Wetlands (2017) 37:145–152
DOI 10.1007/s13157-016-0855-3

ORIGINAL RESEARCH

Effects of Litter Evenness, Nitrogen Enrichment and Temperature on Short-Term Litter Decomposition in Freshwater Marshes of Northeast China

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Received: 17 March 2015 / Accepted: 30 November 2016 / Published online: 14 December 2016

Abstract Knowledge about the effects of global change factors on litter decomposition is critical for accurate prediction of future carbon (C) and nutrient cycles in terrestrial ecosystems. Here, we collected *Deyeuxia angustifolia* and *Carex lasiocarpa* litters from freshwater marshes in Northeast China, and conducted an incubation study to examine the effects of nitrogen (N) enrichment (0 and 25 mg N g^{-1} litter), temperature (5, 15, and 25 °C), and litter evenness on litter mixing effect and decomposition. Non-additive effects were more common than additive effects during decomposition of litter mixtures, and synergistic effect was detected in two thirds of the litter mixtures. Moreover, litter mixing effects on decomposition varied with N enrichment, incubation temperature, and litter evenness. Both increased proportions of *D. angustifolia* in litter assemblages and elevated temperature generally accelerated litter decomposition. However, N enrichment slowed litter decomposition at 5 and 15 °C, but had positive or neutral effect at 25 °C. Our results highlight the importance of the interactive effects of N enrichment, temperature, and plant community structure on litter mixing effects during decomposition, and suggest that accelerated litter decomposition induced by climate warming and altered vegetation community would be modulated by N enrichment in freshwater marshes of Northeast China.

Keywords *Carex lasiocarpa* · *Deyeuxia angustifolia* · Litter mixing effects · Microbial respiration · The Sanjiang Plain · Wetland

Introduction

Plant litter decomposition not only is the main source of nutrients for biological activity in most terrestrial and aquatic ecosystems, but also plays a key role in the global carbon (C) cycle (Aerts 1997; Gessner et al. 2010). Litter decomposition studies regarding single species have been widely performed in natural or managed ecosystems (Aerts 1997). However, most ecosystems contain multiple plant species and consequently plant litters from a number of species usually become mixed. Gartner and Cardon (2004) have found non-additive effects (where the decomposition rate of litter mixture is not equal to the average of each species alone) on decomposition in 67% of approximately 30 mixed-litter studies. Therefore, decomposition patterns of litter mixtures could not be predicted from the decomposition dynamics of single species in the mixtures.

In recent decades, most terrestrial and aquatic ecosystems have been experiencing nitrogen (N) enrichment (Knorr et al. 2005; Ferreira et al. 2015), altered plant community composition (Handa et al. 2014), and climate warming (Aerts et al. 2007). During litter-mixture decomposition, N enrichment can modify species interaction because increased N

Electronic supplementary material The online version of this article (doi:10.1007/s13157-016-0855-3) contains supplementary material, which is available to authorized users.

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availability reduces the distinction in nutrient contents among plant litters through inorganic N enrichment of the litters induced by microbial colonization (Rosemond et al. 2010). Moreover, litter mixing effects during decomposition generally vary with litter evenness (the relative mass ratio of component litters in the mixtures) (Bonanomi et al. 2010; Mao and Zeng 2012) and climate conditions (Madritch and Cardinale 2007; Butenschoen et al. 2011). To date, little is known about the interactive effects of N enrichment, temperature, and litter mixing proportion on litter mixing effects, and thus decomposition rates.

Temperate freshwater wetlands in the northern hemisphere store a large amount of organic C in soils due to the low decomposition rates relative to production rates (Bridgham et al. 1995; Bernal and Mitsch 2012). In these ecosystems, decomposition is mainly limited by low temperature, nutrient-poor conditions, and biochemically recalcitrant substrates (Thormann et al. 1999; Breeuwer et al. 2008; Song et al. 2011). Previous studies have observed that N enrichment, climate warming, and altered plant community composition and structure could exert substantial influences on soil nutrient availability, litter quality, and soil microbial activities (Knorr et al. 2005; Aerts et al. 2007; Breeuwer et al. 2008; Song et al. 2013), which may result in alterations in litter mixing effects and thus decomposition rates in temperate freshwater wetlands.

