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REGULAR ARTICLE

Differential responses of litter decomposition to climate between wetland and upland ecosystems in China

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Abstract
Background and aims In upland ecosystems, climate and initial litter quality are the two major factors influencing decomposition rates regionally and globally. Litters are exposed to a different decomposition environment in wetlands than in upland ecosystems, but the driving factors of litter decomposition in wetlands at a large scale are still unclear.
Methods We established a comprehensive database of litter decomposition in China, including 249 datasets and 27 pairs of sites, to examine the controlling factors of decomposition in both wetland and upland ecosystems at the regional scale.
Results Both ecosystems showed similar climatic conditions, but the average litter decomposition potential was higher in wetlands than in upland ecosystems, as indicated by a higher initial K content and lower initial carbon content. The average decomposition rate in wetlands was almost 3 times higher than that in upland ecosystems. In both ecosystems, the decomposition rate increased with the mean annual temperature, mean annual precipitation, and initial N content. However, linear regressions of these variables with the decomposition rate indicated steeper slopes in wetlands than in upland ecosystems.
Conclusions The litter decomposition rate responded to climate and initial N content in both ecosystem types, but these responses were more rapid in wetlands than upland ecosystems. Wetland ecosystems should be given more attention when studying the responses of litter dynamics to future climate changes.

Keywords Litter decomposition rate · Wetlands · Mean annual temperature · Mean annual precipitation · Initial litter quality

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Introduction

Litter decomposition is essential to the carbon and nutrient cycling of ecosystems (Aerts 2006; Shiels 2006). Climate (mainly temperature and precipitation) and initial litter quality (i.e., nutrient, C, and lignin content) are the two major factors controlling litter decomposition rates directly on large spatial scales (Zhang and Wang

2015; Waring 2012). Climate also indirectly influences decay rates by modifying litter qualities (Bontti et al. 2009; Alvarez-Clare and Mack 2011). Understanding the distribution of litter decomposition rates along climate gradients is critical for the accurate prediction of long-term ecosystem C and N cycling in future climatic scenarios (Cheng et al. 2010). Several comprehensive databases have revealed that the litter decomposition rate in upland ecosystems increases with temperature, precipitation or litter nutrients regionally and globally (Meentemeyer 1978; Silver and Miya 2001; Liski et al. 2003; Zhang et al. 2008; Kang et al. 2010; Zhang and Wang 2015). Litters are exposed to permanent or temporary high moisture of water in wetlands, which is different from the conditions in upland ecosystems. However, it is still not entirely clear how wetland litter decomposition rates are distributed on a large spatial scale.

Under the Ramsar wetland conservation treaty, wetlands are "areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water with a depth at low tide that does not exceed 6 m" (Davidson and Max 2018). High moisture in wetlands often results in variation of physico-chemical conditions, which in turn regulate litter decomposition processes (Torremorell and Gantes 2010). Due to the high moisture content in wetlands, litter decomposition might be hindered since decomposers' respiration declines under anoxic and cold conditions (Torremorell and Gantes 2010; Fonseca et al. 2013). However, in other studies, decomposition was enhanced by easy leaching and fragmentation due to the presence of high moisture (Larmola et al. 2006). The overall effects of high moisture are site-specific, as reported by many studies (Trinder et al. 2008; Datry et al. 2011; Straková et al. 2011; Fonseca et al. 2013; Duan et al. 2018).

Various types of wetlands (e.g., riparian zones, lakes, peatlands, swamps, ponds, marshes, mangroves, alpine wetlands, and estuaries) are widely distributed across China. In this study, a comprehensive database was established of litter from both wetland and upland ecosystems in China to evaluate the major controlling factors of litter decomposition rates in both ecosystem types. We hypothesized that 1) the decomposition rate increased with increasing temperature and precipitation in both ecosystems and 2) the response of the decomposition rate to temperature and precipitation was more rapid in wetlands than in upland ecosystems.

