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Non-additive effect of species diversity and temperature sensitivity of mixed litter decomposition in the alpine meadow on Tibetan Plateau

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ABSTRACT

Few studies of the effects of litter diversity on the temperature sensitivity of mixed litter mass loss (MLML) are available. We tested the hypothesis that high litter diversity would reduce the magnitude of effects of climate and environmental change on MLML with 0.5/1 mm litter bags and sampling once after 1 yr of decomposition, using 51 combinations of litter mixtures from 25 dominant species at 3200 and 3800 m elevations on the Tibetan Plateau. Generally, our study supported our hypothesis. High temperature (i.e. lower elevation) reduced the dependency of MLML and non-additive effects on species richness. Species composition significantly affected MLML and its Q_{10} (i.e. the ratio of litter mass loss rate at a temperature T_1 that is 10 °C lower than a temperature T_2) when species richness was less than 8. Shrubs significantly decreased the Q_{10} of MLML when the species richness of litter mixture was less than 4. These findings suggest that the influence of future warming on MLML may depend on the balance between the magnitude of the impacts of climate change on shrub invasion and loss of species diversity in alpine region.

1. Introduction

The relationship between biodiversity and ecosystem function has received a great deal of attention due to increasing global species decline (Loreau et al., 2002; Tilman et al., 2006; Meier and Bowman, 2008; Srivastava et al., 2009). Although effects (i.e. non-additive effects) of litter diversity (i.e. species richness and composition) on mixed litter mass loss (MLML) have been observed in terrestrial ecosystems (Wardle et al., 1997; Kaneko and Salamanca, 1999; Hector et al., 2000; Hättenschwiler et al., 2005; Srivastava et al., 2009) and in aquatic ecosystems (Gessner et al., 2004; LeRoy and Marks, 2006; Moore and Fairweather, 2006; Lecerf et al., 2007; Kominoski et al., 2007; Schindler and Gessner, 2009; Swan et al., 2009; Rosemond et al., 2010), no general relationship exists between litter species diversity and MLML, as both synergistic and antagonistic effects may result in an overall neutral trend (Gartner and Cardon, 2004; Hättenschwiler et al., 2005; Srivastava et al., 2009). The relative uncertainty of litter diversity effects on MLML may be due to differences in climate and environmental conditions, experimental design and choice of litter species (Gartner and Cardon, 2004; Hättenschwiler et al., 2005; LeRoy and Marks, 2006; Srivastava et al., 2009; Rosemond et al., 2010). Therefore, a broad comparison among studies should be interpreted with great caution (Hättenschwiler et al., 2005). In particular, grassland ecosystems are critically underrepresented because few studies on the effects of litter mixture on decomposition have previously been reported for alpine ecosystems (Hector et al., 2000; Gartner and Cardon, 2004).

Global warming and associated environmental changes are predicted to affect most regions of the northern hemisphere and

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will be peculiarly pronounced at high northern latitudes and high elevation during this century (ACIA, 2005; IPCC, 2007). Warming increased invasion of shrubs in the alpine region (Klein et al., 2007); and decomposition of shrub litters was lower which had higher temperature sensitivity of decomposition (Xu et al., 2010). In particular, litter decomposition rates may change owing to the shifts of species composition and lower litter quality induced by climate change (Cornelissen et al., 2007) which may alters microbial activity (Henry et al., 2005; Parton et al., 2007). Some results have been reported on the potential responses of single species litter decomposition to climate change (Murphy et al., 1998; Liski et al., 2003; Fierer et al., 2005; Cornelissen et al., 2007; Xu et al., 2010). However, recent results show that single species litter decomposition may not adequately represent natural ecosystems where litter from multiple species decomposes together (Gartner and Cardon, 2004; Hăttenschwiler et al., 2005), because litter interactions may alter the response of decomposition rates extrapolated from single-species studies to climate change. Moreover, a lack of experiments with the same litter species richness under different climate conditions limits our understanding of the response of litter decomposition to future climate change. Therefore, evaluating the overall response of decomposition in mixed species litter to climate and environmental changes is critical to our understanding of litter decomposition and for modeling carbon and nutrient processes in terrestrial ecosystems under future climate change.

The objective of this study was to test the hypothesis that high litter diversity reduced the effect of warming on MLML. To meet this objective, the study involved 25 dominant litter species and 51 combinations of litter mixtures at five species richness levels at two elevations (i.e. 3200 and 3800 m a.s.l.) on the Tibetan Plateau. Our study addressed the following four hypotheses: 1) the dependencies of MLML and non-additive effects on litter species richness differ under different environmental conditions; 2) high litter species richness reduces the temperature sensitivity of MLML (i.e. Q_{10}, the ratio of litter mass loss rate at a temperature T_1 that is 10 °C lower than a temperature T_2); 3) non-additive effects of MLML vary with species composition and elevation; and 4) the effect of species composition, especially for shrubs, on the Q_{10} value decreases with increasing litter species richness.

