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ORIGINAL ARTICLE

Decomposition of *Abies faxoniana* litter varies with freeze–thaw stages and altitudes in subalpine/alpine forests of southwest China

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Abstract
Freeze–thaw events in winter may affect litter decomposition in cold biomes but few reports are available. We characterized the fir (*Abies faxoniana*) litter decomposition over a whole winter (November 2008 to April 2009) during the late autumn, deep winter, and early spring stages. The mass loss, nutrient release, and quality change of fir litter were determined using the litterbag method at 2700, 3000, 3300, and 3600 m altitude in southwest China. Over the winter an average of 18% mass, 27% C, 50% N, 40% P, 36% K, 30% cellulose, and 14% lignin were lost. Of these total losses, a majority loss of mass (70%), C (65%), N (50%), P (58%), K (42%), cellulose (70%), and lignin (68%) occurred during the deep winter stage. The highest loss rate of mass (19.2%) and lignin (16.4%) but the lowest N loss (47.9%) was at the highest 3600 m altitude. Soil freeze–thaw cycle resulted in significant losses of mass, while mass loss rate did not increase under the higher mean soil temperature during each stage. Our results confirmed that the physical process seemed to be the most important process for cold season decomposition in the cold biome.

Keywords: Abies faxoniana, *altitude, freeze–thaw cycle, litter decomposition, nutrient release, subalpine/alpine forest.*

Introduction

Seasonal freezing and thawing is one of the most significant environmental changes at high latitudes and high altitudes including alpine and subalpine regions (Joseph & Henry, 2008). Physical or chemical losses of organic compounds from leaching and other processes related to the duration or cycles of freezing and thawing may alter the quality of plant litter and contribute to the litter decomposition (Manzoni et al., 2010). Our previous results (Wu et al., 2010a) and other studies (Hobbie & Chapin, 1996; Moore, 1983) have documented that litter is mainly decomposed during winter in the first year in cool climates, and nutrients released from the litter decomposition during winter are favorable to plant nutrition and growth in the following growing season (Berg & Ekbohm, 1993; Berg & McClaugherty, 2008; Berg & Tamm, 1994; Freppaz et al., 2007). Changes in litter quality because of temperature fluctuations as soil freezing and thawing proceeded may also affect the later process of litter decomposition (Weintraub et al., 2007). However, the detailed process of such freeze–thaw-induced litter decomposition as affected by significant temperature fluctuations is less studied, particularly when the dynamics of both temperature and moisture have been greatly altered by an ongoing global warming (Henry, 2008).

Predicting warming effects (air temperature) on decomposition in subalpine/alpine ecosystems seems complicated even significant loss of litter mass and nutrients could take place during litter decomposing in winter (Baptist et al., 2010; Bleak, 1970; Hobbie & Chapin, 1996). Given the temperature sensitivity of litter decomposition and the strong relations between litter decomposition rates and climatic variables (Meentemeyer, 1978; Mugendi & Nair, 1997), it is obvious that global warming will lead to an increased rate in litter decomposition and thus a higher flux of carbon dioxide (CO_2) into the atmosphere (Aerts, 2006; Tufekcioglu et al., 1999).

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In addition, because of the insulating effects of snow cover, the warming events may have different effects on soil temperature in a cold than in a warm season (Baptist et al., 2010). These differences must be considered when predicting warming events on winter decomposition. Furthermore, multiple environmental factors including soil temperature fluctuations around 0°C, soil frost intensity and snowpack patterns, could essentially affect litter decomposition in cold biomes (Edwards et al., 2007). Our previous study found that there are significant variations of freezing and thawing events in four different forests with different altitudes, and variations in landscapes and environments at different altitudes are mainly driven by temperature patterns (Tan et al., 2010). Contrary to the general theory that the litter decomposition rate decreases with the increase of altitude, it might be relatively higher at a higher altitude during winter, but no available information has demonstrated this. A better understanding of wintertime litter decomposition processes along an altitudinal gradient is therefore important under global warming scenarios in particular.

Fir (*Abies faxoniana*) is a representative tree species for most subalpine zones in southwest China (Yang et al., 2005). The dynamics surrounding freezing development and subsequent thawing around half a year from winter to early spring may have significant effects on fir litter decomposition (Wang 2004; Yang & Wang, 2004). We did observe that above 60% of fir litter decomposition occurred in the winter of the first year (Wu et al., 2010a), and that there were three distinctive stages of temperature fluctuations in winter in the proposed experimental site (Tan et al., 2010). However, less attention has been paid to the whole three stages (late autumn, deep winter, and early spring) of the cold season, although litter decomposition in the different stages with different decomposition characteristics could be essential to understand the entire litter decomposition process.

To characterize fir litter decomposition along an altitudinal gradient at the different stages of the winter season, mass loss, nutrient release, and changes in its quality of fir litter were studied at the late autumn, deep winter, and early spring stage, using the litterbag method under four representative subalpine forests at different altitudes (from 2700 to 3600 m) in southwest China. The objectives were to (1) characterize the fir litter decomposition rate at each different winter stage and (2) study the effects of altitude-controlled temperature fluctuations with freezing and thawing events on fir litter decomposition.

Materials and methods

Site description

This study was conducted in the Bipenggou Nature Reserve (102°53′–102°57′E, 31°14′′–31°19′N, 2458–4619 m a.s.l.), located in Li County, Sichuan, southwest China. This region is a transitional area between the Qinghai–Tibet Plateau and the Sichuan Basin. The annual mean air temperature is 3°C. The coldest month is January (−18°C) and the warmest month is July (23°C). Annual mean precipitation is about 850 mm. The cold season starts in November as the soil temperatures goes down below 0°C after snow falls and the soil remains frozen for 5–6 months.