Materials and methods

Data collection

We collected published papers relating to litter decomposition, climate and/or initial litter quality using the Web of Science database. The database included decomposition rates (k values) or mass loss, at least one index of initial litter quality (namely, contents of carbon (C), nitrogen (N), phosphorus (P), potassium (K), lignin and cellulose), climate (namely, mean annual temperature (MAT) and mean annual precipitation (MAP)), and site latitude and longitude. Some data were absent in the climate information; thus, we used a climate database to infer MAT and MAP through latitude and longitude information (Kang et al. 2010). For missing litter qualities, the data were obtained from other papers that used the same litter from the same study site (Silver and Miya 2001).

For each site, data were collected from wetlands and upland ecosystems. The distance between the two pairs of ecosystems types was mostly less than 80 km. The paired Student's t test results showed no significant differences in MAT or MAP between ecosystem types ($p > 0.05$).

Criteria used to filter collected data

Only litter decomposition in its native environment was used due to the possible potential influences of the home-field advantage (Ayres et al. 2009). In addition, we only selected data from studies that used the litterbag method to reduce the effect of measurement protocols. Although this method has some limitations, including burial of surface bags by falling litter through time, microclimatic effects, and potential exclusion of soil fauna (De Santo et al. 1993; Kurz-Besson et al. 2005), it remains the best method available for generating a large decomposition database (Kurz-Besson et al. 2005). Studies on the decomposition of mixed litter were excluded due to the fact that decomposition rates are often more variable in mixtures than in single litter (Xie et al. 2016a). Beyond that, in the studies on decomposition designed for special purposes (i.e., fire, fertilization and clear-cut), only data from the control treatment were kept, litter decomposition rates obtained from greenhouse experiments were discarded.

In addition, as litter decomposition is dependent upon the phase of the decomposition process (Adair et al. 2008; Freschet et al. 2012), the relative importance of abiotic factors versus litter chemistry can vary throughout the process of decay. Therefore, only data with incubation periods from 9 to 18 months were selected (Zhang and Wang 2015).

A total of 249 datasets were included, encompassing 181 litter species, 30 wetlands and 37 upland ecosystems from 27 sites (Appendix 1). The sites were distributed relatively evenly across China (Fig. 1a, b) and included the main wetlands in China (Hu et al. 2014). The sites ranged from 18°11′ N to 48°23′ N in latitude, from 99°39′ N to 133°31′ N in longitude, from −1 to 24 °C in MAT, and from 447.9 to 2651.6 mm in MAP. The types of wetlands included riparian, stream, lake, swamp, mash, pond, mangrove, sandy beach, and alpine wetlands. The salty site was included because of its large area in China and its ecological significance.

