Chin. Geogra. Sci. 2017 Vol. 27 No. 5 pp. 760–771
doi: 10.1007/s11769-017-0898-2

Springer Science Press
www.springerlink.com/content/1002-0063

Litter Decomposition of Emergent Plants along an Elevation Gradient in Wetlands of Yunnan Plateau, China

LIU Guodong[1], SUN Jinfang[1], TIAN Kun[2], YUAN Xingzhong[3], AN Subang[4], WANG Hang[2]

(1. *College of Geography and Tourism*, *Qufu Normal University*, *Rizhao* 276826, *China*; 2. *National Plateau Wetlands Research Center/Southwest Forestry University*, *Kunming* 650224, *China*; 3. *College of Resource and Environmental Science*, *Chongqing University*, *Chongqing* 400030, *China*; 4. *Key Laboratory of Wetland Ecology and Environment*, *Northeast Institute of Geography and Agroecology*, *Chinese Academy of Sciences*, *Changchun* 130102, *China*)

Abstract: The decomposition of plant litter is a key process in the flows of energy and nutrients in ecosystems. However, the response of litter decomposition to global climate warming in plateau wetlands remains largely unknown. In this study, we conducted a one-year litter decomposition experiment along an elevation gradient from 1891 m to 3260 m on the Yunnan Plateau of Southwest China, using different litter types to determine the influences of climate change, litter quality and microenvironment on the decomposition rate. The results showed that the average decomposition rate (K) increased from 0.608 to 1.152, and the temperature sensitivity of litter mass losses was approximately 4.98%/℃ along the declining elevation gradient. Based on a correlation analysis, N concentrations and C∶N ratios in the litter were the best predictors of the decomposition rate, with significantly positive and negative correlations, respectively. Additionally, the cumulative effects of decomposition were clearly observed in the mixtures of *Scirpus tabernaemontani* and *Zizania caduciflora*. Moreover, the litter decomposition rate in the water was higher than that in the sediment, especially in high-elevation areas where the microenvironment was significantly affected by temperature. These results suggest that future climate warming will have significant impacts on plateau wetlands, which have important functions in biogeochemical cycling in cold highland ecosystems.
Keywords: plateau wetland; climate change; elevation gradient; litter decomposition; carbon cycle; Yunnan Plateau

Citation: Liu Guodong, Sun Jinfang, Tian Kun, Yuan Xingzhong, An Subang, Wang Hang, 2017. Litter decomposition of emergent plants along an elevation gradient in wetlands of Yunnan Plateau, China. *Chinese Geographical Science*, 27(5): 760–771. doi: 10.1007/s11769-017-0898-2

1 Introduction

Global climate warming and the associated environmental changes are predicted to affect most regions of the Northern Hemisphere, and climate change will likely cause longer and more frequent heat waves by the end of the 21st century (IPCC, 2014). Additionally, climate warming will likely lead to increased litter decomposition rates and higher fluxes of carbon dioxide into the atmosphere. These effects are predicted to be greater in cold biomes (high-latitude and high-elevation sites) because warming is predicted to be greatest in these areas, and the litter decomposition in these regions is strongly limited by temperature (Meentemeyer, 1978; Hobbie, 2000; Robinson, 2002; Aerts, 2006).

The decomposition of plant litter is a key ecosystem process that plays an important role in the carbon cycle (Coûteaux *et al*., 1995; Robinson, 2002; Berg and McClaughtery, 2008). Litter decomposition involves the physical and chemical processes that reduce litter to its

Received date: 2016-05-09; accepted date: 2016-09-21
Foundation item: Under the auspices of Special Projects of National Key Basic Research Program of China (No. 2012CB426509), National Natural Science Foundation of China (No. 40971285, 31370497, 31500409), Yunnan Innovation Talents of Science and Technology Plan of China (No. 2012HC007)
Corresponding author: LIU Guodong. E-mail: lgd102378@163.com; TIAN Kun. E-mail: tlkunp@126.com

elemental chemical constituents (Swift *et al*., 1979; Aerts, 2006). Litter decomposition rates are mainly controlled by environmental conditions, litter quality and decomposer organisms (Coûteaux *et al*., 1995; Cadish and Giller, 1997; Gavazov, 2010). Among these factors, climate is considered the most important because it acts at global and regional scales (Aerts, 1997; Bonanomi *et al*., 2013).

Environmental gradient studies can be used to analyze and quantify the influences of environmental conditions on ecosystem processes (Dunne *et al*., 2004; Malhi *et al*., 2010). Elevation gradient studies represent a natural approach to evaluating the impacts of climatic parameters on ecological processes (KÖrner, 2007; Gavazov *et al*., 2014). Therefore, these studies can potentially provide information regarding the sensitivity of ecosystem processes to temperature, although the covariance of temperature with other elevation-dependent variables necessitates caution in such interpretations (Salinas *et al*., 2011). Furthermore, ecological field experiments along elevation gradients can be performed to identify direct environmental factors and other site-dependent factors, such as species traits and compositions (van de Weg *et al*., 2009; Pellissier *et al*., 2010; Averill and Finzi, 2011).

Plateau wetlands play an important function in the carbon balance of China (Fan *et al*., 2008; Pei *et al*., 2009). Compared to other ecosystems, plateau wetland ecosystems are more severely impacted by climate change because the wetland organisms in cold and high-elevation environments are more sensitive to temperature (Beniston *et al*., 1997; Kusler, 2007; Xue *et al*., 2014). In most temperate aquatic ecosystems, litter decomposition occurs mainly in winter because the decomposer community is synchronized with the pulse of organic matter entering the aquatic ecosystems in autumn (Giller and Twomey, 1993; Haapala and Muotka, 1998). However, this pattern is different for plateau wetland ecosystems because low temperatures limit the litter decomposition process during winter (Rief *et al*., 2012). Despite the importance of aquatic ecosystems in this region, little is known about the effects of global warming on litter decomposition, which could in turn affect carbon storage in plateau wetlands. In this study, we conducted a litter decomposition experiment using plateau wetland plants along an elevation gradient from 1891 m to 3260 m on the Yunnan Plateau of Southwest China. In this study, we address four questions. How do the decomposition rate and mean residence time of litter vary with elevation? Does litter quality influence the decomposition rate? How sensitive is the litter decomposition of plateau wetland plants to temperature? How much does the microenvironment influence litter decomposition?

2 Materials and Methods

2.1 Study area

We established a litter decomposition experiment along an elevation gradient on the Yunnan Plateau of Southwest China. The Yunnan Plateau (23°N–27°N, 100°E–110°E) is on the southeast of the Qinghai-Tibet Plateau, with elevations ranging from 5000 m in the northwest to less than 1000 m in the southeast. The plateau was the result of the uplift of the Himalayas and Qinghai-Tibet Plateau due to the collision of the Indian subcontinent with the Eurasian Plate. The plateau is characterized by a low-relief upland landscape (relict landscape), and this topography extends from the southeastern margin of the Qinghai-Tibet Plateau toward the South China Sea (Schoenbohm *et al*., 2004; Clark *et al*., 2005). Numerous wetlands are located on this plateau, and they were formed by the long-term solution of calcareous strata. Surrounded by mountains, these wetlands have no channels connecting them to the outside environment, and the surface water in these wetlands only flows underground via funnels; thus, these typical closed and half-closed wetlands are very fragile (Tian *et al*., 2015; Liu *et al*., 2017).