Four sites were selected covering a 900 m vertical transition zone at elevations around 2700 m (A_1), 3000 m (A_2), 3300 m (A_3), and 3600 m (A_4) with similar topographic and environmental factors such as slope, aspect, and canopy density. The forest is dominated by birch (*Betula albosinensis*) and spruce (*Picea asperata*) with dense shrubs including dwarf bamboo (*Fargesia nitida*) at A_1; by spruce and fir (*A. faxoniana*) with dwarf bamboo, *Lonicera* spp. and *Rubus corchorifolius* at A_2; by spruce, fir, and birch dwarf bamboo at A_3; and by fir and larch (*Larix mastersiana*) with shrubs of a few azaleas (*Rhododendron* spp.) and willow (*Salix paraplesia*) at A_4. Frequent freezing and thawing events occur before and after the soil freezes in these forests (Tan et al., 2010).

Experimental design

Litterbag technique was used to quantify the leaf litter decomposition rate (Bocock & Gilbert, 1957). In October 2008, fresh fir senesced leaves were collected from the floor of the sampled fir forests. To avoid the structure damage of the litter during oven-drying, the fresh leaf litter was air-dried for more than two weeks at room temperature, 15 g of the air-dried litter ($9.15 \pm 0.02\%$ moisture) were then placed in a 0.50 mm nylon bag (20×20 cm) and the edges of the bag were sealed. Chemical analyses of the initial litter were based on the oven-dried mass (Table II, also for other data).

Our previous studies on soil temperature data (Tan et al., 2010; Wu et al., 2010a) have shown a cold winter season in this sample forest could be divided into three stages as the late autumn, deep winter, and early spring stage. The late autumn stage is characterized by frequent soil temperature fluctuations around 0°C. The labile component of litter, cold-tolerance microorganisms (Uchida et al., 2005), frequent freeze–thaw cycles (FTCs) (Taylor & Parkinson, 1988), or physical leaching

events (Bokhorst et al., 2010) may lead to a rapid litter decomposition during this stage. Soil temperature is constantly below 0°C in the second deep winter stage with a permanent snow cover. Physically destructive processes dominate this stage, and litter quality could be significantly changed due to the high-frost intensity. The last early spring stage is also characterized by the significant fluctuation of soil temperature around 0°C as the temperature increases. The selection of sampling dates was based on our previous field observation between 2005 and 2007 (Tan et al., 2010; Wu et al., 2010a). A total of 60 fir litter bags (four altitudes × three stages × five replicates) were placed on the floor of the four sampled forests on 6 November 2008. Litterbags were randomly sampled from each forest at 8 December 2008 (Late autumn stage), 24 March 2009 (Deep winter stage) and 22 April 2009 (Early spring stage). The retrieved litter was then oven-dried at 70°C for 48 h to determine dry mass. Five subsamples of each litter type were oven-dried at 70°C for 48 h at the time of initial deployment to determine the ratio between air-dried and oven-dried mass. This ratio was used to convert the initial air-dried mass of the litter to oven-dried mass. Soil temperature close to the litterbags was measured every 2 hours between 6 November 2008 and 22 April 2009 using a Buttony DS1923-F5 Recorder (Maxim Integrated Products, Inc., San Gabriel Drive Sunnyvale, USA) that was placed on the floor (Figure 1). A FTC was defined whenever the temperature dropped below 0°C for at least 3 h, followed by a rise above 0°C for at least 3 h, or whenever the temperature rose above 0°C for at least 3 h followed by a drop below 0°C for at least 3 h (Konestabo et al., 2007).

Chemical analysis

The residual litter in the litterbags was oven-dried at 70°C for 48 hours to a constant weight, and then ground (1 mm sieve) for C, N, P, K, cellulose, and lignin analysis. Analyses of C, N, P, and K were followed Lu (1999). In brief, the C content was determined by the dichromate oxidation–ferrous sulfate titration method. Subsamples of 0.2500 g were acid digested with 8 mL H_2SO_4 ($\rho = 1.84$ g cm^{-3}) and 3 mL H_2O_2 solution at 190°C for 10 min. The digested solution was then transferred to a 100 mL volumetric flask, subsampled, and stored for N, P, and K measurements. The N, P, and K contents were determined by Kjeldahl determination for N, phosphorus molybdenum-blue colorimetry for P, and flame photometry for K. Lignin and cellulose were measured using the Acid Detergent Lignin method (Graca et al., 2005).

Litter dry mass loss (L_i), and the release (R_i) of C, N, P, and K, lignin and cellulose during each stage of the freeze–thaw season were calculated as follows:

$$L_i(\%) = 100 \times (M_{i-1} - M_i)/M_0$$

$$R_i(\%) = 100 \times (M_{i-1}C_{i-1} - M_iC_i)/M_0C_0$$

Wintertime decomposition rates in cold biomes are poorly understood and the rates of leaf litter may not absolutely follow an exponential decay pattern. We focus on the rate in a relatively shorter period, that is half-year, not one year, and suppose that the litter decomposition in such a short period may not fit to the traditional litter decomposition model (Olson, 1963). As a consequence, dry mass loss rate per 30 days (V_m) is used here as:

$$V_m(\%) = 30 \times L_i/D_{Ti} (i = 1, 2, 3)$$

where M_0 is the dry mass of the initial litter; M_i and M_{i-1} are the dry masses of the remaining litter in the bag at the end of T_i and T_{i-1} stages after sampling; C_0, C_i, and C_{i-1} are the concentration (g kg^{-1}) of C, nutrients, lignin, and cellulose in the initial litter and remaining litter at the end of T_i and T_{i-1} stages after sampling; and D_{Ti} is the length (d) of each stage (T_i) as mentioned earlier. The mass loss (L) and element released (R) during the whole freeze–thaw stage was the sum of the losses and releases during each stage.

