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Original Research

Effect of Litter Quality on Leaf-Litter Decomposition in the Context of Home-Field Advantage and Non-Additive Effects in Temperate Forests in China

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Abstract

Litter quality is often considered the main driver of rates of decomposition. Litter decomposes faster in its home environment than in any other environment, which is called the home-field advantage (HFA). However, evidence for this phenomenon has not been universal. In addition, litter mixtures of different species can induce a non-additive effect (NAE) on decomposition processes. However, the direction and magnitude of NAE vary and underlying mechanisms remain unclear. The aim of our study was to assess the effect of litter quality on leaf-litter decomposition in the context of HFA and NAEs in temperate forests in China. Litterbags containing aspen (*Populus davidiana*), birch (*Betula platyphylla*), and oak (*Quercus liaotungensis*) litter were incubated *in situ* in pure aspen and broadleaved mixed forests in Chinese temperate forests for 360 days. The main results were:

1. Aspen litter with a low C/N ratio and high initial N concentration decomposed faster than birch litter, both of which decomposed faster than oak litter, which had the lowest quality.
2. The rate of decomposition of oak litter was significantly higher in the broadleaved mixed forest than in pure aspen stands; however, the rate of decomposition of birch litter was not significantly different from pure aspen stands and broadleaved mixed forest.
3. Contrary to what was predicted, the mixture of aspen and birch litter decomposed faster than expected. However, both the aspen/oak and birch/oak mixtures had a neutral mixing effect where the rates of decomposition were slightly faster than expected.
4. Controlling factors based on linear models show that the order of the relative importance of their effect on litter decomposition was as follows: litter quality, forest floor environment, and litter mixtures.

This study indicates that:

1. The various litter species exhibited different litter-environment interactions, such as favoring or contradicting the HFA hypothesis.

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2. Litter mixture treatments can induce different mixing effects.
3. Compared with environment and litter mixtures, litter quality is the dominant factor in controlling the rate of litter decomposition.

Keywords: litter decomposition, monospecific litter, litter mixtures, mass loss, non-additive effects, home field advantage

Introduction

Leaf litter decomposition is an important ecological process that regulates the cycle of matter, such as the release of CO_2 into the atmosphere and nutrient mineralization into soil [1-3], providing the main source of nutrients for biological activity and playing a crucial role in the maintenance of soil fertility in forest ecosystems [4].

Generally, the rate of litter decomposition is positively correlated with N content of initial litter, while it is negatively correlated with C/N and lignin/N ratios of initial litter over a wide range of ecosystems [5-7]. Moreover, the rate of litter decomposition is affected by dominant external factors indirectly. In the first place, a distinct forest floor in terms of soil nutrients, pH, and structure could affect the rate of decomposition in the forest floor-litter interface [8]. Secondly, environmental incubation conditions influence litter decomposition indirectly through temperature and moisture. Simultaneously, litter decomposition is indirectly affected by the microclimate on soil formation and nutrient cycling [9]. Finally, the decomposer food webs, consisting of faunal and microbial communities, will vary underneath different forest soils [10-11], which should in turn affect the rate at which various litter fractions are mineralized [12]. From this exposure, it should be clear that litter decomposition is not only affected by litter quality but also by the micro-environmental conditions under which the litter originated [13-15]. Hence, the interaction is derived from its home field advantage (HFA) due to an adaptation of the local micro-environmental conditions to the litter produced by the prevailing plant species [16-17]. Compared to any other plant cover, litter decomposes faster at the site of its origin. For example, Gholz et al. discovered that litter from broadleaved trees decomposes more quickly in broadleaved than in conifer habitats [13]. Knowledge of HFA for decomposition has rarely been explored. And the relative importance of litter quality remains unclear versus the effect of the forest floor environment on decomposition [18].

Litter decomposition studies have very often dealt with the decomposition of single-species litter [19], but in natural forest ecosystems litter from various species becomes mixed in the litter layer after shedding and decomposing together. A great many studies have found that mixing litter could have non-additive or additive effects on litter decomposition. Compared with non-additive effects, the additive effects can be predicted from the rates of decomposition in the monocultures of each component species [19]. According to Ostrofsky, there exist some primary mechanisms in driving non-additive (synergism or antagonism) effects [20]. Firstly, through transferring from high-quality to low-quality litter, nutrients could favor rapid colonization of microorganisms and accelerate the decomposition of recalcitrant litter in the mixture [21]. Secondly, specific secondary compounds (tannins or phenolics) render the N unavailable to the organisms of decomposition and consequently reduce the rate of litter decomposition [22]. Thirdly, litter beds could offer more suitable microclimatic conditions for decomposer communities to accelerate the rate of litter decomposition. Meanwhile, litter beds could protect labile soluble compounds from leaching [23]. Finally, synergistic or antagonistic effects on the decomposition of various types of species in mixed litter may occur simultaneously; therefore, the net effect of mixed-litter decomposition could present different mixing effects in various processes [20].