The Sanjiang Plain, one of the largest freshwater marsh regions in China, has been experiencing N enrichment (Mao et al. 2013) and climate warming (Yan et al. 2002). Meanwhile, *Carex lasiocarpa* (CL)-dominated wetlands have been gradually replaced by *Deyeuxia angustifolia* (DA)-dominated wetlands, due to the drainage of wetlands for agricultural use and climate warming (Song et al. 2009). Will N enrichment, increased temperature, and altered plant community composition change litter decomposition in the freshwater marshes in the Sanjiang Plain, Northeast China? To answer the question, we used a short-term laboratory incubation experiment to assess the effects of N enrichment, temperature, and litter mixing proportion on litter mixing effects and decomposition rates of foliar litters. Meanwhile, we attempted to investigate how temperature sensitivity of litter decomposition responded to N enrichment and altered litter mixing proportions.

Materials and Methods

Plant Litter Collection and Preparation

Plant foliar litters used for the decomposition experiment were taken from the Sanjiang Experimental Station of Wetland Ecology (47°35’N and 133°31’E), which is located in the central portion of the Sanjiang Plain, Northeast China. The study site has a temperate continental monsoon climate, with a mean annual temperature of 2.5 °C and precipitation of 558 mm. *C. lasiocarpa*- and DA-dominated wetlands are two main wetland types in the Sanjiang Plain. Detailed information about the study site was described by Song et al. (2009).

In April 2011, standing foliar litters of DA and CL were collected from freshwater marshes. For each species, foliar litters were mixed carefully, oven dried at 65 °C, and divided into two subsamples. The first group of subsample was cut into approximately 1 cm^2 pieces and used for the incubation experiment, and the second group was ground to pass through a 0.25 mm sieve for the analysis of the initial chemical properties. Organic C concentration was determined using the $K_2Cr_2O_7$–H_2SO_4 wet oxidation method (Nelson and Sommers 1996). To determine the total N and P concentration, plant litters were first digested using concentrated H_2SO_4 and H_2O_2 solution (Lu 2000). Total N and P concentrations were analyzed by the indophenol blue method and the molybdenum blue method, respectively (Lu 2000). The initial chemical properties of litter mixtures were calculated based on the initial chemical properties of individual components and their weight ratios. The initial chemical properties of plant litters were showed in Table 1.

Experimental Design and Laboratory Incubation Study

We established five litter types: DA, CL, and the two species litters mixed with three proportions (DA-dominated uneven mixture, 75%DA + 25%CL; even mixture, 50%DA + 50%CL; and CL-dominated uneven mixture, 25%DA + 75%CL). Meanwhile, an unamended treatment (without plant litters) was included as a blank. For each litter type, N was added as NH_4NO_3 solution at two levels (Control, 0 mg N g^{-1} litter; and N enrichment, 25 mg N g^{-1} litter). Considering that the mean temperature in the whole year, growing season, and July was 2.5, 14.0, and 21.6 °C, we created three incubation temperature degrees (5, 15, and 25 ± 0.5 °C) for the litter decomposition experiment. These resulted in 36 litter treatments with four replicates (six litter types × two N enrichment treatments × three temperature degrees × four replicates =144 microcosms).

Plant litter decomposition was measured using a modified short-term incubation method similar to that described by Briones and Ineson (1996). We determined litter decomposition rates by measuring cumulative CO_2 production. Initial short-term litter respiration correlates well with field-determined long-term litter decomposition rates (Aerts and de Caluwe 1997), and thus is widely used to identify the effect of particular factors on litter decomposition (Briones and Ineson 1996; Powers and Salute 2011). For each litter type, one gram of plant litters was rewetting until saturation with distilled water, placed in 1 L glass jar, and inoculated with 1

Table 1 Initial chemical properties of foliar litters from freshwater marshes in the Sanjiang Plain of Northeast China