Statistical analyses

Differences in litter mass loss of different winter stages and sites from the field were analyzed with repeated measures ANOVA. Kruskall–Wallis test was used to test the differences in loss of mass, nutrient, lignin, and cellulose among altitudes during each decomposition stage. When significant differences occurred, Least Significant Difference (LSD) multiple range test was used to determine where differences existed. Linear regressions were performed to determine correlations between mass loss against mean soil temperature and the soil FTCs during each decomposition stage. All statistical analyses were performed using the SPSS 17.0 for Windows (SPSS Inc., IL, USA).

Results

Temperature dynamics

Soil surface temperature varied along the altitude gradient (Figure 1), and mean temperature at the upper A_3 and A_4 altitudes was higher during the deep winter stage, but lower at the late autumn and early spring stage (Table I). Over the winter, soil temperature remained close to 0°C and ranged

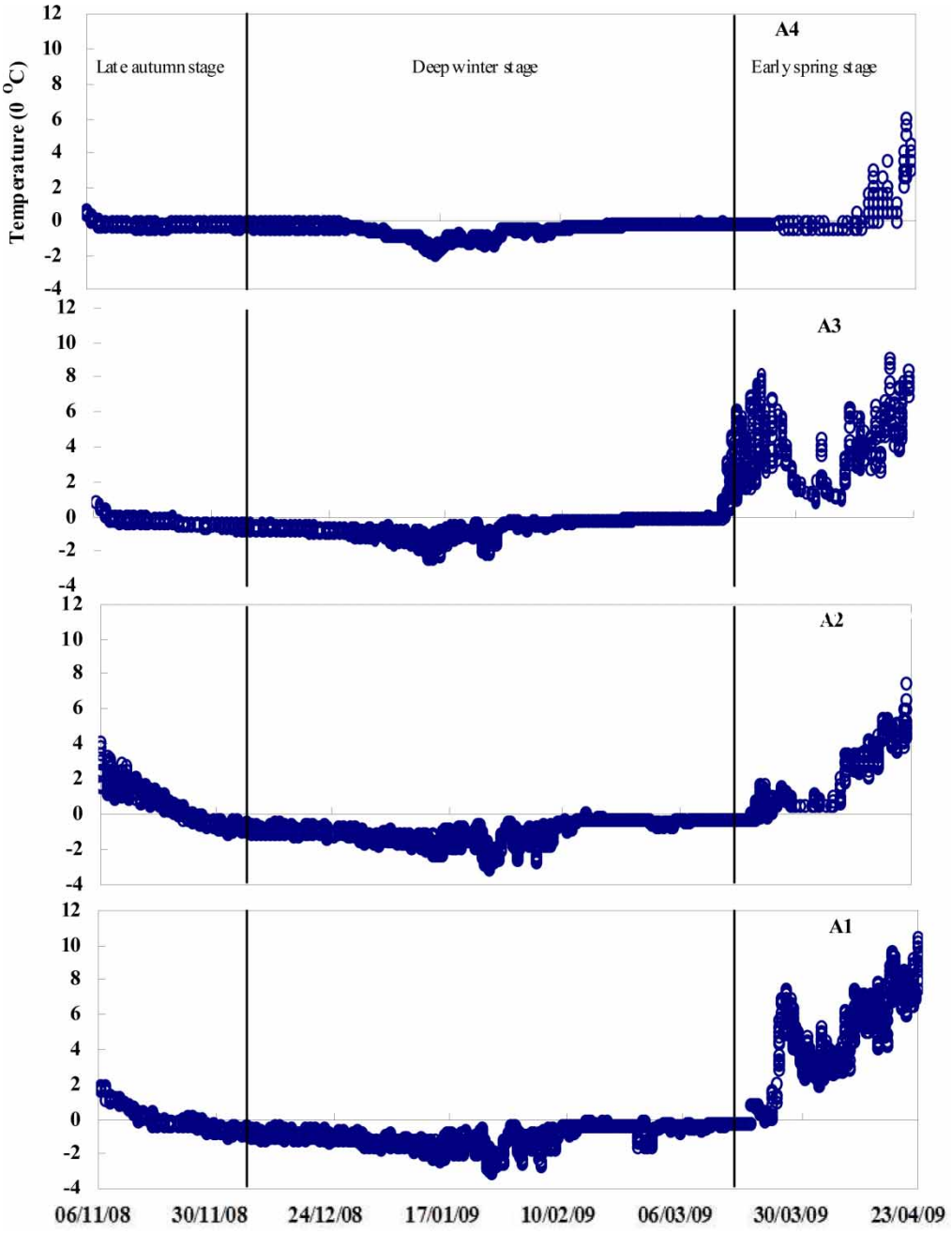

Figure 1. Variations of floor temperature at four altitudes over the winter. A_1, 2700 m; A_2, 3000 m; A_3, 3300 m; A_4, 3600 m.

Table I. Frequency of soil freeze–thaw cycles around 0°C at different altitudes during three decomposition stages of the winter.

Decomposition	Frequency of soil freeze–thaw cycles around 0°C at different altitudes (times)/ mean soil temperature (°C)			
Stage	A_1 (2700 m)	A_2 (3000 m)	A_3 (3300 m)	A_4 (3600 m)
Late autumn stage	10/0.1	4/0.4	13/–0.2	13/–0.1
Deep winter stage	1/–0.7	3/–0.7	2/–0.1	2/–0.4
Early spring stage	0/5.5	0/2.4	0/3.9	12/1.0
Total	11/0.5	7/0.0	15/0.6	27/0.3

from -2 to 2°C. Moreover, the minimum soil temperature was higher as -2.96°C at both the A_1 and A_2, -2.35°C at the A_3 and -1.80°C at the A_4 altitude in the deep winter stage. During the late autumn stage, the FTC frequencies were greater at both the A_3 and A_4, less at the A_1 and least at the A_2 altitude (Table I). No soil temperature fluctuations around 0°C were detected at the A_1, A_2, and A_3 altitude during the early spring stage, but with the greatest 12 soil FTCs at the A_4 altitude.