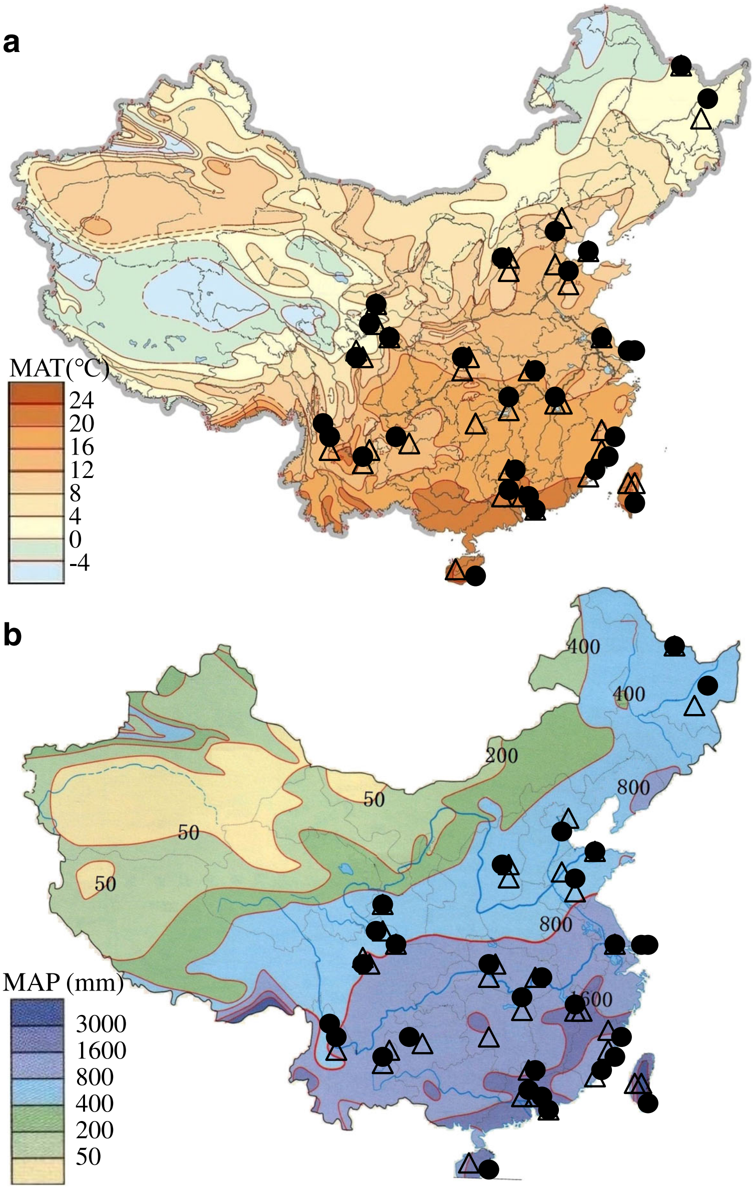

Fig. 1 Geographic distribution of the wetland (*black circles*) and upland sites (*open triangles*) contained in the database according to the mean annual temperature (MAT, A) or mean annual precipitation (MAP, B)

Data processing

For missing k values, the data were calculated by a single exponential decay function as in Eq. 1 (Olson 1963) when only mass loss was reported

$$W_t/W_0 = e^{-kt} \tag{1}$$

where W_0 is the initial litter mass and W_t is the mass remaining at time t (year).

To ensure data comparability, k values expressed by g g^{-1} d^{-1} in the original paper were converted to g g^{-1} y^{-1} (y^{-1} for short) by multiplying the values by 365. The unit mg g^{-1}, which is used by some authors for the initial litter quality, was converted to units of percentage (%).

A two-way analysis of variance (ANOVA) was used to test the differences in climate between ecosystem types, with 1 fixed variable (ecosystem type) and 1 random variable (site). For initial litter quality and litter decomposition rate, a non-parametric ANOVA was used instead, due to the unbalanced sample size or nonnormal distribution. Correlations were calculated to determine if the variables varied with each other in both wetland and upland ecosystems. Then, for the variables significantly correlated with the litter decomposition rate (k), simple linear regressions were calculated. An ANCOVA was used instead to test the differences in slopes, with MAT or MAP as covariate. Values were natural log transformed to homogenize the variances among groups if necessary. All statistical analyses were performed using the statistical software SPSS 21.

Results

Climate, initial litter quality and decomposition rate in wetlands and upland ecosystems

For 27 sites, litters from wetlands had initially less C chemical components (namely, C, lignin, and cellulose) ($p < 0.05$ or 0.01) but more K and N ($p < 0.05$ or 0.01, Table 1) compared with those from upland ecosystems, which might result from the richer soil nutrient in wetlands than upland ecosystems (Larmola et al. 2006). Other litter chemical components were not significantly different among ecosystem types ($p > 0.05$, Table 1). These results demonstrate that the initial decomposition potential (i.e., lower C chemical components and higher K content) was higher in litters from wetlands than those from terrestrial ecosystems.

The litter decomposition rates in wetlands and upland ecosystems ranged from 0.169 to 4.86 y^{-1} and 0.205 to 20.44 y^{-1}, respectively. They were significantly different among ecosystem types ($p < 0.01$, Table 1). The average decomposition rate in wetlands was almost 3 times the rate in upland ecosystems (Table 1). Although salt might have a significant negative impact on decomposition in the beach, mangrove and estuary sites, the average decomposition rate for the 5 salty sites (1.68 ±

Table 1 Comparison of climate, initial litter quality and decomposition rate at both wetlands and upland ecosystems in China