	Organic C mg g^{-1}	Total N mg g^{-1}	Total P mg g^{-1}	C/N ratio	C/P ratio
DA	451	9.08	1.58	49.7	285
DA-dominant uneven mixture	452	8.55	1.64	52.9	276
Even mixture	453	8.02	1.69	56.6	268
CL-dominant uneven mixture	454	7.49	1.75	60.7	260
CL	455	6.96	1.81	65.5	252

DA D. angustifolia foliar litter, *CL C. lasiocarpa* foliar litter

mL fresh marsh water from the study site. For the N enrichment treatments, N was added as NH_4NO_3 solution. Meanwhile, an equal volume of distilled water was added for litter treatments without N enrichment. All the jars were weighed, closed with rubber stopper, and then incubated in darkness for 42 days. After 4, 8, 12, 17, 22, 27, 32, 37, and 42 days of incubation, 20-ml gas samples were taken from the jars using a syringe and analyzed for CO_2 concentration on a gas chromatograph (Hewlett Packard 4890, Hewlett Packard, PA, USA). Following gas sampling, the jars were weighed, and distilled water was added to maintain constant humidity when necessary. After that, the jars were purged with fresh air for 30 min and then closed. The amounts of oxygen in 1 L jars were much greater than the amounts of CO_2 produced from the microbial decomposition during sampling intervals (less than 25 mg CO_2-C), so we assumed that sufficient oxygen was available to maintain aerobic conditions during litter decomposition. The blanks were included within every set of microcosm to account for background concentrations of CO_2. For each litter treatment, cumulative CO_2 production was calculated as the sum of the difference between the CO_2 production from the treatment and that from the blank at each sampling time, and expressed as mg CO_2-C g^{-1} litter. Temperature sensitivity of litter decomposition was characterized by Q_{10} value that described the change in reaction rate with an increase of 10 °C in temperature (Conant et al. 2011). The Q_{10} value of litter decomposition was calculated according to Conant et al. (2011): $Q_{10} = (k_2/k_1)^{[10/(T_2-T_1)]}$, where k_1 and k_2 are cumulative CO_2 production at two incubation temperatures T_1 and T_2.

Statistical Analyses

The data were analyzed statistically using SPSS 13.0 for Windows and the accepted significance level was $\alpha = 0.05$. Three-way analysis of variance (ANOVA) was used to examine the effects of litter type, N enrichment, and incubation temperature on cumulative CO_2 production during decomposition. Meanwhile, two-way ANOVA was used to examine the effects of litter type and N enrichment on the Q_{10} value of litter decomposition. For each litter type, one-way ANOVA was performed to detect the significant effect of N enrichment on litter decomposition and Q_{10} value. Multiple comparisons among cumulative CO_2 production were performed with Tukey's honestly significant difference test.

For all litter mixtures, expected cumulative CO_2 production was calculated as follows (after Bonanomi et al. 2010): $eCO_2 = \sum_{i=1}^{n} oCO_{2i} \times P_i$, where eCO_2 is the expected cumulative CO_2 production, oCO_{2i} is the observed cumulative CO_2 production in single litters of species i, and P_i is the initial proportion of litters of species i in the mixture. The relative litter mixing effect was calculated as the follows (after Lecerf et al. 2011): relative litter mixing effect (%) = $(oCO_2 - eCO_2) \times 100/\, eCO_2$. For the litter mixture treatments, one-way ANOVA was used to test the differences between the relative litter mixing effect and zero. According to the results of the statistical analysis, we defined litter mixing effects as additive (no significant difference between the relative litter mixing effect and zero) and non-additive (significant difference between the relative litter mixing effect and zero) effects (after Gartner and Cardon 2004). Furthermore, non-additive effects were divided into synergistic (the relative litter mixing effect greater than zero) and antagonistic (the relative litter mixing effect lower than zero) effects (after Hättenschwiler et al. 2005).

Results

At each incubation temperature, DA generally had greater cumulative CO_2 production than CL under both control and N enrichment conditions. During the decomposition of single litter treatments, cumulative CO_2 production increased with increasing incubation temperature, irrespective of N enrichment. By the end of single litter decomposition, N enrichment generally caused a decrease in cumulative CO_2 production at both 5 and 15 °C, and had no effect at 25 °C (Table 2 and Supplemental Material Fig. S1).