While a number of field and laboratory studies have largely focused on the effect of litter quality on decomposition [12, 24], few studies have been carried out regarding the effect of litter quality on the mixture of litter and the environment of the forest floor [25-26]. Wu et al. found that litter quality on the basis of species composition affects litter-mixing effects on decomposition rates in temperate forests in China, which only took litter quality and litter mixtures into consideration [27]. Wang et al. found that litter quality plays a primary role in controlling litter decomposition, with site conditions being a secondary factor contributing to the local variations in litter decomposition in temperate forest ecosystems in China, which only took litter quality and forest environment into consideration [28]. It should be pointed out that litter mixtures and their forest floor environment are real existing factors controlling litter decomposition as found from various forest field studies. Their results would have been inaccurate or even wrong if the litter decomposition of litter mixture or environment had been neglected. Therefore, in order to improve insight into the drivers of litter decomposition, it is worthwhile to study the effect of litter quality on leaf-litter decomposition in the context of non-additive effects and HFA in natural litter layers of temperate forest ecosystems in China. We had three specific objectives for our study:

1. To evaluate the effects of litter species on their decomposition in a distinct environment that contains the same litter species, in order to demonstrate the HFA decomposition theory.
2. To investigate whether the rates of decomposition of litter mixtures deviate from theoretically predicted patterns that are based on the rates of decomposition of single-litter components and show non-additive

Table 1. Site characteristics of the two forest types. Pure forest refers to pure *Populus davidiana* forest, while mixed forest refers to *Populus davidiana - Betula platyphlla - Quercus mongolica* mixed forest (mean±SE, $n = 3$).

Forest types	Tree density (of trees hectare)	Slope angle (º)	Aspect	Elevation (m)	Mean DBH (cm) (mean±SE)	Tree height (m) (mean±SE)
Pure forest	910	20	West	989	7.28±2.22	7.81±1.20
Mixed forest	840	20	West	1067	16.22±6.16	11.26±3.92

effects because of synergism or antagonism species interactions.

3. To determine the effects of relative importance of the three drivers – i.e., litter quality, forest floor environment, and litter mixtures – on the rate of litter decomposition.

Material and Methods

Study Site

The study was conducted in the Liao River Source Nature Reserve (LRSNR, 41°01′-41°21′N, 118°22′-118°37′E) in Pingquan County, Hebei Province, China. This nature reserve consists of an area of 3.355×10^4 ha with elevations ranging from 625 to 1,738 m. The region is in China's temperate zone – part of a semi-humid and semi-arid continental monsoon mountain climate. The long-term mean annual precipitation is 550 mm and the mean annual temperature is 7.3ºC, with monthly average temperatures ranging from -10.8ºC (January) to 22.9ºC (July) [29]. By and large, the reserve has a brown and cinnamon type of soil, classified as Eutriccambisol [30]. The typical vegetation of its mixed forests is one of deciduous broadleaved trees, i.e., aspen (*Populus davidiana*), birch (*Betula spp.*), oak (*Quercus spp.*), and shrubs (e.g., *Prunus spp.*, *Vitex negundo var. Hetertophylla*, and others), while the typical vegetation of the pure forest in this region consists of highly homogeneous deciduous broadleaved trees dominated by aspen (*Populus davidiana*), while shrubs (e.g., *Ostryopsis davidiana Decaisne*, *Weigela florida*, etc.) are often found in the understorey. Detailed information for these two sites is shown in Table 1.

Experimental Design

We conducted our work based on the "Observation Methodology for Long-term Forest Ecosystem Research" forestry standards of the People's Republic of China (LY/T 1952-2011) [31]. In late September 2012, when maximum litter fall occurred, we collected freshly senesced leaves of birch (*Betula platyphylla*), aspen (*Populus davidiana*), and oak (*Quercus liaotungensis*) from the forest floor. All of our litter was air-dried at room temperature until constant weight immediately after collection and stored for further use. In order to calculate the correction factor from air-dried weight to oven-dried weight, five sub-samples of the three litter species were dried to a constant weight at 75ºC. A detailed description of the chemical compositions of the three litter species can be seen in Table 2.

A litterbag method was used for estimating rates of leaf litter decomposition (a widely used technique to determine litter mass loss) during a 12-month period. Each litterbag (20 × 30 cm) was made of polyethylene netting of 1.0 × 1.5 mm mesh size. The mesh size was intended to impede the incorporation of mesofauna decomposers and to minimize the physical loss of small litter fragments [32].