In this study, three sites along an elevation gradient, at 3260 m, 2437 m, and 1891 m above sea level (a.s.l.), were selected to represent a climate gradient (Fig. 1 and Table 1). The first site, at an elevation of 3260 m, is located at the Napahai Wetland Research Station. The mean annual temperature at this site is 6.15℃. The Napahai wetland supports approximately 115 species of wetland plants that belong to 38 families and 82 genera, and it is an important over-wintering and breeding site for migrating birds in China; more than 60 wintering water bird species are found in this area (Liu *et al*., 2016). The second site is located at the Lashihai Wetland Reserve, with an elevation of 2437 m and a mean annual temperature of approximately 12.50℃. The third site with the lowest elevation is located at the Dianchi

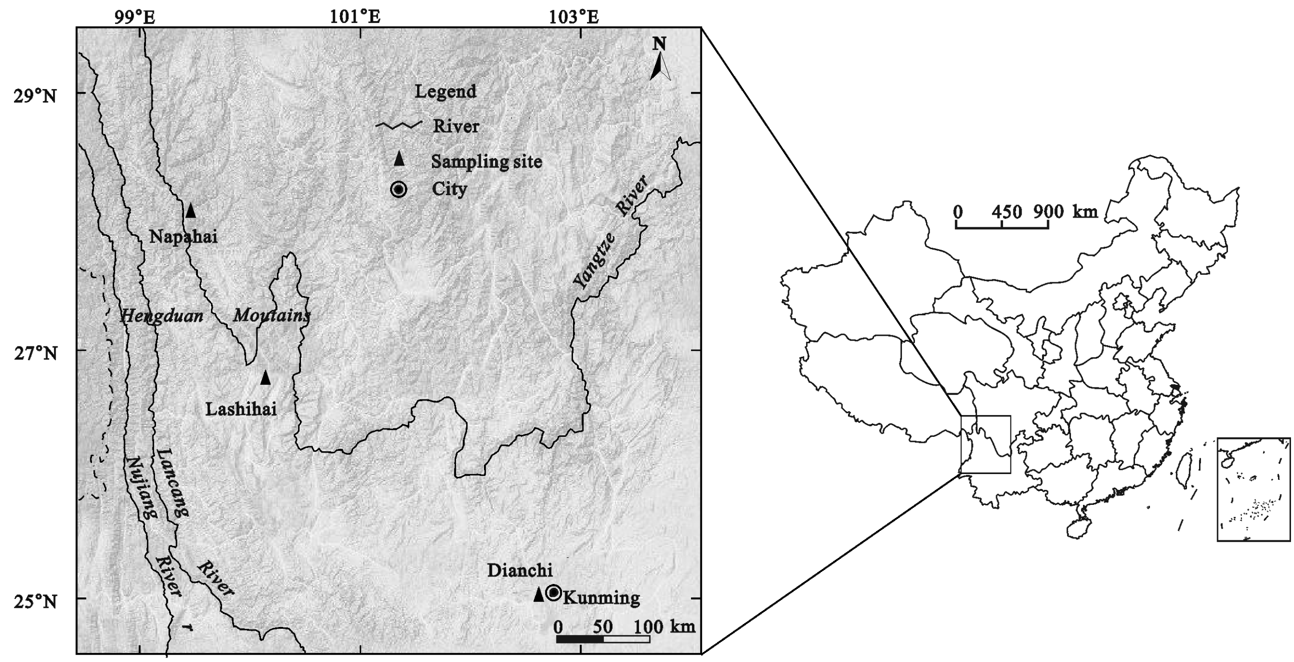

Fig. 1 Locations of study sites along elevation gradient on Yunnan Plateau, China

Table 1 Site characteristics at three sites along elevation gradient

Experimental site	Latitude	Longitude	Elevation (m)	Mean annual precipitation (mm)	Mean annual temperature (℃)
NP	27°52′N	99°41′E	3260	619.9	6.15
LS	26°53′N	100°08′E	2437	1000.0	12.50
DC	25°02′N	102°42′E	1891	584.0	15.80

Notes: NP is Napahai wetland; LS is Lashihai wetland; and DC is Dianchi watershed

Watershed Research Station, with an elevation of 1891 m and a mean annual temperature 15.80℃.

2.2 Experimental design

The study was conducted using a plant-sediment transplant experiment at the three sites: the Napahai wetland (NP), the Lashihai wetland (LS) and the Dianchi watershed (DC). At each experimental site, six identical pools were set up, and each pool was 3.0 m long, 1.5 m wide, and 1.0 m deep. In May 2011, the dominant emergent plants in the Napahai wetland, *Scirpus tabernaemontani* and *Zizania caduciflora,* together with the in situ sediment, were transplanted into the pools of the three sites. Each species of plant was transplanted into three pools, and the depth of sediment in each pool was approximately 50 cm. Each pool was irrigated with tap water, and the depth of water above the sediment was maintained at approximately 25 cm year round. *S. tabernaemontani* and *Z. caduciflora* are both perennial worldwide plants, and therefore, after two years of growth, they adapted to the local climate.

In October 2013, litter samples from these two emergent plants were collected from the pools of the three sites, oven dried (65℃ until a constant weight was reached) and stored at room temperature. Litter samples (single and mixed species treatments) of 8.0 g were placed in 10 cm × 15 cm litterbags of 1.5 mm nylon mesh cloth, and the species mixtures included 4.0 g of each species. In total, 324 litterbags were prepared, with 108 bags from each of the three sites. In November 2013, these litterbags were placed in the original pools of the three sites where the litter samples were collected. Specifically, 162 litterbags were suspended in the water at a depth of 10 cm, and the other 162 litterbags were buried in the sediment at a depth of 5 cm. In addition, all of these litterbags were attached to wooden poles fixed in the sediment using fishing line. Eighteen litterbags were collected from each of the three sites every tow months from January to November 2014. Nine litterbags (3 replicates × 3 litter types) from the water and nine litterbags (3 replicates × 3 litter types) from the sediment were removed during each collection. The retrieved litter was gently cleaned under flowing tap water in the laboratory, oven dried at 65℃ and weighed to determine the remaining litter mass.

2.3 Data calculation and analyses

2.3.1 Sample analyses

The total carbon and total nitrogen of the litter were determined using a Vario EL elemental analyzer. At each of the three sites, the air temperature was measured at 5-min intervals with a Rain Wise Portable Weather Logger (PORTLOG, New York, USA). Meanwhile, the temperatures of the microenvironment in the sediment and water were measured hourly with data loggers (Onset Computer, Pocasset, MA, USA) placed 5 cm below the sediment surface and 10 cm below the water surface.

2.3.2 Calculation of decomposition

A comparison of litter decay rates was performed using the decomposition rate constant (K value) from a negative exponential model: $M_t = M_0 e^{-Kt}$ (Olson, 1963), where M_t is the mass in the litter bags at time t, M_0 is the initial mass in the litterbags and K is the decay constant. The temperature sensitivity of litter mass loss was defined as the relative difference between the litter mass losses (%) at different elevations divided by the annual average temperature difference between the corresponding elevations.

2.3.3 Statistical analyses

The significant differences in the litter decomposition based on the different elevations, species and microenvironments were analyzed using a three-way ANOVA model. Linear regression analysis was performed to test the dependence of the annual average percentage of litter mass losses on the differences in the annual average sediment temperature at 5 cm depth and water temperature at 10 cm depth at different elevations. The relationships between the litter mass losses and chemical contents were tested using a Pearson correlation analysis. All tests discussed in the text were significant at the 0.05 level.