For all litter mixture treatments, N enrichment generally caused a decrease in cumulative CO_2 production at both 5 and 15 °C. However, N enrichment only increased cumulative CO_2 production of even litter mixture at 25 °C. During decomposition of litter mixtures,

Table 2 Effect of litter evenness, N enrichment, and incubation temperature on cumulative CO_2 production by the end of litter decomposition

Litter treatments	Cumulative CO_2 production (mg CO_2-C g^{-1} litter)								
	5 °C			15 °C			25 °C		
	Control	N enrichment	N enrichment effect (*p*-value)	Control	N enrichment	N enrichment effect (*p*-value)	Control	N enrichment	N enrichment effect (*p*-value)
DA	37.4(0.6)ab	35.1(0.7)a	0.042	93.0(1.4)b	79.8(1.6)a	0.001	126.3(2.3)a	119.4(2.0)b	0.069
DA-dominant uneven mixture	37.5(0.4)a	33.6(0.3)a	<0.001	100.3(0.9)a	80.0(0.9)a	<0.001	125.6(1.5)a	132.4(4.0)a	0.162
Even mixture	37.4(1.1)ab	34.6(0.9)a	0.096	93.7(0.8)b	78.5(1.9)a	<0.001	113.2(1.6)b	132.2(2.4)a	0.001
CL-dominant uneven mixture	34.6(0.3)b	32.6(0.5)ab	0.017	85.3(0.5)c	74.2(1.4)a	<0.001	115.5(3.2)b	120.4(0.8)b	0.187
CL	31.3(0.7)c	30.3(0.5)b	0.325	77.5(1.2)d	64.6(0.7)b	<0.001	109.4(2.5)b	111.7(1.9)b	0.493

Data are mean values (with standard errors in parentheses, *n* = 4). Different letters indicate significant differences in cumulative CO_2 production by the end of litter decomposition at each incubation temperature*DA D. angustifolia* foliar litter, *CL C. lasiocarpa* foliar litter

cumulative CO_2 production increased with elevating incubation temperature. In addition, increased proportion of DA in litter assemblages generally caused an increase in cumulative CO_2 production during the process of decomposition (Table 2 and Supplemental Material Fig. S1).

During the decomposition process of the 18 litter mixture treatments, 12 litter mixture treatments exhibited a synergistic effect on cumulative CO_2 production, and one litter mixture treatment exhibited an antagonistic effect (Fig. 1). At the coolest incubation temperature (5 °C), N enrichment transformed synergistic effect to additive effect during decomposition of litter mixtures. However, N enrichment did not affect litter mixing effects at 15 °C. In addition, N enrichment caused a shift in litter mixing effects from additive or antagonistic effect to synergistic effect on cumulative CO_2 production at 25 °C (Fig. 1).

For all litter treatments, Q_{10} values of litter decomposition at the 5–15 °C range were greater than the corresponding values at the 15–25 °C range (Fig. 2). During litter decomposition, N enrichment generally decreased Q_{10} values at the 5–15 °C range, but increased at the 15–25 °C range. Nitrogen enrichment only enhanced the Q_{10} values of decomposition at the 5–25 °C range for litter mixture treatments. Under control conditions, both DA- and CL-dominated uneven mixtures had the greatest Q_{10} values among the five litter treatments at the 5–15 °C and 15–25 °C ranges, whereas even mixture had lower Q_{10} value than the other four litter treatments at the 5–25 °C range. In addition, there was no difference in Q_{10} value among the three litter mixtures at each temperature range under N enrichment conditions (Fig. 2).

Discussion

In this study, we observed non-additive effects on decomposition in 13 out of 18 litter mixtures, and additive effect in five out of 18 litter mixtures. Our result was consistent with the majority of litter diversity experiments (Gartner and Cardon 2004; Bonanomi et al. 2010; Barantal et al. 2014; Handa et al. 2014), and further confirmed that non-additive effect was more common than additive effect during the decomposition process of litter mixtures. Although decomposition dynamics of single plant litters have been widely studied in these freshwater marshes (Zhang et al. 2014, 2015), our result clearly implies that litter decomposition rates at the ecosystem level could not be predicted from the litter species decomposing singly, and that litter mixing effect should be incorporated into the further litter decomposition studies.