Parameter	Wetland ecosystem		Upland ecosystem		p value
	Mean ± S.E.	n	Mean ± S.E.	n	
MAT (°C)	13.3 ± 0.64	121	13.49 ± 0.59	128	0.163
MAP (mm)	1146 ± 48	121	1201 ± 49	128	0.894
C (%)	41.16 ± 1.07	104	47.71 ± 0.95	100	< 0.01
N (%)	1.08 ± 0.07	95	1.20 ± 0.05	114	0.035
P (%)	0.168 ± 0.033	78	0.137 ± 0.012	105	0.459
K (%)	0.963 ± 0.064	19	0.480 ± 0.039	69	< 0.01
Lignin (%)	20.86 ± 1.54	44	33.06 ± 1.46	59	< 0.01
Cellulose (%)	22.48 ± 1.11	30	17.91 ± 0.88	48	< 0.01
k (y^{-1})	2.4073 ± 0.3093	119	0.8302 ± 0.0631	127	< 0.01
Ratio of C:N	38.11 ± 0.25	90	39.85 ± 0.23	103	0.434

MAT and MAP indicate the mean annual temperature and mean annual precipitation, respectively. Differences in MAT and MAP were tested by two-way ANOVA with site and ecosystem type as main factors. Non-parametric ANOVA was used for comparison of initial litter quality as well as decomposition rate

0.18 y^{-1}) was still higher than that of the upland sites (1.12 ± 0.17 y^{-1}) ($p < 0.01$).

Linear correlations between initial litter quality, climate, and decomposition rate

Litter decomposition rates were influenced by climatic and initial litter quality variables (Tables 2 and 3). The litter decomposition rate was positively correlated with MAT, MAP and initial litter N content in both wetlands ($p < 0.01$, Table 2) and upland ecosystems ($p < 0.05$, Table 3). In upland ecosystems, the estimated litter decomposition rates tended to increase with initial litter K content ($p < 0.05$, Table 3) but decrease with initial litter C content ($p < 0.05$, Table 3).

Additionally, the initial contents of C chemical components were influenced by climate variables (Tables 2 and 3). In wetlands, initial litter C content was positively correlated with both MAT and MAP ($p < 0.01$) and initial litter lignin content with MAP ($p < 0.01$, Table 2). In upland ecosystems, initial litter lignin and cellulose contents were positively correlated with both MAT and MAP ($p < 0.01$ or $p < 0.05$, Table 3). However, in any of the ecosystem types, no significant linear correlation was shown between climatic conditions and the initial N, P and K contents in litter ($p > 0.05$, Tables 2 and 3).

Regressions of climate and initial litter quality parameters with litter decomposition rates

The variation in *k* values was larger in the sites where MAT >10 °C (or MAP >1100 mm) than the sites where MAT <10 °C (or MAP <1100 mm) (Fig. 2a, b). In the linear correlations of *k* values versus climate variables, the coefficients of the slope were very significant in wetlands ($p < 0.001$), and significant in upland ecosystems (for MAT, $p = 0.0218$; for MAT, $p = 0.0438$). The regressions of the litter decomposition rate with climate and initial litter quality showed that the slope value was greater for wetlands than upland ecosystems (Table 4 and Fig. 2a, b). The ANCOVA results proved steeper slopes for climate in wetlands than in upland ecosystems ($p < 0.05$ or 0.01). The slope values for MAT, MAP, and initial litter N for wetlands were approximately 7, 13, and 5.3 times higher than those for upland ecosystems, respectively.

Discussion

The average decomposition rate in upland ecosystems in China was consistent with the results of the other humid zones (MAP >591 mm) with low or middle latitude (from 54°N to 41°S) (Zhang and Wang 2015). Litter

Table 2 Correlation coefficient (r) and sample size (n) obtained between initial litter quality, climate, and decomposition rate in wetland ecosystems

		MAT	MAP	C	N	P	K	Lignin	Cellulose
C	r	0.388**	0.303**						
	n	104	104						
N	r	0.181	0.163	−0.070					
	n	95	95	94					
P	r	−0.120	−0.112	−0.054	0.430**				
	n	78	78	77	78				
K	r	0.161	−0.311	−0.641**	−0.047	0.174			
	n	19	19	19	19	19			
Lignin	r	0.142	0.421**	0.516**	−0.034	0.087	−0.994**		
	n	44	44	44	44	39	17		
Cellulose	r	0.208	−0.119	−0.390*	−0.007	−0.294	0.711**	−0.402*	
	n	30	30	30	30	28	17	30	
k	r	0.328**	0.486**	−0.057	0.372**	0.185	−0.229	0.148	−0.326
	n	119	119	102	95	78	19	44	30