3 Results

3.1 Climatic gradient

As the elevation decreased, the mean annual water temperature at a depth of 10 cm and the mean annual sediment temperature at a depth of 5 cm increased from 8.6℃ and 6.1℃ at the NP site (3260 m a.s.l.) to 13.8℃ and 12.2℃ at the LS site (2437 m a.s.l.) and then to 16.2℃ and 15.6℃ at the DC site (1891 m a.s.l) (Fig. 2). In general, there were significant differences between elevations ($F_{2,69}$ = 50.3, P = 0.002), and the difference between the water temperature and sediment temperature was significant ($F_{1,69}$ = 37.8, P = 0.027), especially at the NP site ($F_{1,22}$ = 85.8, P < 0.001). The observed gradients in the water temperature and sediment temperature at the different sites were mainly due to the variations in the air temperature along the elevation gradient.

3.2 Litter mass remaining and decomposition rates

The decomposition of the three types of litter was significantly different at the NP, LS and DC sites (Fig. 3). The mean mass remaining of the litter were 61.9%, 52.3% and 39.0% for *S. tabernaemontani*, *Z. caduciflora* and mixed species treatments, respectively, at the NP site; 52.6%, 48.6% and 34.1% at the LS site; and 42.4%, 29.9% and 25.0% at the DC site. Overall, the mixed species treatment decomposed more rapidly compared to the *S. tabernaemontani* ($F_{1,34}$ = 26.1, P < 0.001) and *Z. caduciflora* ($F_{1,34}$ = 97.3, P = 0.012) treatments at each of the three sites. In addition, the litter mass loss along the elevation gradient was positively correlated with the water temperature (R^2 = 0.9538, P < 0.001) and sediment temperature (R^2 = 0.9078, P = 0.007) (Fig. 4).

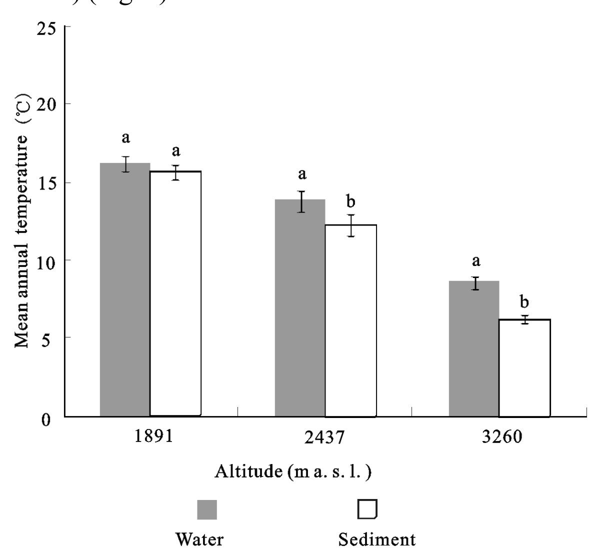

Fig. 2 Changes in mean annual temperature in water at a depth of 10 cm and in sediment at a depth of 5 cm along elevation gradient

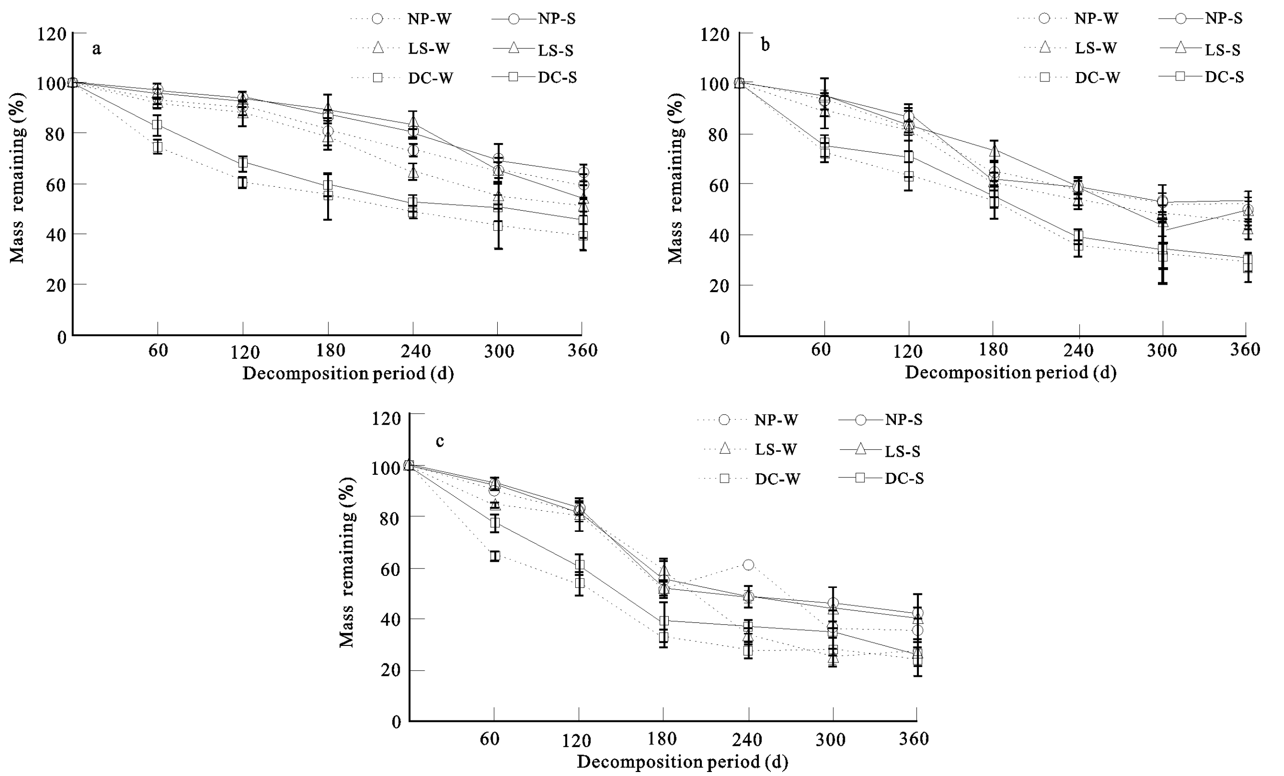

Fig. 3 Changes in litter masses remaining of *S. tabernaemontani* (a), *Z. caduciflora* (b) and mixed species treatments (c) in litterbags. W represents water; S represents sediment; and NP (3260 m), LS (2437 m) and DC (1891 m) represent three experimental sites