Losses of mass, lignin, and cellulose

The decomposition of litter was gradually increased with the time extended and the amount of litter loss was similar (ranged from 17.1 ± 1.2 to $19.2 \pm 0.8\%$) among the four altitudes over the whole winter (Figure 2). Among the three stages, percentage of litter mass loss was significantly greatest at the deep winter ($12.9 \pm 0.5\%$), less at the late autumn ($4.2 \pm 0.3\%$), and least at the early spring ($1.5 \pm 0.9\%$, Asymp. Sig. $= 0.003$). Among different altitudes, significant mass loss patterned as $A_1 = A_4 = A_3 > A_2$ at the late autumn stage, $A_1 > A_4 = A_2 = A_3$ at the deep winter stage, and $A_4 > A_3 > A_2 = A_1$ at the early spring stage (Asymp. Sig. $= 0.043$). The mass loss rates per 30 d (V_m) among the different altitudes were averaged $4.0 \pm 0.3\%$ and $3.6 \pm 0.1\%$ during the late autumn and deep winter stage. In addition, the mass loss rates during the early spring stage for each site were $0.3 \pm 0.2\%$ (A_1), $0.7 \pm 0.3\%$ (A_2), $1.2 \pm 0.9\%$ (A_3), and $2.4 \pm 0.5\%$ (A_4), respectively. A regression analysis of mass loss rate in each altitude against number of FTCs and the location's mean soil temperatures (Figure 5) showed a positive effect of soil FTC on mass loss rate ($R^2 = 0.31$, $F = 20.054$, $P = 0.001$). Without any FTCs, litter decomposition rate was significantly lower than the rate at the site where FTCs happen, however more numbers of FTC resulted in little additional change ($R^2 = 0.01$, Figure 5). But an adverse effect of the mean soil temperature on mass loss rate ($F = 19.807$, $P = 0.001$). The mean temperature $\times$ FTCs was never significant ($F = 1.175$, $P = 0.307$).

Over the winter, percentage of the total losses of cellulose and lignin ranged from 26.6–39.3% and 11.1–16.4% depending on the altitude (Figure 3). Among the three stages, percentages of both cellulose and lignin losses were highest at the deep winter (23.1 and 9.4%), less at the late autumn (7.6 and 3.5%), and least at the early spring (2.9 and 1.0%) stage. Among different altitudes, cellulose loss was generally highest at the A_3 altitude in both the deep winter and early spring stage, whilst was similar among the four altitudes in the late autumn stage. In contrast, lignin loss was generally highest at the A_4 altitude, whilst least at the A_2 altitude in all three stages.

Releases of C, N, P, and K

Over the winter an average of $26 \pm 6\%$ the total C was released from the fir litter among the different altitudes (Figure 4a). Among the three stages, significantly highest C loss occurred at the deep winter, less at the late autumn and least at the early spring stage. Among the four altitudes, the highest C release was in the A_2 and the least was at the A_3 altitude during the deep winter stage, and similar during both the late autumn and early spring stage,

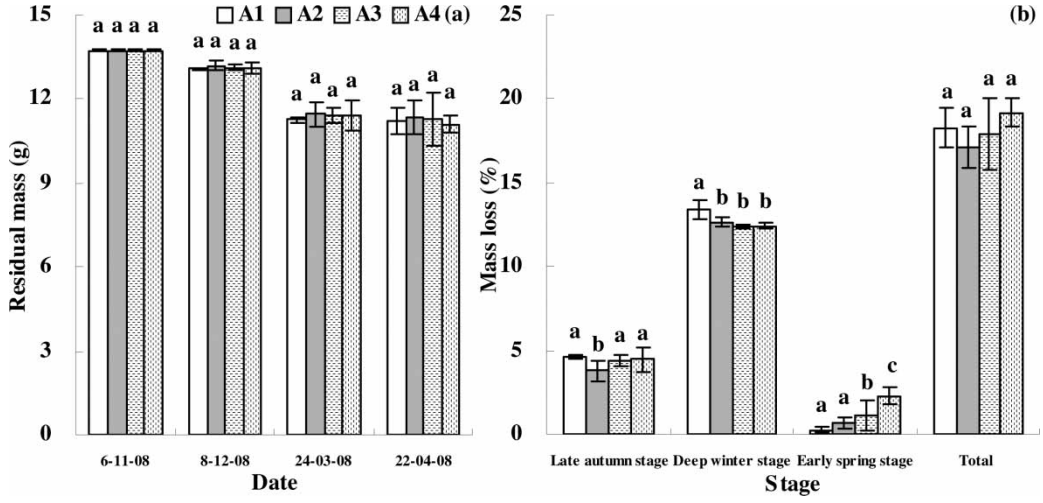

Figure 2. Residual mass weight (a) and mass loss (b) of fir leaf litter at four altitudes and three decomposition stages over the winter. Different letters denote significant differences at $P < 0.05$. Data are means $\pm$ SE, $n = 5$. A_1, 2700 m; A_2, 3000 m; A_3, 3300 m; A_4, 3600 m; Total, the total loss over the three stages. Note that the residual mass was based on oven-dried, not air-dried.