2. Materials and methods

2.1. Experimental site

The experimental site is located at the Haibei Alpine Meadow Ecosystem Research Station (HBAMERS), a facility run by the Northwest Institute of Plateau Biology of the Chinese Academy of Sciences. HBAMERS is situated at latitude 37° 37′N, longitude 101° 12′E. The station lies in the northeast of the Tibetan Plateau in a large valley surrounded by the Qilian Mountains. The station experiences a typical plateau continental climate which is dominated by the southeast monsoon from May to September in summer and high pressure from Siberia in winter. Summers are short and cool, and winters are long and severely cold. Mean annual temperature is −2 °C, and mean annual precipitation is 500 mm, over 80% of which falls during the summer monsoon season. Mean elevation of the valley bottom is 3200 m.

At 3200 m, the vegetation is dominated by *Kobresia humilis*, *Festuca ovina*, *Elymus nutans*, *Poa* spp., *Carex* spp., *Scripus distigmaticus*, *Gentiana straminea*, *Gentiana farreri*, *Leontop odiumnanum*, and *Potentilla nivea*. Litter samples of the 25 species based on the aboveground biomass of coloring leaves were collected randomly from this alpine meadow community grazed during winter by sheep in September 2008 at 3200 m, air-dried and stored indoors for 9 months until the beginning of the decomposition experiment. The chemical properties were shown in supplementary information Table 1. In briefly, there were 3 litter functional groups: 2 shrubs with a high lignin:N ratio (mean 10.9, ranging from 8.5 to 13.2), 3 graminoids with a medium lignin:N ratio (mean 6.1, ranging from 4.2 to 7.6) and 20 forbs with low lignin:N ratios (mean 2.6, ranging from 0.1 to 8.8, and only 4 out of 20 litter species had a lignin:N ratio of more than 4) (SI Table 1).

2.2. Experimental design

At the HBAMERS and about 3 km from HBAMERS, two 10 × 20 m plots were fenced in autumn 2005 and 2006 at 3200 and 3800 m above sea level along the southern side of the Qilian Mountains. The coverage of the vegetations at the two sites is more than 90%. Air-dried litter samples (4.0 g oven-dry mass at 65 °C) of single species and mixed litter samples of the community were placed in 4 × 6 cm litter bags with nylon cloth of 1 mm mesh for upper side and 0.5 mm mesh for bottom side. Species mixtures were assembled with the total mass of 4.0 g partitioned equally among mixed species, recording the exact mass of litter used. Because testing all combinations of species mixtures was impractical, species combinations were drawn at random for each of 5 species richness levels: 2, 4, 8, 16 and 25 species. Finally 19, 10, 11, and 10 combinations for the first four levels were adopted. Thus the experiment encompassed 76 treatments with 2 replicates, including 25 single-species litters decomposing in isolation, one 25-species mixture, and a total of 50 random species-mixtures comprising 2–16 species. There were 4 sites totally and two at each elevation used in the study. Litter bags were randomly distributed within each location at spacings of 20–30 cm apart on 20 June 2009. Litter samples with bag were cleaned quickly with tap water to remove dust of bag surface, dried at 65 °C for 48 h, and weighed on 21 June 2010.

2.3. Data calculation

Chemical traits in litter were determined in 4 sub-samples. Ash-free dry mass (AFDM) was determined after combustion of subsamples at 550 °C for 4 h. Four unexposed samples of each litter species were used to determine the initial dry mass and AFDM in the same way. The initial carbon and nitrogen (N) content of the 25 litter species was determined as per the methods described in AOAC (1984). Litter chemistry was measured by sequentially digesting material into fractions that correspond with soluble cell contents, cellulose, hemicellulose, lignin and acid insoluble ash

Table 1
ANOVA of effects of species composition at each species richness level and elevation on mass loss and non-additive effects of mixed litter mass loss.

Species richness	Model	Mass loss			Non-additive effect		
		df	*F*	*P*	df	*F*	*P*
1	Elevation (*E*)	1	211.822	<0.001	/	/	/
	Composition (*C*)	24	26.552	<0.001	/	/	/
	E × *C*	24	1.607	0.078	/	/	/
2	Elevation (*E*)	1	172.265	<0.001	1	1.137	0.293
	Composition (*C*)	18	19.184	<0.001	18	5.307	<0.001
	E × *C*	18	1.109	0.381	18	1.296	0.245
4	Elevation (*E*)	1	59.740	<0.001	1	0.199	0.660
	Composition (*C*)	9	3.165	0.015	9	3.439	0.010
	E × *C*	9	1.147	0.378	9	0.722	0.684
8	Elevation (*E*)	1	41.684	<0.001	1	4.323	0.049
	Composition (*C*)	10	4.914	<0.001	10	6.038	<0.001
	E × *C*	10	0.721	0.927	10	0.646	0.760
16	Elevation (*E*)	1	30.891	<0.001	1	3.932	0.061
	Composition (*C*)	9	1.863	0.118	9	2.336	0.055
	E × *C*	9	1.279	0.307	9	1.411	0.248