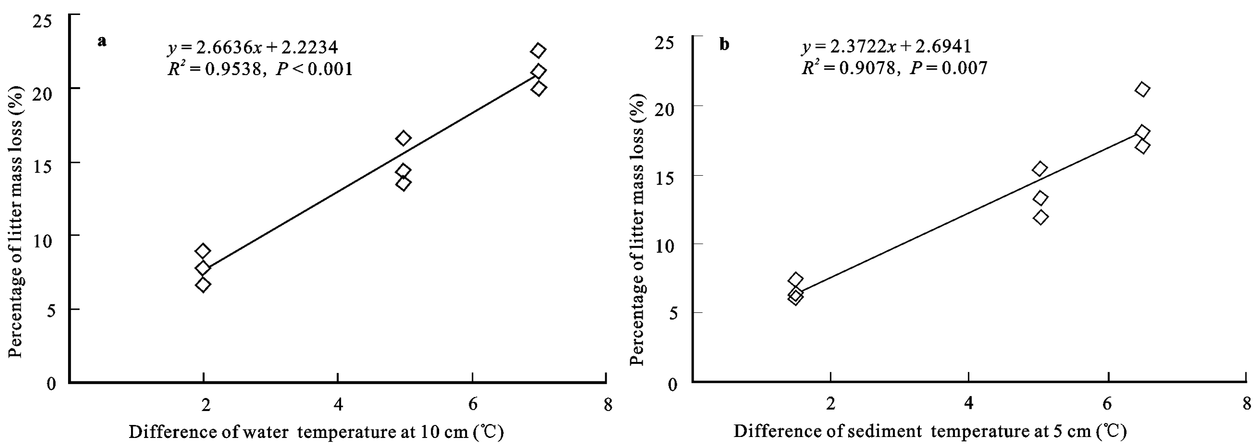

Fig. 4 Temperature sensitivities of litter mass losses (%/℃) in water (a) and sediment (b) along elevation gradient

The variation in the decomposition rate (K) for all litter types at each elevation site is shown in Fig. 5 over the one-year decomposition period. In our study, the average rate of decomposition was lowest (K = 0.608) at NP (3260 m a.s.l.), intermediate (K = 0.888) at LS (2437 m a.s.l.), and highest (K = 1.152) at DC (1891 m a.s.l.), and significant differences were observed between different elevations ($F_{2,51}$ = 13.6, P = 0.003), species ($F_{2,51}$ = 50.6, P < 0.001) and microenvironments ($F_{1,52}$ = 21.3, P = 0.025) (three-way ANOVA, Table 2). The mean value of K increased by 100.1% for *S. tabernaemontani*, 64.1% for *Z. caduciflora* and 120.8% for the mixed species treatment, and this result was consistent with the mass loss rates of the three types of litter. In addition, the litter in the sediment decomposed more slowly than that in the water, especially at the NP site ($F_{1,16}$ = 47.3, P < 0.001).

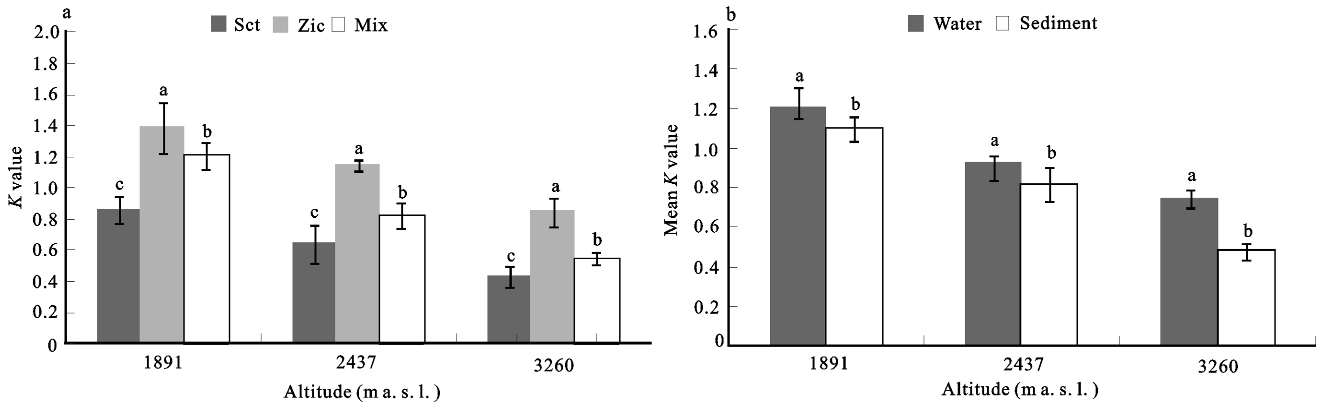

Fig. 5 Litter decomposition rates (*K* values) of different species (a) and mean decomposition rates (*K* values) of the three types of litter in different microenvironments (b) along the elevation gradient. Sct, Zic and Mix represent the three types of litter: *S. tabernaemontani*, *Z. caduciflora* and mixed species treatment, respectively; a.s.l. represent above sea level.

Table 2 Results of three-way ANOVA: effects of elevations (*E*), species (*S*), microenvironments (*M)* and their interactions on litter decomposition rate (*K* value)

Sources of deviation	*E*	*S*	*M*	*E* × *S*	*E* × *M*	*S* × *M*	*E* × *S* × *M*
df	2	2	1	4	3	3	5
F	13.6	50.6	21.3	16.5	24.0	33.4	14.7
P	0.003	<0.001	0.025	0.009	0.032	0.014	0.063

3.3 Litter chemistry

Overall, after litter decomposition, the C concentration and C∶N ratio decreased significantly, with the decreases of 22.8% ($F_{1,106}$ = 23.5, P = 0.018) and 52.7% ($F_{1,106}$ = 112.3, P = 0.006), respectively; however, the concentration of N increased significantly by 64.7% ($F_{1,106}$ = 23.5, P < 0.001) (Fig. 6). In addition, the C∶N ratio of the litter in the water was slightly lower than that in the sediment during decomposition, and the difference was not significant ($F_{1,52}$ = 45.5, P = 0.079), but the N concentration in the water was significantly higher than that in the sediment ($F_{1,52}$ = 18.1, P = 0.002).

After one year of decomposition, the C∶N ratio of the mixed species treatment at the NP site was 19.7, which was lower than those of *S. tabernaemontani* (35.2) and *Z. caduciflora* (25.3) ($F_{1,34}$ = 11.2, P = 0.003). Meanwhile, as the elevation decreased, the difference in the C∶N ratio between the mixed species treatment and the other two species increased. In general, all three types of litter at low elevations had low C concentrations, low C∶N ratios and high N concentrations.

4 Discussion

4.1 Climatic gradient effects

Elevation gradients can be considered natural, long-term analogues for climate change, and the loss of litter mass as mediated by temperature has been corroborated by natural gradient studies (Berg *et al*., 1993; Vitousek *et al*., 1994; Murphy *et al*., 1998; Aerts, 2006). As the elevation decreased, the mean values of *K* ranged from 0.608 to 1.152 (Fig. 5), indicating the strong influence of elevation on the decomposition rate. In our study, the temperature change explained approximately 93% of the variation in the losses of litter mass, and the temperature sensitivity of the litter mass losses was approximately 4.98%/℃ (Fig. 4), which was close to the study result (6%/℃) of Luo *et al*. (2010) on the Qinghai-Tibet Plateau. Litter decomposition is an ecological process governed by decomposer organisms, and therefore, an increase in temperature will likely stimulate litter decomposition by creating conditions favorable for decomposer populations and activity (Davidson and Janssens, 2006; Chacon and Dezzeo, 2007; Cusack *et al*., 2009).