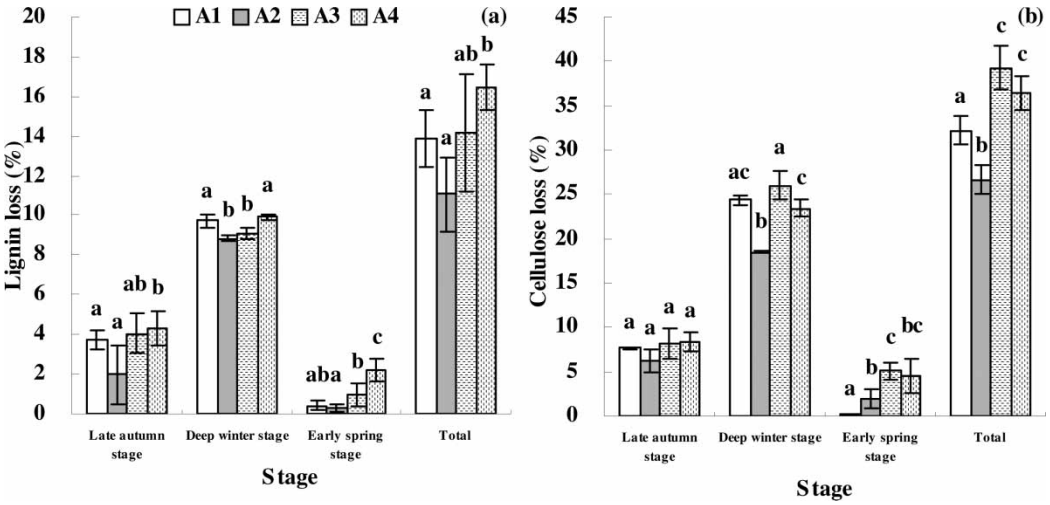

Figure 3. Lignin (a) and cellulose loss (b) in fir leaf litter at four altitudes and three decomposition stages over the winter. Different letters denote significant differences at $P < 0.05$. Data are means $\pm$ SE, $n = 5$. A_1, 2700 m; A_2, 3000 m; A_3, 3300 m; A_4, 3600 m; Total, the total loss over the three stages.

except at the A_1 altitude during the early spring stage.

The total release of N, P, and K from the fir litter varied with the altitude and was 48–55%, 36–42%, and 32–38%, respectively (Figure 4b–d). The highest N, P, and K release rate (25, 22, and 15%) occurred during the deep winter stage, accounting for 50, 58, and 42% of the total N, P, and K releases.

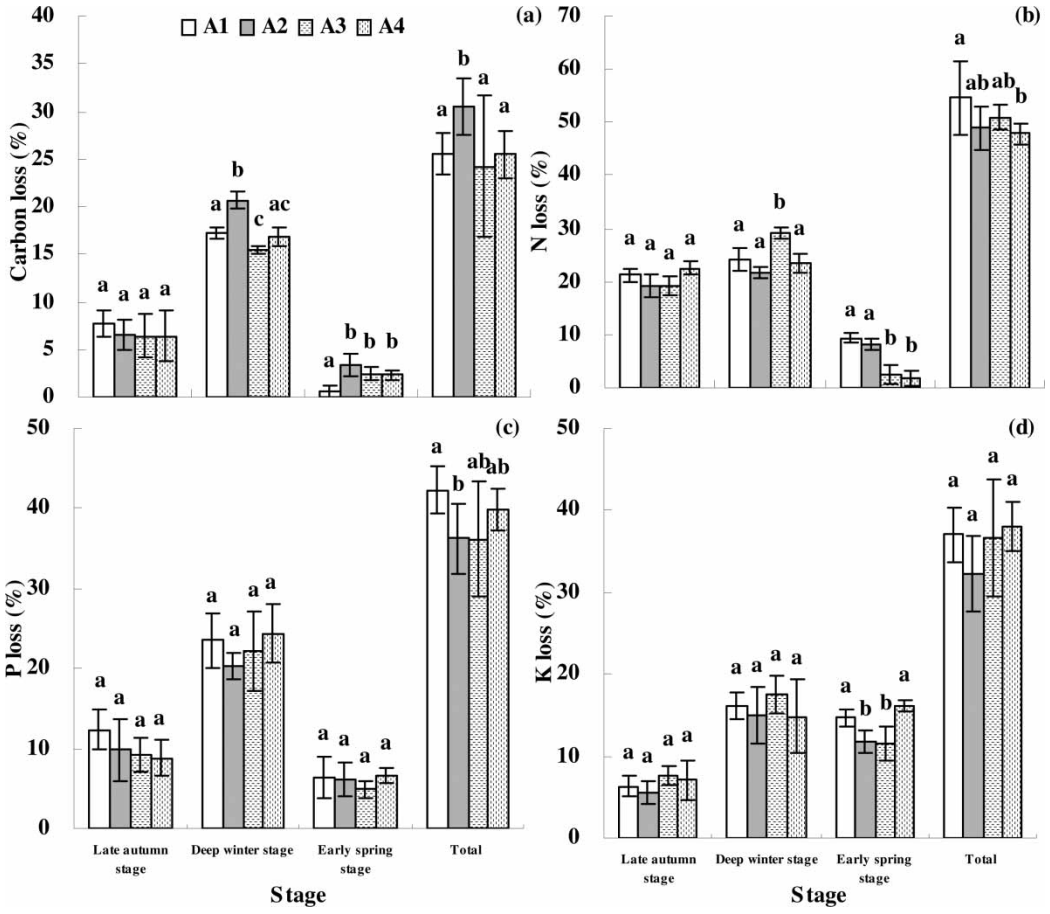

Figure 4. Release of C (a), N (b), P (c) and K (d) from fir leaf litter at four altitudes and three decomposition stages over the winter. Different letters denote significant differences at $P < 0.05$. Data are means $\pm$ SE, $n = 5$. A_1, 2700 m; A_2, 3000 m; A_3, 3300 m; A_4, 3600 m; Total, the total loss over the three stages.