Litter mixing effect during decomposition substantially varied with incubation temperature. In the absence of N addition, synergistic effect during litter mixture decomposition was detected at both 5 and 15 °C, and antagonistic or additive effect was detected at 25 °C. In a recent meta-analysis

Fig. 1 Effect of N enrichment and incubation temperature on the relative litter mixing effect during 42 days of incubation. Data are mean values and vertical bars are standard errors (*n* = 4). The significant differences between the relative litter mixing effects and zero were indicated by ns ($P > 0.05$), * ($P < 0.05$), ** ($P < 0.01$), and *** ($P < 0.001$). DA, *D. angustifolia* foliar litter; CL, *C. lasiocarpa* foliar litter

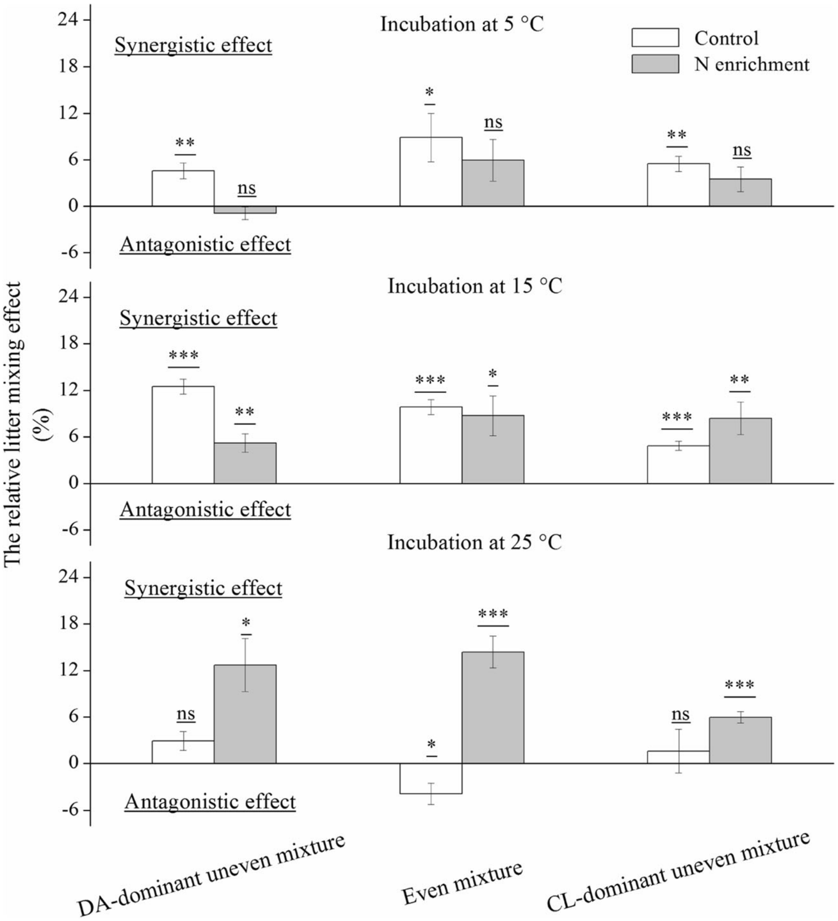
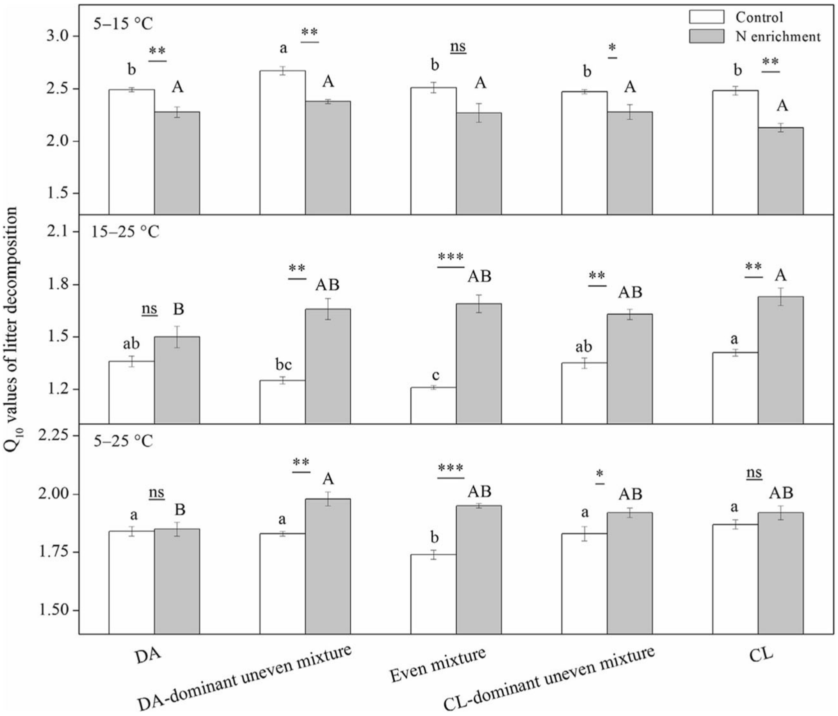