Each bag was filled with 10 g of air-dried litter with a weight accuracy of 10-3 g, labeled, and sealed with rustproof staples. We prepared the following six types of litter bags: the first set of three bags contained the litter of each single species (i.e., birch, aspen, and oak); the second set consisted of the three possible two-species mixtures with loading ratio 1:1, which reflected the heterogeneity of litter composition in the inner broadleaved mixed forests.

Pure aspen stands and mixed forests of birch, aspen, and oak are found randomly distributed in the study area. For the two forest types, litterbags were deployed in three replicate plots 50 m apart, with similar landscape position, topographic features, elevation, and exposure (north facing) to ensure comparability between test results. The pure aspen plots contained all three single species (birch, aspen, and oak), while mixed forest plots contained all three single species and all three possible two-species mixtures. On 19 October 2012, 108 litter bags (three litter

Table 2. Initial chemical properties of three leaf litter species, poplar (*Popolus davidiana*), birch (*Betula platyphylla*) and oak (*Quercus liaotungensis*) (mg/g) (mean±SE, $n = 3$).

Species	C	N	C/N	Lignin	Lignin/N
Populus	509.33±11.32c	8.49±0.22a	59.99±2.1c	252.12±0.32c	29.70±0.21c
Betula	527.35±9.13b	7.52±0.25b	70.13±2.6b	263.61±0.31b	35.05±0.27b
Quercus	551.67±10.48a	6.87±0.20c	80.3±2.2a	290.01±0.33a	42.21±0.33a

Different letters in the same column indicate significantly different means ($p<0.05$)

types × three litter-bag replicates × three plot replicates × four harvests) were deployed on the forest floor and fastened to the ground with non-corrosive nails in pure aspen plots. Similarly, 216 litter bags (six litter setups × three litter-bag replicates × three plot replicates × four arvests) were placed in the mixed plots.

Litterbags of each treatment were randomly retrieved and brought to the laboratory after 180, 240, 300, and 360 days of decomposition. The litter remaining in each bag was cleaned from extraneous matter, such as attached soil particles, in-growth plant materials, and small animals using tweezers and a brush. The contents of the mixed-leaf litter samples were separated into their component species. Litter species identification was relatively easy (even after 360 days) due to the strong morphological and structural differences among the species. In the end, the separated litter samples were oven-dried at 70ºC for 72 h to reach a constant mass and then weighed to determine the remaining dry leaf mass. In total, 12 leaf litter types were obtained consisting of pure birch (*Betula platyphylla*), aspen (*Populus davidiana*), and oak (*Quercus liaotungensis*) leaf-litter (both from pure aspen stands), and from mixed forests, as well as separated birch (*Betula platyphylla*), aspen (*Populus davidiana*), and oak (*Quercus liaotungensis*) leaf-litter (each from the three two-species litter mixtures). We recorded each litter component species, the mixed setting, and the forest type where litterbags had been deployed, allowing us to quantify the importance of the non-additive effect (NAE) relative to the litter quality and litter incubation environments.

Calculations

The remaining litter mass (RM) within each litterbag was calculated as the percentage of the initial litter dry weight (X_o) by species at each sampling time (X_i), using the following formula:

$$RM = X_i / X_O \times 100. \quad (1)$$

To quantify the dynamics of mass loss, we did some fitting change in the amount of litter over time as a negative exponential decay function, developed by Olson [33] and further refined by Barlocher [34], i.e., $W_t = W_0 \times e^{-kt}$, where W_t is the remaining mass at time t, W_o the initial mass of the litter, k the rate of decomposition, and t the incubation time of the litterbags. The times required for 50% and 95% mass loss were calculated as $t_{50\%} = -ln\ 0.5/k$ and $t_{95\%} = -ln\ 0.5/k$, respectively [33].

The predicted relative remaining mass of each litter mixture was calculated based on the observed rates of decomposition in the monocultures of each component species and their initial ratios in the mixtures. This was calculated as follows [35]:

$$\text{Predicted remaining mass (\%)} = [M_1/(M_1 + M_2)] \times R_1 + [M_2/(M_1 + M_2)] \times R_2$$

…where R is the remaining mass (%) of the single litter species and M the initial dry weight of each litter species in the mixture (the subscript 1 and 2 designate two leaf litter species in the mixture). The NAE of each litter mixture was calculated as the ratio [(*expected-observed*)/*expeced*] × 100% [36] that refers to remaining mass, where negative NAE ratios suggest antagonistic mixture effects, while positive NAE ratios indicate synergistic mixture effects. At each sampling time we calculated expected mass loss of litter mixtures on the basis of measured rates of decomposition within the monocultures of each component species as well as their ratios in the mixtures initially.