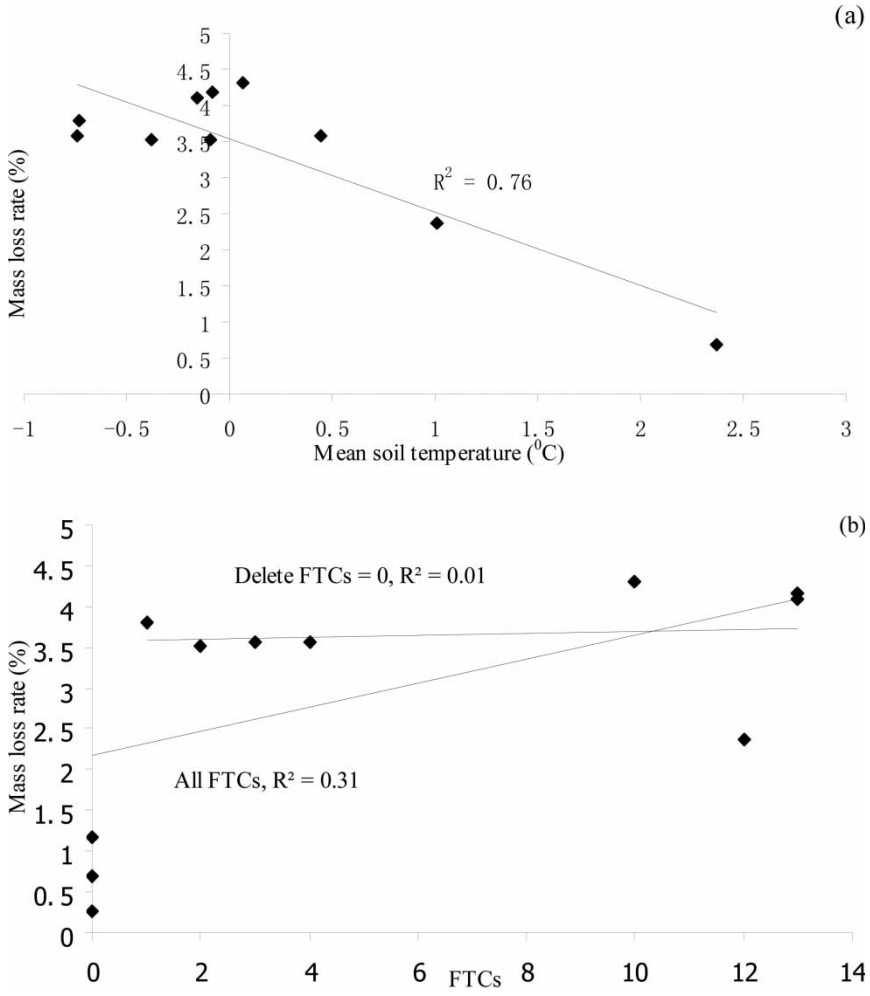

Figure 5. Mass loss rate in relation to mean soil temperature (a) and FTCs (b). Data are means ± SE, $n = 5$.

Meanwhile, N losses were similar among the four altitudes in the late autumn stage, highest at the A_3 altitude in the deep winter but higher at both the A_1 and A_2 altitude in the early spring stage. In contrast, the loss of both P and K were similar among the four altitudes in the three stages, except a lower K loss at the A_2 and A_3 altitude in the early spring stage.

Changes of litter quality

The concentrations of C, N, P, K, and cellulose in the litter showed a decreasing tendency as the decomposition proceeded, although the concentrations of lignin, C/N, L/N, and lignin/cellulose were increased regardless of the altitude (Table II). Concentrations of C, N, and P were generally decreased more rapidly during the late autumn stage than during the other two stages ($P < 0.05$), except a significant K loss during the early spring stage. The lignin/cellulose ratio was increased more significantly during the deep winter stage compared with the other two stages. In addition, all these litter quality changes varied with altitudes.

Discussion

The majority ($> 60\%$) of mass loss occurred when the temperature was consistently below 0°C in the deep winter stage, and less than 26% and 12% in the late autumn and early spring stage, respectively. Generally, almost 20% of mass loss occurred during the first cold season decomposition in the cold biomes (Abouguendia & Whitman, 1979; Hobbie & Chapin, 1996; Moore, 1983). However, Bokhorst et al. (2010) stated that about 90% of that 20% litter decomposition occurred during the first week after the litter fall and only about 2% mass loss occurred during the deep winter. These varied observations might be related to the variation in litter quality and environment factors including the freeze–thaw cycle and microbial activity. Despite the differences, results from both ours and others imply that decomposition

Table II. Variations of fir leaf litter quality at different altitudes during the three decomposition stages over the winter.