Fig. 2 Effect of N enrichment and litter evenness on Q_{10} values of litter decomposition during 42 days of incubation. Data are mean values and vertical bars are standard errors (*n* = 4). Means with different capital- (A and B) and lowercase (a–c) letters indicated significant difference in Q_{10} values among litter treatments under control and N enrichment conditions, respectively. The significant differences between the control and N enrichment treatments were indicated by ns ($P > 0.05$), * ($P < 0.05$), ** ($P < 0.01$), and *** ($P < 0.001$). DA, *D. angustifolia* foliar litter; CL, *C. lasioarpa* foliar litter



regarding litter mixture decomposition in streams, Lecerf et al. (2011) found that litter mixing effect and mean water temperature followed a U-shaped relationship, and additive or antagonistic effect occurred at the lowest (< 4 °C) and highest (> 25 °C) temperatures. Given that the mechanisms behind the effects of climate on litter mixing effect were still poorly understood, we speculated that incubation temperature would modulate the diversity and activity of decomposer, and thus species interactions during litter mixture decomposition. At both 5 and 15 °C, the synergistic effect during litter mixture decomposition may be caused by the fungi-driven nutrient transfer among component litters and complementary use of resources by decomposers (Gartner and Cardon 2004; Hättenschwiler et al. 2005; Swan et al. 2009). In contrast, the antagonistic or additive effect of litter mixing on decomposition at 25 °C may result from the reductions in consumer diversity and altered interactions across trophic levels (Hättenschwiler et al. 2005; Srivastava et al. 2009).

In agreement with the results obtained in field studies (Rosemond et al. 2010; Vivanco and Austin 2011), we also found that N enrichment altered litter mixing effect on decomposition in six out of the nine mixed litter assemblages. Moreover, the effect of N enrichment on litter mixing effect varied with incubation temperature and litter evenness. At low temperature (5 °C), N enrichment might decrease the diversity and activity of decomposer and suppress the transfer of nutrients among species (Rosemond et al. 2010; Ferreira et al. 2015), leading to a shift in litter mixing effects from synergistic effect to additive effect. At high temperature (25 °C), increased N availability might alleviate the N limitation of decomposer activity and diversity (Song et al. 2011; Vivanco and Austin 2011), which could exceed the negative effect of temperature on the decomposer diversity. Hence, N enrichment transformed the litter mixing effect from antagonistic or additive effect to synergistic effect at 25 °C.

