indirect controls over litter decomposition

Besides a consistent effect of snowmelt location, the main determinant of litter decomposition remained species identity (Experiment I). Correspondingly, strong interspecific variability in winter decomposi-

tion rate suggests that the nature of available substrates exerts an important control over microbial activity (Experiment II): *A. gerardi* exhibited the highest decomposition rate during Winter 1 followed by *C. foetida* and *K. myosuroides* then *D. octopetala* and *S. herbacea*.

Similarly, Nadelhoffer et al. (1991) showed that C mineralization was more strongly related to organic matter quality than to temperature in arctic

Table 5 Two-way ANOVA results for litter N (proportion of initial N) comparing period and site effects (Experiment II)

Source	F value$_{(df)}$	P
C. foetida		
Periods	$2.8_{(2,17)}$	0.08
Sites	$0.31_{(2,17)}$	0.73
Periods × Sites	$0.37_{(4,\ 17)}$	0.82
K. myosuroides		
Periods	$11.0_{(2,\ 18)}$	<0.001
Sites	$7.0_{(2,\ 18)}$	0.005
Periods × Sites	$1.0_{(4,\ 18)}$	0.42
A. gerardi		
Periods	$2.1_{(2,\ 16)}$	0.15
Sites	$2.2_{(2,\ 16)}$	0.14
Periods × Sites	$1.3_{(4,\ 16)}$	0.31
S. herbacea		
Periods	$6.3_{(2,\ 18)}$	0.008
Sites	$3.0_{(2,\ 18)}$	0.07
Periods × Sites	$0.83_{(4,\ 18)}$	0.52
D. octopetala		
Periods	$9.2_{(2,\ 17)}$	0.002
Sites	$2.9_{(2,\ 17)}$	0.07
Periods × Sites	$0.65_{(4,\ 17)}$	0.63

tundra. However, the reciprocal transplant litter experiment underlined that, despite distinct dominant functional traits along the snowmelt gradient (Baptist and Choler 2008; Choler 2005), species effect was mainly determined by lignin rather than by leaf nitrogen concentration (Table 1). Hence, interspecific variations in litter decomposition largely mirrored growth form diversity in alpine tundra, underlying the importance of lignin in decomposition process (Cornelissen 1996; Meentemeyer 1978; Melillo et al. 1982). These results are in agreement with previous studies, which showed that shrubs generally had lower decomposition rates compared to sedges in arctic and sub-arctic ecosystems (Cornelissen et al. 2007; Hobbie 1996).

Implications for N cycling

No significant effect of snowmelt location on N immobilization was detected. Earlier N release from the late snowmelt locations was primarily the result of faster decomposition, whereas the inconsistent snowpack in early snowmelt locations may delay the final stage of N mineralization, limiting inorganic N availability in the ecosystem. However, this phenomenon may also contribute to limit N loss during snowmelt as a result of steep slopes between early and late snowmelt locations and thus promote N retention in the ecosystem, even in an organic form (Steltzer and Bowman 2005). Litter quality, especially initial N concentration, is a main driver of N release or immobilization (Parton et al. 2007). However, no significant relationship could be drawn between initial litter N concentration and N dynamic after one year of decomposition (Experiment I). Despite low litter N concentration (Table 2), *D. octopetala* exhibited important net N immobilization, whereas *K. myosuroides* had the greatest net N release. Different patterns of N dynamic depend on interspecific differences in nutrient concentration as well as on resorption and leaching from dead leaves. As a result, they are more likely to be idiosyncratic effects that are difficult to predict.

Conclusion

Our experiment highlight that winter deep snowpack creates an abiotic environment that is more stable and favourable for litter decomposition. However, the results also showed that growth form was a more important driver of decomposition than snowpack depth. Thus, changes in litter quality resulting from community-level shifts in dominant growth forms will likely have a stronger impact on litter decomposition in alpine tundra than the direct effect of changing snow regimes. A recent study suggested that experimental warming affected only sligthly alpine plant community composition (Wilson and Nilsson 2009). However associated to changes in snow cover duration and depth, the effects of global climate change on vegetation may be especially pronounced in alpine meadows (Theurillat and Guisan 2001). In this context, this study indicates that a shift in growth form composition, as observed in arctic ecosystem (Sturm et al. 2001; Walker et al. 2006), might have significant effects on biogeochemical cycling in alpine ecosystems.

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