Stage	Site	C (g kg^{-1})	N (g kg^{-1})	P (g kg^{-1})	K (g kg^{-1})	Cellulose (g kg^{-1})	Lignin (g kg^{-1})	C:N ratio	L:N ratio	L:Cel ratio
Initial		545.8 ± 6.9a	13.8 ± 0.3a	1.3 ± 0.1a	7.1 ± 0.0a	248.5 ± 6.1a	328.2 ± 5.0a	39.5 ± 0.8a	23.8 ± 0.5a	1.3 ± 0.0a
Late autumn stage	A_1	527.7 ± 10.5b	11.4 ± 0.3b	1.2 ± 0.0a	7.0 ± 0.1a	240.5 ± 7.6ab	331.3 ± 2.8a	46.2 ± 0.8bc	29.0 ± 0.3b	1.4 ± 0.0a
	A_2	530.6 ± 16.8ab	11.6 ± 0.6b	1.2 ± 0.1a	7.0 ± 0.1a	242.5 ± 8.3ab	334.4 ± 7.2ab	45.6 ± 1.4bc	28.8 ± 0.8b	1.4 ± 0.1a
	A_3	534.3 ± 15.5ab	11.7 ± 0.4b	1.3 ± 0.0a	6.9 ± 0.1ab	238.7 ± 8.2ab	329.2 ± 5.0a	45.7 ± 1.1b	28.2 ± 0.5b	1.4 ± 0.1a
	A_4	534.6 ± 12.4ab	11.2 ± 0.3b	1.3 ± 0.0a	6.9 ± 0.1ab	238.3 ± 3.1b	328.8 ± 7.3a	47.7 ± 1.2bc	29.4 ± 0.7b	1.4 ± 0.0a
Deep winter stage	A_1	499.6 ± 8.0c	9.2 ± 0.4cd	1.0 ± 0.1b	6.8 ± 0.1b	206.0 ± 9.2c	346.4 ± 9.4b	54.2 ± 0.9d	37.6 ± 0.9cd	1.7 ± 0.1bc
	A_2	475.5 ± 5.1d	9.8 ± 0.5c	1.1 ± 0.0b	6.8 ± 0.1b	224.0 ± 7.9b	350.3 ± 12.0b	48.6 ± 0.6c	35.8 ± 1.1c	1.6 ± 0.1b
	A_3	512.5 ± 6.7bc	8.6 ± 0.6d	1.1 ± 0.1ab	6.4 ± 0.1c	196.5 ± 4.1c	342.3 ± 5.9b	59.8 ± 0.9f	39.9 ± 0.7d	1.7 ± 0.0b
	A_4	504.9 ± 10.6c	9.0 ± 0.5cd	1.1 ± 0.1ab	6.7 ± 0.1b	204.0 ± 8.0c	339.2 ± 12.3ab	56.1 ± 0.9e	37.7 ± 1.2cd	1.7 ± 0.1bc
Early spring stage	A_1	497.3 ± 6.7c	7.4 ± 1.7d	0.9 ± 0.1b	5.5 ± 0.1d	206.0 ± 8.0c	346.1 ± 11.1b	65.2 ± 1.0g	45.4 ± 1.0f	1.7 ± 0.1bc
	A_2	457.4 ± 8.1e	8.5 ± 0.9d	1.0 ± 0.1b	5.8 ± 0.2d	220.1 ± 9.8bc	352.0 ± 8.5b	53.9 ± 1.0d	41.5 ± 0.9e	1.6 ± 0.1b
	A_3	502.9 ± 15.5c	8.3 ± 0.2d	1.0 ± 0.1b	5.5 ± 0.2d	183.9 ± 8.0d	343.7 ± 6.6b	60.7 ± 1.2f	41.5 ± 0.7e	1.9 ± 0.1c
	A_4	503.3 ± 10.0c	8.9 ± 0.5d	1.0 ± 0.1b	5.5 ± 0.1d	195.6 ± 6.1c	339.5 ± 10.0ab	56.5 ± 1.1e	38.1 ± 1.1d	1.7 ± 0.1bc

Note: Different letters in a column denote significant differences at $p < 0.05$ in different stages under different forests.
A_1, 2700 m; A_2, 3000 m; A_3, 3300 m; A_4, 3600 m; L, lignin, Cel, cellulose.

during winter is a key process for litter loss, which might limit or promote later decomposition by changing litter quality (e.g. Bokhorst et al., 2010; Wu et al., 2010a). It seems that understanding litter decomposition during the three key stages of the winter is essential to resolve the inconsistent results described earlier.

Litterfall at our study sites mainly occurs at the onset of soil freezing stage (late autumn). This stage is characterized by the duration of FTCs as the temperature decreases before the temperature falls down consistently below 0°C (Tan et al., 2010; Withington & Sanford, 2007). Therefore, litter may exhibit a relatively rapid decomposition rate due to the presence of fresh litter with relatively more labile components, the physically destructive effects of frequent FTCs (Hobbie & Chapin, 1996; Taylor & Parkinson, 1988; Wu et al., 2010a,b), an altered microbial activity, and their interactions (Moorhead & Sinsabaugh, 2006; Schadt et al., 2003; Weintraub et al., 2007). In this study, soil FTC increased mass loss rate after one FTC, but more FTCs resulted in little additional change. This result confirmed that freezing and thawing events improved litter decomposability in the field (Edwards et al., 2007) and mass loss rate did not increase with increasing number of FTCs in this cold biome. The detected adverse effect of the mean soil temperature on mass loss rate demonstrated that a higher frost intensity as an important physical factor in cold season decomposition could destroy the litter function while enhancing litter decomposability. These results agree the general theory (Baptist et al., 2010; Edwards et al., 2007), which states the temperature sensitivity of litter decomposition. Meanwhile, for this specific season a deep insulating snow cover resulted in the soil temperature close to 0°C (usually between −2°C to 2°C) throughout the day and the highest mass loss rate under this 0°C (Figure 5). Although these results confirmed that physical processes including frost/cryoturbation (Edwards et al., 2007), FTC (Taylor & Jones, 1990; Wu et al., 2010a,b) and probable fragmentation (Hobbie & Chapin, 1996) might be the most important process for the cold season decomposition, we cannot exclude the role of microbial activities in mass loss (Brooks et al., 1996). Nevertheless, the correlations between mass loss and temperature dynamics showed that higher mass loss rate did not occur under the highest mean soil temperature but under the mean temperature mostly closed to 0°C.