The decomposition of plant litter, especially in cold biomes, is hierarchically controlled by the following factors: climate > litter quality > sediment organisms (Aerts, 2006). Meanwhile, temperature and moisture in combination are the most important climatic controls that affect litter decomposition rates, and litter mass loss will increase in a warming environment if the sediment moisture is sufficiently high (Berg *et al*., 1993; Murphy

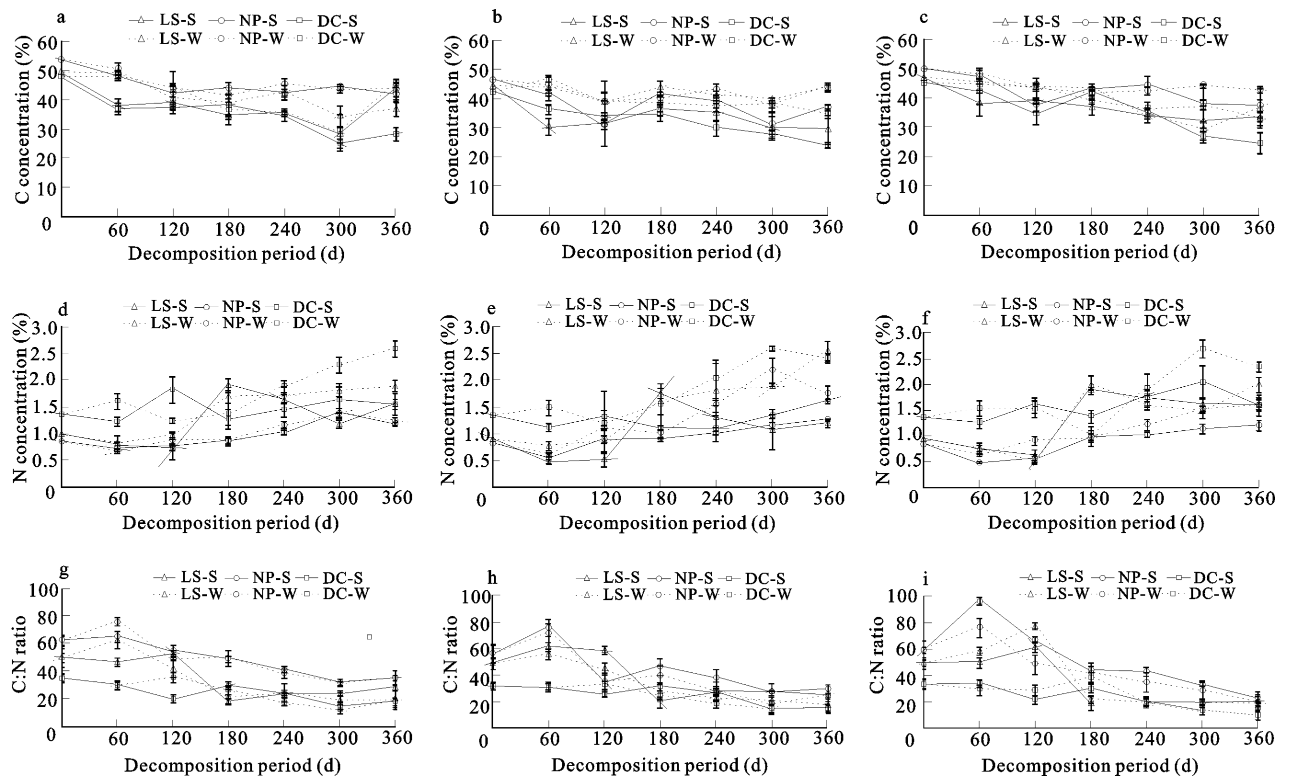

Fig. 6 Concentrations of C and N and C∶N ratio in *S. tabernaemontani* (a, d, g), *Z. caduciflora* (b, e, h) and mixed species treatment (c, f, i) at three sites during decomposition process. W represents water; S represents sediment; and NP (3260 m), LS (2437 m) and DC (1891 m) represent three experimental sites

et al., 1998; Gholz *et al*., 2000). Because the decomposition of aquatic plants in plateau wetlands mainly occurs in the water or in the sediment, where moisture is sufficient, the litter mass loss in plateau wetlands will likely increase with future climate warming. This finding was confirmed by Guo *et al*. (2013), who found that the decomposition rates of *S. tabernaemontani* and *Z. caduciflora* in the Napahai plateau wetland increased with increasing monthly mean temperature. Recently, Boyero *et al*. (2011) conducted a global litter decomposition experiment using a latitudinal temperature gradient in streams. Although the interpretation of latitudinal gradients is complex, they found that climate warming will reduce carbon sequestration in streams because CO_2 production through litter decomposition will increase with climate warming (Seastedt, 1984; Baldy *et al*., 2007), while the generation and sequestration of recalcitrant organic particles could be reduced (Yoshimura *et al*., 2008).

4.2 Litter chemistry effects

The N concentration and C∶N ratio of the litter have been identified as the most reliable predictors of litter decomposition (Berg *et al*., 1982; Taylor *et al*., 1989; Blair *et al*., 1990; Aerts and De Caluwe, 1997; Shaw and Harte, 2001). Generally, good litter quality, with a high initial N concentration (Bosatta and Staaf, 1982) and low initial C∶N ratio (Swift *et al*., 1979; Holub *et al*., 2001) yields a fast decomposition rate. In our study, the litter of *Z. caduciflora*, which had a low initial C∶N ratio, lost mass more quickly than did the litter of *S. tabernaemontani*, and this effect has been observed in other mesic systems (Taylor *et al*., 1989; Luo *et al*., 2010). Litter decomposition can be divided into two phases. The early phase (before 20% to 40% of the mass loss) is mainly determined by the litter chemistry, while the later phase (after 20% to 40% of the mass loss) is mainly controlled by the decomposition of lignin and the microbial community (Berg and McClaughtery, 2008; Bray *et al*., 2012; Gavazov *et al*., 2014). Therefore, in the early phase, the litter of *S. tabernaemontani*, which had a high C∶N ratio and poor litter quality, decomposed slower than the other two types of litter.

In our study, litter decomposition could be described as seasonal. Notably, decay generally occurs from winter to the late growing season, as a majority of the labile material is decomposed by freezing and thawing events during the winter (Hobbie and Chapin, 1996). This variation in the decomposition rate, which shifts from low to high, was consistent with the change in the C∶N ratio in the early phase, which increased slightly and then decreased (Fig. 6). These findings have been confirmed by the studies of Coûteaux *et al*. (1995) and Duboc *et al*. (2012), who found that in addition to litter chemistry, climate might also influence the decomposition rate in the early phase of decomposition. Meanwhile, in our study, the litter quality was highly correlated with the decomposition rates at the high-elevation site (NP), especially the N concentration and C∶N ratio (Table 3). Theoretically, the low temperatures in high-elevation regions seriously limit the processes involved in organic matter cycling; however, the physical and chemical losses of organic compounds from leaching and other processes related to the duration of freezing and thawing may change the litter quality and contribute to litter decomposition (Taylor *et al*. 1989; Hobbie and Chapin, 1996; Edwards *et al*., 2007). Therefore, the litter quality plays an important role in controlling decomposition and determining decomposer activity in high-elevation regions (Moorhead and Sinsabaugh, 2006; Bray *et al*., 2012; Liu *et al*., 2017).