In order to evaluate the HFA hypothesis, litter species and location were used as factors to examine the litter-environment interactions. HFA indices (HFAI) were pair-wise calculated on the basis of Ayres [37]:

$$HFAI = [100(RML_{Aa} + RML_{Bb})/(RML_{Ab} + RML_{Ba})] - 100 \quad (2)$$

…where RML denotes the relative mass loss of the litter (capital letters in subscripts stand for the litter species, while lower case letters designate the site where the litterbags have been deployed). Specifically, subscript *A* designates birch and *B* refers to pair-wise comparisons with oak; the small subscript *a* indicates the mixed species stand and *b* the pure aspen stand.

A positive HFA index in our pair-wise comparisons of tree species indicates that the litter species decomposes more rapidly under the tree species from where it originated than from below other tree species. Otherwise, a zero HFA index suggests no difference in terms of litter decomposition between home field and away field, while a negative index suggests that the litter decomposes more slowly in its home field than in other fields.

Statistical Analysis

In order to test whether non-additive (synergistic or antagonistic) litter mixture effects were significant or not, the differences between predicted and observed mass loss of decomposition of mixtures were assessed by paired t-tests across the sample dates. In addition, correlation analysis was used to investigate which initial litter parameters correlated with mass remaining in the monoculture litters at the end of the study.

One-way ANOVA was applied to examine the differences in species-specific initial litter quality (three replicate plots for each of the forest types and three replicated litter samples). Two-way ANOVA was applied to examine: 1) differences in mass loss among the six monoculture leaf-litter treatments (aspen, birch, and oak litter in pure aspen stands and in mixed forests) with litter types and time as the major factors, and 2) differences in mass loss of individual amounts in litter decomposing as a single species compared to individual amounts of litter in a mix-

Table 3. Decomposition parameters and time (t) required for different levels ($t_{50\%}$ and $t_{95\%}$ mass loss) of decay of leaf litter in pure poplar and mixed plots of all three leaf litter species (mean±SE, n = 3)

Litter type	Forest type	Parameter *a*	Coefficient *k* (year^{-1})	R^2	$t_{50\%}$(year)	$t_{95\%}$(year)
Populus	pure	102.212±0.12d	0.613±0.01a	0.92	1.13±0.06d	4.89±0.19d
Populus	mixed	102.706±0.18c	0.646±0.01a	0.91	1.07±0.07d	4.64±0.21d
Betula	pure	100.621±0.17e	0.524±0.01b	0.93	1.32±0.05c	5.72±0.17c
Betula	mixed	99.886±0.11f	0.545±0.01b	0.91	1.27±0.07c	5.49±0.22c
Quercus	pure	103.825±0.17b	0.310±0.01d	0.92	2.23±0.05a	9.66±0.18a
Quercus	mixed	104.238±0.13a	0.384±0.01c	0.89	1.81±0.06b	7.81±0.19b

Values followed by different lower letters in the same line indicate significant difference between means (p<0.05)

ture of species (we carried out separate analyses for each sampling time). For post-hoc comparisons of mass loss, we used Tukey's multiple mean comparison test. The two-way ANOVA was used in testing differences in mass loss among the three mixture treatments (the aspen/birch mixture, the aspen/oak mixture, and the birch/oak mixture), with treatment and time as the major factors.

Because of the hierarchical structure of the data, ANOVAs were conducted using linear models to test the effects of our experimental factors (litter quality, mixed litter, and forest type) and their interactions on the remaining mass. This analysis allowed us to express the relative importance of each factor as its sum of squares as a proportion of the total sum of squares (r^2). All statistical analyses were carried out using SPSS version 13.0.1 statistical software (SPSS, Chicago, IL, USA), with the level of significance set as 0.05 in all cases.

Results

Decomposition in the Monospecific Litter

Litter quality variables such as initial leaf litter chemistry were tested and then used to classify litter species from high to low quality (Table 2). Among all three tested litter types, Aspen litter had the highest litter quality due to its high N concentration and low C/N ratio, while oak litter had the poorest litter quality with the lowest N concentration and highest C/N ratio among all three tested litter types. Values of birch litter were intermediate among the three tested litter species.

Results from the linear model showed that litter quality was the strongest determinant of the rate of leaf litter decomposition (r^2 = 0.618, p < 0.01; Table 5). Decomposition of leaf litter with high quality was faster than that of leaf litter with low quality. The rate of decomposition of leaf litter in the same plot decreased by the following order: aspen> birch> oak (p < 0.05; Table 3). The rates of decomposition of aspen and birch were significantly higher than that of oak, given that their decomposition rate was on average 18.61% and 15.66% higher than for oak in pure *Populus davidiana* forest (Table 3).