More rapid losses of lignin and cellulose, and more significant releases of K in response to the higher frequencies of soil FTCs and lower but close to 0°C were also observed during the late autumn stage (Figures 3 and 4d; Table I). Of these total

losses over the winter, 18–29% of lignin and 22–29% of P losses during the entire winter occurred during the late autumn stage. Physical processes such as soil cryoturbation (Edwards et al., 2007), cold-resistant microorganisms (Grogan & Jonasson, 2006; Larsen et al., 2007), and leaching (Harris & Safford, 1996; Melick & Seppelt, 1992) were probably response to the mass loss during the deep winter stage. In addition to the FTC, temperature dynamics (Figure 1) were also different at the four altitudes, each of the temperature dynamics could also influence the litter decomposition during the late autumn stage. Furthermore, changes in litter quality including the decrease of C, N, P, K, and cellulose, and the increase of lignin and the C/N and L/N ratio (Table II) might limit and/or affect the decomposition processes in the later stage (Melillo et al., 1982; Taylor et al., 1989).

The second stage of the freeze–thaw season was characterized by deep freezing (the deep winter stage) as the temperature was consistently below 0°C. Because of methodological limitations to measure the low temperature and low activity of soil microorganisms (Uchida et al., 2005), litter decomposition at this stage is less studied (Aerts, 2006; Hobbie & Chapin, 1996). The majority ($>60\%$) of the mass loss and nutrient releases occurred during the deep winter stage in this study are consistent with other previous studies (Edwards et al., 2007; Wu et al., 2010a,b). Three reasons may be related to this observed mass loss during the deep winter stage. First, the labile components are not completely lost during the short late autumn stage (<30 days), which can be seen in the relatively high concentrations of cellulose, N, and P, and lower C:N and L:N ratios during the deep winter stage compared with the later stage (Table II). Although the decomposition rate was lower during the deep winter stage than that during the late autumn stage, the longer (>109 days) decomposition time might contribute to the loss of components at the deep winter stage. Second, the snow cover may provide an insulated layer as a stable environment for cold-resistant microorganisms at the deep winter stage (Baptist et al., 2010; Grogan & Jonasson, 2006; Larsen et al., 2007), and thus continual microbial activities might lead to a rapid litter decomposition (Brooks et al., 1996). Third, the effects of soil cryoturbation may destroy litter structure after the freeze–thaw season and hence increase the C substrate and nutrient availability for microorganisms, and consequently lead to more mass loss and nutrient release during the deep winter stage.

Our results from this experiment showed that the losses of mass, lignin, and cellulose and the release of C were far greater during the deep winter stage than during the other two stages, and the greater losses of lignin and cellulose were observed at the upper A_3 and A_4 altitudes with a higher soil temperature. These are also most likely due to the deeper snow cover in the higher altitude, which provides a more stable abiotic environment for a favorable litter decomposition as discussed earlier (Baptist et al., 2010; Grogan & Jonasson, 2006; Larsen et al., 2007). Lignin loss and the destruction of the litter structure by freezing during the deep winter stage could be thus beneficial to the later litter decomposition. In addition, lower proportions of mass loss and C release but larger proportions of lignin and cellulose loss, N and P release occurred during the deep winter stage at the upper A_3 and A_4 altitude. These results agreed with the notion that mass loss and release during the litter decomposition process can be not only attributed to microbial activities (Moorhead & Sinsabaugh, 2006; Schadt et al., 2003), but also to the soil freeze–thaw events, especially during the winter.

The last stage of the freeze–thaw season is characterized by frequent FTCs as the temperature increases after the deep winter stage (Tan et al., 2010). However, the highest FTCs (12 times) was only detected at the A_4 altitude. More frequently repeated FTCs might have probably promoted the mass loss by awaking microorganisms and stimulating their interactions, although only 0.26–2.29% of mass loss occurred during this short early spring stage. A comparatively larger proportion of K release occurred during this early spring stage was likely due to a leaching event when the snow melts (Nykvist, 1961). Larger loss proportions of mass, lignin, and cellulose also occurred at the higher A_3 and A_4 than at the lower A_1 and A_2 altitudes during the early spring stage. These results confirmed that the duration of freezing and thawing events can exert significant impacts on the structure of decomposed litter during the freeze–thaw season.

During the freeze–thaw season in this study, the total losses of litter mass at the A_4 altitude with the highest FTCs occurred significantly higher than at the other three altitudes. Meanwhile, larger proportions of lignin and cellulose loss, and K release occurred during the entire freeze–thaw season at both the higher A_3 and A_4 altitude, but a larger proportion of N release occurred at the lower A_1 and A_2 altitude. A possible explanation may relate to the lower temperature limits on microbial activity, implying that N might be the limiting factor in these forests since N is immobilized by microorganisms. Further studies are thus required to determine how the changed litter quality after the early spring stage could influence the litter decomposition process in the following growing season.

Conclusion

There were large amounts of mass, lignin, cellulose, C and N, P, and K losses during the fir litter decomposition in the freeze–thaw season. The litter decomposition rate was highest at the late autumn stage, but the majority of mass loss and nutrients releases occurred during the deep winter stage, and a small amount of their losses occurred during the early spring stage. Physical processes accompanied with the various soil temperature dynamics seemed to be the most important process for the cold season decomposition in this subalpine/alpine forest. Although we observed these significantly different processes of litter decomposition during the three different stages of a freeze–thaw season, interactions among the physical, chemical, and microbial processes during these stages and their influences on litter decomposition were not characterized in detail. Further research is guaranteed to determine these interactions during the different stages over a whole freeze–thaw season.

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