During the one-year decomposition period, litter mass losses were significantly positively correlated with the N concentration but were significantly negatively correlated with the C∶N ratio, which is broadly consistent with the results of other studies of litter decomposition (Aerts, 2006; Jacob *et al*., 2010; Gavazov *et al*., 2014) (Table 3). Meanwhile, the correlation between the litter mass loss and litter chemistry of the mixed species treatment was higher than those of *S. tabernaemontani* and *Z. caduciflora* because the decomposition rate of the mixed species treatment was significantly higher than those of the other two species. Mixed litters have different chemical and physical properties that alter the resource quality and physical habitat complexity within leaf packs, resulting in changes in decomposition rates and decomposer abundance and activity (Hector *et al*., 2000; Kominoski *et al*., 2007). Mass loss often increases when litters of different species are mixed, mainly due to nutrient transfer between the decomposing species, which is mediated by fungal mycelia (Gartner and Cardon, 2004; Quested *et al*., 2005). Therefore, in addition to litter decomposition, the nutrient transfers in the mixed litter became more frequent and more convenient, and the synergistic effects of the decomposition rates became more significant in the mixed litter than in the treatments of the other two species (Williamsa and Alexandera, 1991; Antoine and Bill, 2015). In addition, in the studied cold-region plateau wetlands, future climate warming may increase the carbon losses from the litter of aquatic plants, especially from mixed litter.

4.3 Microenvironment effects

Climate and litter quality are considered the most important controls of litter decomposition rates at global and regional scales (Aerts, 2006; Gavazov, 2010), while at the local scale, with nearly uniform climate and litter quality, the effects of the microenvironment are more important (Belyea, 1996; Hector *et al*., 2000). The microenvironment affects litter decomposition mainly through changes in physical environmental variables such as temperature, moisture and pH (Hobbie *et al*., 1999) or through changes in the decomposer community, which includes bacteria, fungi and arthropods

Table 3 The relationship coefficients (*r* values) between litter mass loss and chemical contents during one year of litter decomposition

Experimental site (evelvation)	Microenvironment	C			N			C∶N		
		Sct	Zic	Mix	Sct	Zic	Mix	Sct	Zic	Mix
NP (3260 m)	Water	–0.694	–0.461	–0.654*	0.868*	0.838*	0.930**	–0.871*	–0.814*	–0.936**
	Sediment	–0.646	–0.461	–0.647	0.801**	0.766*	0.846*	–0.863**	–0.760*	–0.906*
LS (2437 m)	Water	–0.430*	–0.251	–0.548*	0.728**	0.819**	0.886*	–0.754*	–0.838**	–0.886*
	Sediment	–0.280	–0.429	–0.588	0.395	0.716	0.740	–0.570	–0.801**	–0.810*
DC (1891 m)	Water	–0.632	–0.766*	–0.815*	0.678	0.701	0.690	–0.698*	–0.707	–0.748*
	Sediment	–0.665*	–0.625*	–0.533*	0.392	0.761	0.703	–0.813	–0.668*	–0.732*

Notes: NP, LS and DC represent three experimental sites, and Sct, Zic and Mix represent three types of litter: *S. tabernaemontani*, *Z. caduciflora* and mixed species. * and ** represent significance at 0.05 and 0.01 levels, respectively

(Blair *et al*., 1990; Wardle and Lavelle, 1997; Wardle *et al*., 1997).

In our study, the litter decomposition rate in the water was generally higher than that in the sediment, especially in cold biomes (Fig. 5b). The first reason for this result is that mass loss is dominated by leaching and the decomposition of carbohydrates in the early decomposition phase, and the transfer of soluble compounds is a major driver (Berg and McClaugherty, 2008). Therefore, although the moisture in the sediment at a depth of 5 cm is sufficient, the leaching, decomposition and transfer were still slightly weaker than in the water, and this difference affected the litter decomposition rate in the two microenvironments. Second, the late decomposition phase is mainly driven by the composition of the microbial community (Bray *et al*., 2012; Gavazov *et al*., 2014), and the redox potential of saturated environments generally decreases from the surface downward. Therefore, the oxidation of carbon substrates shifts from aerobic processes to sulfate reduction and, finally, to methanogenesis, with a consequent decrease in the decomposition rate (Belyea, 1996). Third, the temperature of the water at a depth of 10 cm was higher than that of the sediment at a depth of 5 cm, and this difference directly affected the microbial communities and litter chemistry, which improved the decomposition rate (Cusack *et al*., 2009; Bray *et al*., 2012). Therefore, in addition to the large difference in temperature in the two microenvironments at the site with the highest elevation (Fig. 2), the difference in the decomposition rate was more significant (Fig. 5b). This result suggests that litter decomposition in cold biomes is sensitive to changes in the microenvironment and further confirms that the influence of elevated temperature will be more pronounced in high-elevation areas that are additionally stressed by extreme climatic conditions (Aerts, 2006).

4.4 Uncertainties and future work

The decomposition of plant litter is a key and complex ecosystem process that is controlled by many factors (Robinson, 2002; Berg and McClaughtery, 2008). In addition to the above-mentioned factors, the decomposer communities (such as microbial decomposers and shredders), water quality and sediment nutrients can affect the decomposition of litter. For example, environmental temperature changes can directly affect decomposer communities and their activities (Cusack *et al*., 2009; Bray *et al*., 2012); however, Gavazov *et al*. (2014) suggested that the functional composition of decomposer microbial communities (fungal/bacterial ratio) was insensitive to elevation. Therefore, in future studies, we will consider all these factors to more thoroughly and comprehensively understand the influences of global climate warming on litter decomposition in plateau wetlands.

5 Conclusions

Our study showed that temperature increases along a declining elevation gradient can significantly increase litter mass losses, which suggests that global warming will increase litter decomposition in plateau wetlands. The variations in the litter chemistry at different elevations and between different litter types were used to determine that the N concentrations and C∶N ratios in the litter were the best predictors of the decomposition rate. In addition to the climate and litter quality, the microenvironment can also affect litter decomposition, especially in high-elevation areas. Moreover, our results may have important implications for addressing biogeochemical nutrient cycling in cold highland ecosystems. Although the approach based on natural climate gradients cannot separate the effects of temperature on litter mass losses from those of other factors, the relative comparison between the temperature sensitivity and litter mass losses should be credible. Therefore, our study may have important implications for predictions of future changes in litter decomposition in plateau wetlands and possibly other cold regions under global warming scenarios.

Acknowledgements

We acknowledge the teachers and students in the Environment Science and Engineering Laboratory of the Southwest Forestry University, for their help during field work.

References

Aerts R, 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: triangular relationship. *Oikos*, 79(3): 439–449. doi: 10.2307/3546886

Aerts R, 2006. The freezer defrosting: Global warming and litter decomposition rates in cold biomes. *Journal of Ecology*, 94(4): 713–724. doi: 10.1111/j.1365-2745.2006.01142.x

Aerts R, De Caluwe H, 1997. Nutritional and plant mediated controls on leaf litter decomposition of *Carex* species. *Ecology*, 78(1): 244–260. doi: 10.2307/2265993

Antoine T, Bill S, 2015. The relationship between functional dispersion of mixed-species leaf litter mixtures and species' interactions during decomposition. Oikos, 124(8): 1050–1057. doi: 10.1111/oik.01686

Averill C, Finzi A, 2011. Increasing plant use of organic nitrogen with elevation is reflected in nitrogen uptake rates and ecosystem $\delta^{15}N$. *Ecology*, 92(4): 883–891. doi: 10.1890/10-0746.1

Baldy V, Gobert V, Guerold F *et al*., 2007. Leaf litter breakdown budgets in streams of various trophic status: effects of dissolved inorganic nutrients on microorganisms and invertebrates. *Freshwater Biology*, 52(7): 1322–1335. doi: 10.1111/j.1365-2427.2007.01768.x

Belyea L R, 1996. Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. *Oikos*, 77(3): 529–539. doi: 10.2307/3545942

Beniston M, Diaz H F, Bradley R S, 1997. Climatic change at high elevation sites: an overview. *Climatic Change*, 36(3–4): 233–251. doi: 10.1023/A:1005380714349

Berg B, Wessen B, Ekbohm G, 1982. Nitrogen level and decomposition in Scots pine needle litter. *Oikos*, 38(3): 291–296. doi: 10.2307/3544667

Berg B, Berg M P, Bottner P *et al*., 1993. Litter mass loss rates in pine forests of Europe and eastern United States: some relationships with climate and litter quality. *Biogeochemistry*, 20(3): 127–159.