Similar to mass loss, the differences in the half-life ($t_{50\%}$) and 95% mass loss ($t_{95\%}$) periods of decomposing leaf litter were significant among the three tested litter types (p < 0.05) in the same stand (Table 3). The rates of decomposition of litter correlated positively and significantly with the initial N concentration (r = 0.931, p = 0.001), but negatively with the C/N ratios (r = -0.947, p < 0.001), lignin concentration (r = -0.978, p < 0.001), and with the initial lignin/N ratios (r = -0.951, p < 0.001; Fig. 1).

Effects of Forest Type on Litter Decomposition

Results from the linear model showed that forest type had the second strongest effect on the rate of decomposition after litter quality (r^2 = 0.083, p < 0.01; Table 5). In addition, the interaction between litter quality and forest type (litter quality × forest type) significantly affected litter the rate of decomposition (p < 0.01; Table 5).

For the duration of the experiment, mean mass loss rates differed among litter species in monocultures between pure and mixed forests (Table 3). The average mass loss rate of monospecific aspen litter in the mixed forest was slightly higher (0.89%) than in the pure forest (p > 0.05; Table 3). A similar result was obtained in the case of birch litter, with the decomposition constant (k = 0.545) on average 4.01% higher in the mixed forest than in the pure forest (Table 3). With regard to the 50% ($t_{50\%}$) and 95% mass loss ($t_{95\%}$) periods of decomposition, the differences were similar to the mass loss rate and statistically insignificant (p > 0.05; Table 3) between the two forest types. In contrast, the rate of decomposition of oak was significantly higher in the mixed forest (27.95% ± 0.21%) than in the pure forest (22.55% ± 0.18%) (p < 0.05; Table 3). For oak litter, the HFA index reached its maximum positive value at day 240 and then decreased slightly (Fig. 2), indicating that the rate of decay of oak litter was significantly higher under the original oak mixed forest than in the pure aspen stands (p < 0.01; Fig. 2). In contrast, the HFA index of birch litter was not significantly different from zero (p > 0.05; Fig. 2) during the entire incubation process, even though the HFA index