MAT and MAP indicate the mean annual temperature and mean annual precipitation, respectively. *$p < 0.05$; **$p < 0.01$

Table 3 Correlation coefficient (r) and sample size (n) obtained between initial litter quality, climate, and decomposition rate in upland ecosystems

		MAT	MAP	C	N	P	K	Lignin	Cellulose
C	r	−0.001	0.020						
	n	100	100						
N	r	0.024	−0.147	−0.031					
	n	114	114	100					
P	r	−0.053	0.054	−0.246*	0.193				
	n	105	105	86	100				
K	r	0.024	0.178	−0.248	0.422**	0.575**			
	n	69	69	59	67	68			
Lignin	r	0.565**	0.684**	0.055	−0.303*	−0.147	0.183		
	n	59	59	56	57	57	37		
Cellulose	r	0.378**	0.337*	0.116	−0.009	−0.321*	−0.461*	−0.069	
	n	48	48	45	46	46	30	48	
k	r	0.203*	0.179*	−0.211*	0.202*	−0.056	0.247*	0.127	0.111
	n	127	127	99	113	105	69	59	48

MAT and MAP indicate the mean annual temperature and mean annual precipitation, respectively. $^{*}p < 0.05$; $^{**}p < 0.01$

decomposition rates were different among ecosystem types under similar climatic conditions. One explanation is related to the high moisture content in wetlands. In addition to high moisture increasing leaching and physical fragmentation (Wallis and Raulings 2011), a high moisture content might also stimulate litter decomposition by favouring decomposers (Torremorell and Gantes 2010). In fact, our previous studies also provided evidence that, in wetlands, litter decomposition is stimulated not only by inundation events but also by high soil

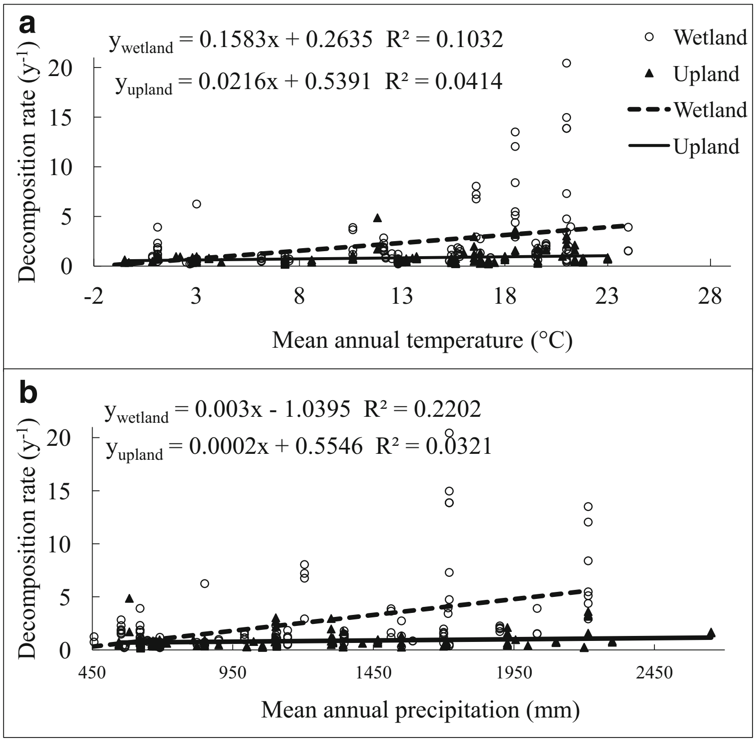

Fig. 2 Variation of litter decomposition rates with mean annual temperature (MAT, A) and mean annual precipitation (MAP, B) in both wetlands and upland ecosystems

moisture content (Xie et al. 2016a, b). Furthermore, the initial litter quality might provide a further explanation. Microbes consuming the litters must assimilate nutrients from available resources (including litters) to maintain the balance in microbial composition (Beth et al. 2012). Compared with those from upland ecosystems, litters from wetlands were richer in initial K content and thus more suitable for microbial consumption.