Berg B, McClaugherty C, 2008. *Plant Litter*: *Decomposition*, *Humus ormation*, *Carbon Sequestration*. Heidelberg: Springer Verlag. doi: 10.1007/978-3-662-05349-2

Blair J M, Parmelee R W, Beare M H, 1990. Decay rates, nitrogen fluxes, and decomposer communities of single- and mixed-species foliar litter. *Ecology*, 71(5): 1976–1985. doi: 10.2307/1937606

Bonanomi G, Incerti G, Giannino F *et al*., 2013. Litter quality assessed by solid state C-13 NMR spectroscopy predicts decay rate better than C/N and Lignin/N ratios. *Soil Biology & Biochemistry*, 56: 40–48. doi: 10.1016/j.soilbio.2012.03.003

Bosatta E, Staaf H, 1982. The control of nitrogen turn-over in forest litter. *Oikos*, 39(2): 143–151. doi: 10.2307/3544478

Boyero L, Pearson R G, Gessner M O *et al*., 2011. A global experiment suggests climate warming will not accelerate litter decomposition in streams but might reduce carbon sequestration. *Ecology Letters*, 14(3): 289–294. doi: 10.1111/j.1461-0248.2010.01578.x

Bray S R, Kitajima K, Mack M C, 2012. Temporal dynamics of microbial communities on decomposing leaf litter of 10 plant species in relation to decomposition rate. *Soil Biology & Biochemistry*, 49: 30–37. doi: 10.1016/j.soilbio.2012.02.009

Cadish G, Giller K E, 1997. *Driven by Nature, Plant Litter Quality and Decomposition*. Wallingford: CAB International.

Chacon N, Dezzeo N, 2007. Litter decomposition in primary forest and adjacent fire-disturbed forests in the Gran Sabana, southern Venezuela. *Biology and Fertility of Soils*, 43(6): 815–821. doi: 10.1007/s00374-007-0180-3

Clark M K, House M A, Royden L H *et al*., 2005. Late Cenozoic uplift of southeastern Tibet. *Geology*, 33(6): 525–528. doi: 10.1130/g21265.1

Couteaux M M, Bottner P, Berg B, 1995. Litter decomposition, climate and litter quality. *Trends in Ecology and Evolution*, 10(2): 63–66. doi: 10.1016/S0169-5347(00)88978-8

Cusack D F, Chou W W, Yang W H *et al*., 2009. Controls on long-term root and leaf litter decomposition in neotropical forests. *Global Change Biology*, 15(5): 1339. doi: 10.1111/j.1365-2486.2008.01781.x

Davidson E A, Janssens I A, 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, 440(7081): 165–173. doi: 10.1038/nature04514

Duboc O, Zehetner F, Djukic I *et al*., 2012. Decomposition of European beech and Black pine foliar litter along an Alpine elevation gradient: mass loss and molecular characteristics. *Geoderma*, 189–190: 522–531. doi: 10.1016/j.geoderma.2012.06.018

Dunne J, Saleska S, Fisher M *et al*., 2004. Integrating experimental and gradient methods in ecological climate change research. *Ecology*, 85(4): 904–916. doi: 10.1890/03-8003

Edwards A C, Scalenghe R, Freppaz M, 2007. Changes in the seasonal snow cover of alpine regions and its effect on soil processes: a review. *Quaternary International*, 162: 172–181. doi: 10.1016/j.quaint.2006.10.027

Fan J W, Zhong H P, Harris W *et al*., 2008. Carbon storage in the grasslands of China based on field measurements of above-and below-ground biomass. *Climate Change*, 86(3–4): 375–396. doi: 10.1007/s10584-007-9316-6

Gartner T B, Cardon Z G, 2004. Decomposition dynamics in mixed-species leaf litter. *Oikos*, 104(2): 230–246. doi: 10.1111/j.0030-1299.2004.12738.x

Gavazov K, Mills R, Spiegelberger T *et al*., 2014. Biotic and abiotic Constraints on the decomposition of Fagus sylvatica leaf litter along an altitudinal gradient in contrasting land-use types. *Ecosystems*, 17(8): 1326–1337. doi: 10.1007/s10021-014-9798-9

Gavazov K S, 2010. Dynamics of alpine plant litter decomposition in a changing climate. *Plant and Soil*, 337(1–2): 19–32. doi: 10.1007/s11104-010-0477-0

Gholz H L, Wedin D A, Smitherman S M *et al*., 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Global Change Biology*, 6(7): 751–765. doi: 10.1046/j.1365-2486.2000.00349.x

Giller P S, Twomey H, 1993. Benthic macroinvertebrate community organisation in two contrasting rivers: between-site differences and seasonal patterns. *Biology and Environment: Proceedings of the Royal Irish Academy*, 93B(3): 115–126.

Guo Xuhu, Xiao Derong, Tian Kun *et al*., 2013. Biomass production and litter decomposition of lakeshore plants in Napahai wetland, Northwestern Yunnan Plateau, China. *Acta Ecologica Sinica*, 33(5): 1425–1432. (in Chinese)

Haapala A, Muotka T, 1998. Seasonal dynamics of detritus and associated macroinvertebrates in a channelized boreal stream. *Archiv Fur Hydrobiologie*, 142(2): 171–189. doi: 10.1127/archiv-hydrobiol/142/1998/171

Hector A, Beale A J, Minns A *et al*., 2000. Consequences of the reduction of plant diversity for litter decomposition: effects through litter quality and microenvironment. *Oikos*, 90(2): 357–371. doi: 10.1034/j.1600-0706.2000.900217.x

Hobbie S E, 2000. Interactions between litter lignin and soil nitrogen availability during leaf litter decomposition in a Hawaiian montane forest. *Ecosystems*, 3(5): 484–494. doi: 10.1034/j.1600-0706.2000.900217.x

Hobbie S E, Chapin F S, 1996. Winter regulation of tundra litter carbon and nitrogen dynamics. *Biogeochemistry*, 35(2): 327–338. doi: 10.1007/BF02179958

Hobbie, S E, Shevtsova A, Chapin F S I, 1999. Plant responses to species removal and experimental warming in Alaskan tussock tundra. *Oikos*, 84(3): 417–434. doi: 10.2307/3546421

Holub S M, Spears J D H, Lajtha K, 2001. A reanalysis of nutrient dynamics in coniferous coarse woody debris. *Canadian Journal of Forest Research*, 31(11): 1894–1902. doi: 10.1139/x01-125

IPCC (Intergovernmental Panel on Climate Change), 2014. *Climate Change 2014 Synthesis Report Summary for Policymakers*. Geneva, Switzerland.