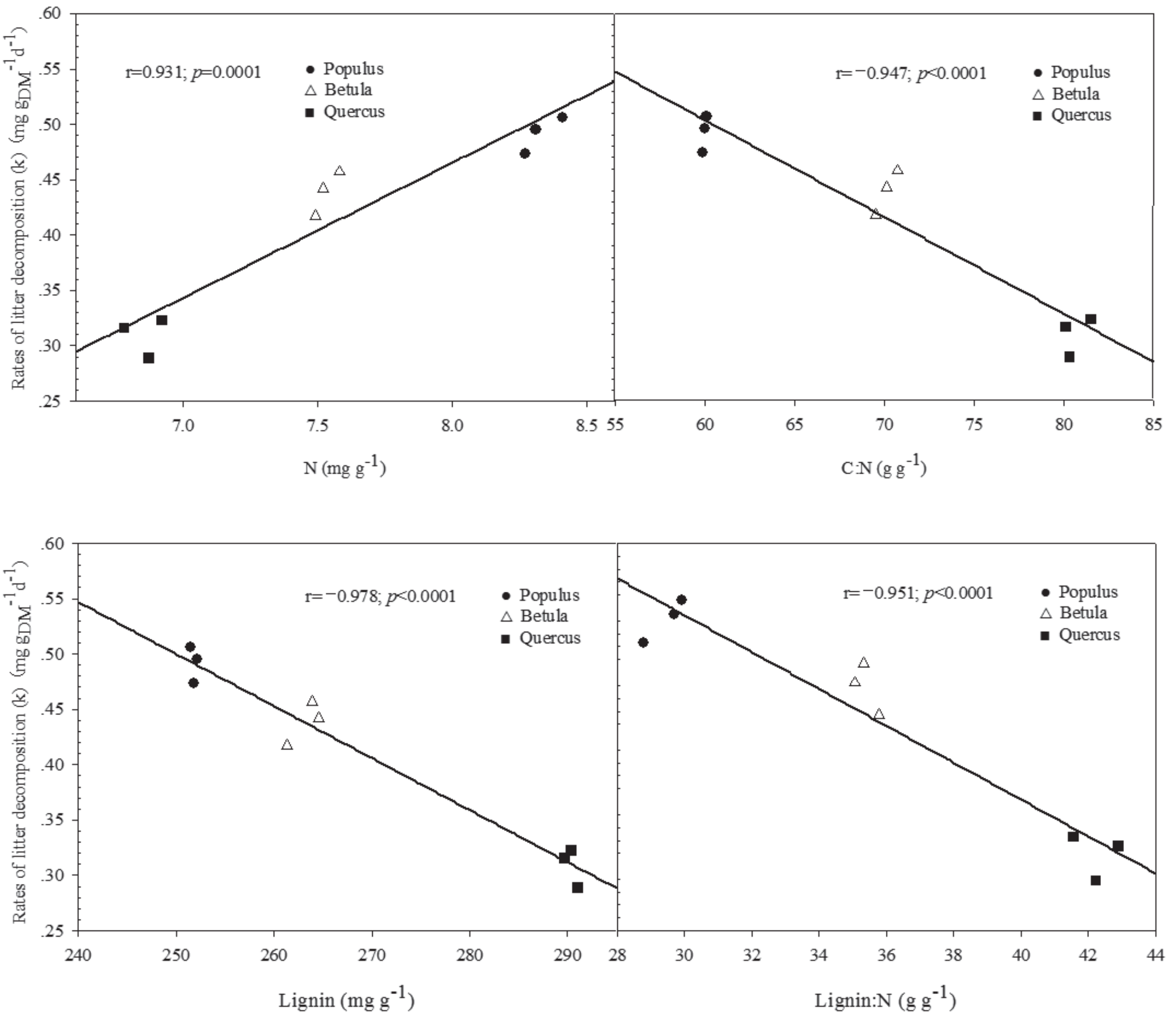

Fig. 1. Rates of litter decomposition (k) as a function of initial chemical concentrations or ratios of nutrients to lignin in three tested MONO litterbags incubated in temperate deciduous forest stands.

was negative at day 180. There was positive interaction between the rate of decomposition of oak litter and the forest where the oak litter originated. Therefore, the HFA hypothesis could be accepted for oak litter but not for birch litter.

Decomposition in Litter Mixtures: Synergistic or Antagonistic Effects

Results from the linear model showed that litter mixture had the least important effect on the rate of decomposition ($r^2 = 0.017$, $p < 0.01$; Table 5). There was no evidence of significant specific pair-wise interactions between litter mixture and the two factors litter quality and forest type, i.e., litter mixture × litter quality ($p = 0.109$; Table 5) and litter mixture × forest type ($p = 0.161$; Table 5).

The observed values of mass loss of the aspen/birch mixture were significantly higher than the predicted values based on the component species decomposing alone ($p < 0.01$; Table 4), showing a prominently synergistic effects at day 240 ($t = -2.48$, $p = 0.035$), at day 300 ($t = -2.54$, $p = 0.032$), and after 360 days ($t = -2.38$, $p = 0.041$; Fig. 3). However, the non-additive effects of all three litter mixtures were not significantly different from zero at day 180 ($t = -1.19$, $p = 0.265$). By contrast, significantly non-additive effects only found at day 300 for the aspen/oak mixture ($t = -2.35$, $p = 0.043$) and for the birch/oak mixture ($t = -2.28$, $p = 0.049$; Fig. 3).

Decomposition of Monospecific Litter and of Individual Litter in Mixed Stands

By separating litter mixtures by species, we detected the effects of individual litter species in the mixtures on mass loss. In the mixture of aspen and birch, the mass loss of aspen or birch litter was significantly higher than that of litter decomposing alone separately over the entire process ($p < 0.05$; Table 4). In addition, when mixed with oak, the mass loss of aspen or birch litter in the mixtures was not significantly different from that of monospecific aspen or birch litter separately over the entire process ($p > 0.05$; Table 4). Similarly, the mass loss of monospe-

Table 4. Mass loss over 360 days of individual types of litter for three tested leaf litter species and litter mixtures in *Populus davidiana* - *Betula platyphlla* - *Quercus mongolica* mixed forest (mean±SE, n = 3).

	Mass loss (%)					
	Individual types of litter			Litter mixtures		
	Populus	*Betula*	*Quercus*	Observed	Predicted	Difference
Monospecific litters	46.55±1.46^{bA}	43.61±1.85^{bA}	27.95±1.29^{aB}			
Populus+Betula	55.83±1.77^{a}	52.87±1.13^{a}		54.35^{A}	45.08^{B}	9.27
Populus+Quercus	49.72±1.59^{b}		30.57±1.93^{a}	40.15^{A}	37.25^{A}	2.89
Betula+Quercus		48.45±1.17^{b}	30.52±1.36^{a}	39.49^{A}	35.78^{A}	3.71

Different letters indicate significant differences. Lower letters denote differences between monospecific litter and litter in mixture. Capital letters denote difference between litter species and difference between observed and predicted mass loss of litter mixtures. Two-way ANOVA for differences (p < 0.05) among individual litters; t-tests for differences (p<0.05) between observed and predicted values. Relative differences of predicted and measured mass loss of litter.

cific oak litter in the mixtures was not significantly different from that of oak litter mixed with aspen or with birch litter (p > 0.05; Table 4).