Notably, N enrichment generally inhibited litter decomposition at 5 and 15 °C, but stimulated the decay of litter mixtures at 25 °C. Previous meta-analysis also found that the effects of N enrichment on litter decomposition were inconsistent, and varied with climate and litter quality (Knorr et al. 2005; Ferreira et al. 2015). Moreover, our previous study observed that N enrichment stimulated decomposition of *D. angustifolia* aboveground litters (with C/N ratio of 133) at 25 °C in experimental microcosms (Song et al. 2011). Therefore, these inconsistent effects of N addition on litter decomposition in these freshwater marshes may be explained by the differences in incubation temperature (Ferreira et al. 2015), initial litter chemical properties (Knorr et al. 2005), and/or litter mixing effect. At both 5 and 15 °C, N addition might reach the toxic levels to decomposers due to the low microbial demand for N during decomposition (Ferreira et al. 2015). As a consequence, increased N availability might suppress decomposer activity (Ramirez et al. 2012) and decrease the magnitude of synergistic effect (Fig. 1), and thus caused a reduction in litter decomposition rate at both 5 and 15 °C. Given that single litter decomposition was not influenced by increased N availability, the positive effect of N enrichment on litter mixture decomposition at 25 °C might result from the shift in antagonistic or additive effect to synergistic effect.

In our study, the Q_{10} values of litter decomposition at 5–25 °C ranged from 1.74 to 1.87, and the lower temperature range (5–15 °C) had greater Q_{10} values of litter decomposition than the higher temperature range (15–25 °C). These change trends in the Q_{10} values of litter decomposition were similar to that of soil organic matter decomposition conducted in both field and incubation experiments (Kirschbaum 1995; Davidson and Janssens 2006; Conant et al. 2011), indicating that most of the overall temperature sensitivity of organic matter decomposition occurred at low temperature. According to the Arrhenius equation, the relative increase in the activation energy decreases with increasing temperature during the process of microbial decomposition (Kirschbaum 1995; Davidson and Janssens 2006). Moreover, elevated temperature could regulate microbial metabolism and activity, and thus the thermal adaptation of decomposer community (Conant et al. 2011). Therefore, temperature sensitivity of litter decomposition decreased with the increasing incubation temperature. In addition, N enrichment generally decreased Q_{10} values of litter decomposition at 5–15 °C range, and increased at 15–25 °C range. These findings implied that N enrichment could modulate increased litter decomposition rates induced by climate warming in freshwater marshes of Northeast China.

In these freshwater wetlands, litter decomposition is generally limited by N availability (Song et al. 2011; Zhang et al. 2014). Compared with *C. lasiocarpa*, *D. angustifolia* litters had greater N concentration, and lower C:N ratio. Hence, increased proportions of *D. angustifolia* in the litter mixtures generally enhanced litter decomposition rates. Moreover, litter-mixing effects varied with litter evenness during decomposition. These results imply that, in temperate freshwater wetlands, the changes in plant community composition and structure would have profound effects on litter decomposition rates through altered substrate quality and litter mixing effects.

Plant litter decomposition generally occurs under both aerobic and anaerobic conditions in wetland ecosystems. In the present study, we only investigated the effects of N availability, temperature, and litter mixing proportion on short-term litter decomposition under aerobic conditions. In temperate freshwater wetlands, the reduced decomposition rate of plant litter induced by waterlogging and associated anaerobic conditions also contributes substantially to ecosystem C and nutrient budgets (Bridgham et al. 1995). Further studies should be conducted to assess the interactive effects of these factors on anaerobic microbial decomposition of plant litters in temperate freshwater marshes.

Conclusions

In conclusion, litter mixing effects during decomposition varied with increased N availability, temperature, and litter mixing proportion. Nitrogen enrichment generally suppressed litter decomposition at 5 and 15 °C, but had neutral or positive effect at 25 °C. Moreover, both elevated incubation temperature and increased proportions of *D. angustifolia* in litter mixtures stimulated litter decomposition. These results highlight the complexity of litter mixing effects on decomposition in the context of N enrichment, climate warming, and alter plant community composition. Meanwhile, our findings suggest that increased litter decomposition rates induced by climate warming and altered plant community composition would be modulated by increased N availability in freshwater marshes of Northeast China.

Acknowledgements This research was supported by National Natural Science Foundation of China (Nos. 31570479, 41103037, and 31100357), "Strategic Priority Research Program – Climate Change: Carbon Budget and Related Issue" of the Chinese Academy of Sciences (No. XDA05050508), and the Youth Innovation Promotion Association of CAS (No. 2013152). We thank the Sanjiang Experimental Station of Wetland Ecology for providing working facilities, and the editor and the anonymous reviewer for their constructive comments on the manuscript.

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