Jacob M, Viedenz K, Polle A *et al*., 2010. Leaf litter decomposition in temperate deciduous forest stands with a decreasing fraction of beech (*Fagus sylvatica*). *Oecologia*, 164(4): 1083. doi: 10.1007/s00442-010-1699-9

Kominoski J S, Pringle C M, Ball B A *et al*., 2007. Nonadditive effects of leaf litter species diversity on breakdown dynamics in a detritus-based stream. *Ecology*, 88(5): 1167–1176. doi: 10.1890/06-0674

KÖrner C, 2007. The use of 'altitude' in ecological research. *Trends in Ecology and Evolution*, 22(11): 569–574. doi: 10.1016/j.tree.2007.09.006

Kusler J, 2007. *Common Questions*: *Wetland*, *Climate Change*, *and Carbon Sequestering*. Association of State Wetland Managers.

Liu G D, Sun J F, Tian K *et al*., 2017. Long term responses of leaf litter decomposition to temperature, litter quality and litter mixing in plateau wetlands . *Freshwater Biology*, 62(1): 178–190. doi: 10.1111/fwb.12860.

Liu G D, Tian K, Sun J F *et al*., 2016. Evaluating the effects of wetland restoration at the watershed scale in Northwest Yunnan Plateau, China. *Wetlands*, 36(1): 169–183. doi: 10.1007/s13157-015-0727-2

Luo C Y, Xu G P, Chao Z G *et al*., 2010. Effect of warming and grazing on litter mass loss and temperature sensitivity of litter and dung mass loss on the Tibetan plateau. *Global Change Biology*, 16(5): 1606–1617. doi: 10.1111/j.1365-2486.2009.02026.x

Malhi Y, Silman M, Salinas N *et al*., 2010. Introduction: Elevation gradients in the tropics: laboratories for ecosystems ecology and global change research. *Global Change Biology*, 16(12): 3171–3175. doi: 10.1111/j.1365-2486.2010.02323.x

Meentemeyer V, 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology*, 59(3): 465–472. doi: 10.2307/1936576

Moorhead D L, Sinsabaugh R L, 2006. A theoretical model of litter decay and microbial interaction. *Ecological Monographs*, 76(2): 151–174. doi: 10.1890/0012-9615(2006)076%5B0151:ATMOLD%5D2.0.CO;2

Murphy K L, Klopatek J M, Klopatek C C, 1998. The effects of litter quality and climate on decomposition along an elevational gradient. *Ecological Applications*, 8(4): 1061–1071. doi: 10.1890/1051-0761(1998)008%5B1061:TEOLQA%5D2.0.CO;2

Olson J S, 1963. Energy-storage and balance of producers and decomposers in ecological-systems. *Ecology*, 44(2): 322–331. doi: 10.2307/1932179

Pei Z Y, Ouyang H, Zhou C P *et al*., 2009. Carbon balance in an alpine steppe in the Qinghai-Tibet plateau. *Journal of Integrative Plant Biology*, 51(5): 521–536. doi: 10.1111/j.1744-7909.2009.00813.x

Pellissier L, Fournier B, Guisan A *et al*., 2010. Plant traits co-vary with altitude in grasslands and forests in the European Alps. *Plant Ecology*, 211(2): 351. doi: 10.1007/s11258-010-9794-x

Quested H M, Callaghan T V, Cornelissen J H C *et al*., 2005. The impact of hemiparasitic plant litter on decomposition: direct, seasonal and litter mixing effects. *Journal of Ecology*, 93(1): 87–98. doi: 10.1111/j.0022-0477.2004.00951.x

Rief A, Knapp B A, Seeber J, 2012. Palatability of selected alpine plant litters for the decomposer *Lumbricus rubellus* (Lumbricidae). *Plos One*, 7(9): e45345. doi: 10.1371/journal.pone.0045345

Robinson C H, 2002. Controls on decomposition and soil nitrogen availability at high latitudes. *Plant and Soil*, 242(1): 65–81. doi: 10.1023/A:1019681606112

Salinas N, Malhi Y, Meir P *et al*., 2011. The sensitivity of tropical leaf litter decomposition to temperature: results from a large-scale leaf translocation experiment along an elevation gradient in Peruvian forests. *New Phytologist*, 189(4): 967–977. doi: 10.1111/j.1469-8137.2010.03521.x

Schoenbohm L M, Whipple K X, Burchfiel B C *et al*., 2004. Geomorphic constraints on surface uplift, exhumation, and plateau growth in the Red River region, Yunnan Province, China. *Geological Society of America Bulletin*, 116(7–8): 895–909. doi: 10.1130/B25364.1

Seastedt T R, 1984. The role of microarthropods in decomposition and mineralization processes. *Annual Review of Entomology*, 29: 25–46. doi: 10.1146/annurev.en.29.010184.000325

Shaw M R, Harte J, 2001. Control of litter decomposition in a subalpine meadow-sage brush steppe ecotome under climate change. *Ecological Applications*, 11(4): 1206–1223. doi: 10.2307/3061022

Swift, M J, Heal O W, Anderson J M, 1979. *Decomposition in Terrestrial Ecosystems*. Berkeley: University of California Press.

Taylor B R, Parkinson D, Parsons W F J, 1989. Nitrogen and lignin content as predictors of litter decay rates: A microcosm test. *Ecology*, 70(1): 97–104. doi: 10.2307/1938416

Tian K, Liu G D, Xiao D R *et al*., 2015. Ecological effects of Dam impoundment on closed and half-closed wetlands in China. *Wetlands*, 35(5): 889–898. doi: 10.1007/s13157-015-0679-6

van de Weg M J, Meir P, Grace J *et al*., 2009. Altitudinal variation in LMA, leaf tissue density and foliar nitrogen and phosphorus along an Andes–Amazon gradient in Peru. *Plant Ecology and Diversity*, 2(3): 243–254. doi: 10.1080/17550870903518045

Vitousek P, Turner D, Parton W *et al*., 1994. Litter decomposition on the Mauna Loa environmental matrix, Hawaii: Patterns, mechanisms and models. *Ecology*, 75(2): 418–429. doi: 10. 2307/1939545

Wardle D A, Lavelle P, 1997. Linkages between soil biota, plant litter quality and decomposition. In: Cadish G and Giller K E (eds.). *Driven by Nature*: *Plant Litter Quality and Decomposition*. Wallingford: CAB International, 107–123.

Wardle D A, Bonner K I, Nicholson K S, 1997. Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. Oikos, 79(2): 247–258. doi: 10.2307/3546010

Williamsa B L, Alexandera C E, 1991. Interactions on mixing litters from beneath Sitka spruce and Scots pine and effects on microbial activity and N-mineralization. *Soil Biology and Biochemis*try, 23(1): 71–75. doi: 10.1016/0038-0717(91)90164-F

Xue Z S, Zhang Z S, Lu X G *et al*., 2014. Predicted areas of potential distributions of alpine wetlands under different scenarios in the Qinghai-Tibetan Plateau, China. *Global and Planetary Change*, 123(A): 77–85. doi: 10.1016/j.gloplacha.2014.10.012

Yoshimura C, Gessner M O, Tockner K *et al*., 2008. Chemical properties, microbial respiration, and decomposition of coarse and fine particulate organic matter. *Journal of the North American Benthological Society*, 27(3): 664–673. doi: 10. 1899/07-106.1