Discussion

Effect of Litter Quality on Decomposition

Initial litter quality has been demonstrated to be an important indicator of litter decomposition in various ecosystems [15, 27, 38]. The quality of litter ranges from chemical qualities to the physical qualities of litter. Different litter species have their own particular combinations of quality parameters, causing the rate of litter decomposition to possibly be affected by several parameters simultaneously [4]. Therefore, Prescott drew the following conclusions: 1) paying attention to some chemical qualities of litter does not necessarily obtain a satisfactory correlation with the ability of litter to decompose, and 2) to conclude long-term rates of decomposition on the basis of early phase rates of decomposition might bring out a biased result [39]. In our study, however, the differences in the chemical quality of litter explained the specific differences in its rate of decomposition.

As predicted, the rates of decomposition of aspen and birch litter were faster throughout the incubation compared to that of oak litter in the same stand. Specifically, the rate of decomposition of litter was positively associated with its initial N concentration, but negatively with lignin concentration and C/N as well as lignin/N ratios [22, 37, 40]. In general, the rate of litter turnover is strongly controlled by the quality of the litter in temperate and boreal forests [41]. In short, the results of our study indicate

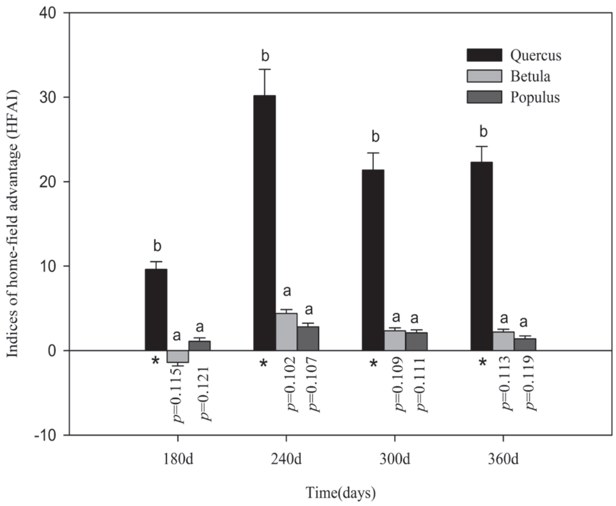

Fig. 2. Indices of home-field advantage (HFAI) calculated for pair-wise comparisons of decomposition of aspen litter vs. decomposition from birch and oak litter.

Notes: HFA indices based on mass loss of litter incubated after 180, 240, 300, and 360 days of litter decomposition in individual/MONO bags incubated in pure aspen and mixed stands. Positive values indicate that litter decomposes faster at "home" (the stand from which the litter had been derived) versus "away" (a stand with a different tree species composition), while negative values show the opposite. T-tests were used to check whether the relative mixture effect was significantly different from zero, indicated by * or p-value (mean±SE, n = 3).

Table 5. ANOVA indicates the statistical significance of three experimental factors (litter quality, litter mixing, and forest type) and their interaction terms that influence decomposition of leaf litter after 360 days of incubation.

Mechanism	df	F	P	r^2
Litter quality(L)	2	960.52	<0.01	0.618
Litter mixing(M)	2	107.56	<0.01	0.017
Forest type(F)	1	141.23	<0.01	0.083
L×M	4	1.63	0.109	0.004
L×F	2	7.78	<0.05	0.007
M×F	2	1.37	0.161	0.002
L×M×F	4	0.98	0.435	0.001

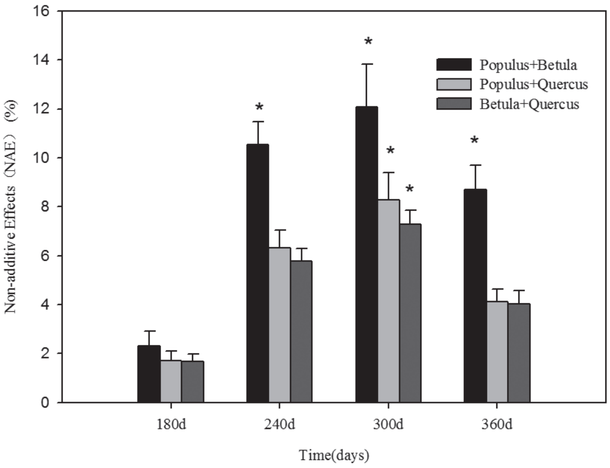

Fig. 3. Non-additive effects (NAE) on mass remaining (mean ±SE, *n* = 3) of all litter mixture treatments over time.
Note: t-tests were used to check whether NAE was significantly different from zero, indicated by *

that the chemical qualities of individual types of leaf litter would be decisive factors of rates of decay, especially in the initial stages of decomposition.

Effect of Forest Floor Environment on Decomposition

As with oak litter, the average mass loss was greater on the mixed forest floor than on the forest floor of pure aspen stands, which may be owed to the obvious differences in microbial communities [39, 42]. Due to the particular chemical compound of one leaf litter species, the forest floor produces specific environmental conditions that will affect the decomposition of its own litter over a long period [4, 43]. Leaf litter does not only affect the chemical component of the soil, but also its physical structure, indirectly controlling temperature and humidity. The organic forest topsoil, in turn, could influence the degree of litter decomposition, leading to the result that the microclimatic conditions and microbial decomposer communities are the most suitable for stand-specific litter decomposition [44]. Hence, there are positive oak litter-environment interactions that could support the HFA hypothesis. However, the data in this study did not support the HFA theory for birch litter decomposition, for the reason that throughout the process of our experiment, the difference in its rate of decomposition was not significant between the mixed forest floor and that of pure aspen stands. Owing to the high N content and low C/N, birch litter has high content of relative degradable chemical substances, which lead to the lower specialized degree in soil microorganisms [45-46]. By contrast, oak litter has lower litter quality than birch litter (such as high content of lignin and cellulose, which are difficult to be degraded), which leads to the higher specialized degree in soil microorganisms [45, 46]. Therefore, the intensity of HFA of oak litter was relatively lower than that of birch litter.

Effect of Litter Mixture on Decomposition

A number of studies have shown that many mixed-litter decompositions exhibit non-additive effects, which is the reason that the rates of decomposition of observed values in the litter mixture generally deviate from predicted values calculated on the rates of decay of single species. Some potential mechanisms have been put forward to account for the non-additive effects of litter mixtures on the rate of decay [23, 47-48].

In this study, our data indicated that the presence of aspen litter increased the rate of decomposition of birch litter in mixtures, and birch litter in this mixture increased the rate of decomposition of the aspen litter in return, which can be explained by the resource complementarity theory [48], since nutrient elements from higher-quality litter (aspen or birch) could be transferred to lower-quality litter (oak) so as to subsidize the microbial community, which accelerates the decomposition of lower-quality litter (oak) [15, 49-50]. However, in our study the data indicated that the rate of decomposition of oak litter in the mixtures was barely influenced by neighboring species, while aspen and birch litter in these mixtures decomposed faster than monoculture separately, resulting in an overall weaker positive non-additive effect in mixtures. The possible underlying reason is that the strongly lignified leaf tissue of oak litter could form high structural stability, which could hamper further decomposition of leaf litter [51]. For the aspen or birch litter mixed with oak litter, the decomposition of recalcitrant lignin from oak litter may coincide with the decomposition of labile compounds from aspen or birch litter, which promote enzyme activities toward lignified structures in cell walls so as to decompose more labile compounds in aspen or birch litter [51-52].

Our results suggest that the positive non-additive effect of litter mixtures changes over time (Fig. 3), which is mainly caused by the temporal variations of litter quality, microbial activity, and microclimate in the decomposition process [53-54]. With the ongoing incubation, litter quality became reduced as leaching and decomposition of labile compounds in litter mixtures progressed, and temperature dropped at the end of the study, which all contributed to the decrease in biomass of microorganism and microbial activity. Therefore, the magnitude of non-additive effects decreased at the end of the study [27].

Effect of Interactions between Factors on Decomposition

As proposed, our original approach was to separate the individual species in the mixtures in order to make it possible to weigh their relative contributions in terms of partitioning the variation. The results of our experiment confirmed the effect of all three factors on litter decomposition. Their effect is ranked in the following order: litter quality followed by forest type and, to a lesser extent, litter mixture. Interactions between litter quality and forest type (litter quality × forest type) also significantly affected litter decomposition. The other interaction terms (litter quality × litter mixture, litter mixture × forest type, and litter quality × litter mixture × forest type) are not discussed, given that their contribution to explaining the total variation of the different parameters was negligible (Table 5).

Conclusions

This study has demonstrated that litter quality, litter mixture, and forest type are the most important drivers of litter decomposition in Chinese temperate forests. In the first instance, we conclude that the rate of decomposition of aspen litter is faster than that of birch and oak under all conditions, indicating that the rate of litter decomposition is negatively correlated with the initial C/N ratio. Secondly, we found that a litter mixture alters the decomposition of individual types of litter and has a synergistic effect on litter mixture with similar leaf texture (aspen and birch) vs. a neutral effect on litter mixture with distinct leaf texture (aspen/oak and birch/oak). In the end, it appears that the mass loss of oak litter was greater in mixed birch forests than in pure aspen stands, favoring the HFA, while the mass loss of birch litter was not significantly different between mixed and pure aspen stands, denying the HFA. Therefore, we conclude that litter decomposition is, essentially, not only mainly affected by litter quality but also, indirectly, by the specific conditions in which decomposer communities differ and by litter mixture. Our results contribute to a better understanding of the effect of controlling factors on litter decomposition processes and should guide future work to reveal the role of drivers in regulating biogeochemical cycles in other forest ecosystems.

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