The litter decomposition rate was positively correlated with MAT and MAP in both types of ecosystems, which is consistent with our first hypothesis. Such positive correlations have been found across different climatic zones (Zhang et al. 2008). High MAT and MAP increase the temperature and moisture of the decomposition environment, respectively, which in turn favour the growth and reproduction of decomposers (Osono et al. 2003; Manzoni et al. 2010). In addition, high moisture also facilitates leaching and fragmentation, which are the key processes of decay (Manzoni et al. 2010).

The linear correlation suggested that, in both ecosystems, with increasing MAT or MAP, the decomposition potential declined (i.e., the initial C chemical components increased), but the decomposition rate increased. Interestingly, the climate did not indirectly influence decay rates via its effects on the initial litter quality. It seems that the decline of decomposition potential linked to the initial quality was overridden by the climatic gradient.. In fact, most studies focusing on litter decomposition at a large spatial scale have proven that climate is more important than initial litter quality in controlling litter decay (Silver and Miya 2001; Prescott 2010).

Previous studies reporting regression slope values of decomposition rate varying with climate are resumed in Table 4. Our estimations of slope values for upland ecosystems are consistent with these results.

Table 4 Linear regressions of litter decomposition rate (k, y^{-1}, by litterbag method) versus climate or initial litter quality variable

Parameter	Regression equation
Wetland ecosystem in China (this study)	
MAP (°C) → MAT (°C)	$k = 0.2635 + 0.1583$ MAT
MAP (mm)	$k = -1.0395 + 0.0030$ MAP
N (%)	$k = 0.6512 + 1.232$ N
Upland ecosystem in China (this study)	
MAT (°C)	$k = 0.5391 + 0.0216$ MAT
MAP (mm)	$k = 0.5546 + 0.00023$ MAP
C (%)	$k = 1.4198–0.0137$ C
N (%)	$k = 0.5022 + 0.2322$ N
K (%)	$k = 0.535 + 0.5957$ K
Global upland ecosystems (Zhang et al. 2008)	
MAT (°C)	$k = 0.0819 + 0.0376$ MAT
MAP (mm)	$k = 0.3156 + 0.0001$ MAP
N (%)	$k = -0.131 + 0.268$ N
K (%)	$k = 0.3333 + 1.4956$ K
Leaf litter in north-central Florida, USA (Bray et al. 2012)	
N (%)	Slope value: 0.75
Forest leaf litter in China (Zhou et al. 2008)	
N (%)	$k = -0.539 + 1.208$ N
Forest leaf litter in Beijing, China (Zhou et al. 2008)	
N (%)	$k = -0.503 + 0.881$ N
Forest in Hawaii, USA (Cusack et al. 2009)	
MAP (mm)	$k = -0.011 + 0.0004$ MAP
Patagonian steppe (Yahdjian and Sala 2008)	
MAP (mm)	$k = 0.14 + 0.0007$ MAP
Scots pine needle litter in Europe (Berg et al. 1993)	
MAT (°C)	$k = 0.189 + 0.0241$ MAT
Pinus sylvestris needle in Europe (Berg et al. 1993)	
MAT (°C)	Slope value: 0.042~0.055
Litter in USA and Central America (Gholz et al. 2010)	
MAT (°C)	Slope value: 0.027~0.068

MAT and MAP indicate the mean annual temperature and mean annual precipitation, respectively. WT indicates water temperature

The slope value in the regression was greater in wetlands than upland ecosystems, which is consistent with our second hypothesis. One explanation might relate to different constraints (climate or initial litter quality) of litter decomposition at different climates (humid or arid, warm or cold). For decomposition to occur quickly and/or completely, conditions must surpass certain thresholds of constraints, i.e., temperature, moisture, and initial litter quality (Prescott 2010). At sites with low MAT, where temperature constrains decomposition, other factors (i.e., moisture and initial litter quality) might be less important in deterging the litter decomposition (Vitousek 2004; Rejmánková and Sirová 2006; Bradford et al. 2016). Therefore, small differences were observed in litter decomposition rates between ecosystem types at these sites. However, at sites with high MAT, the constraint of temperature might be weakened. Thus, factors such as high moisture or a high nutrient content in water in wetlands might be more important in controlling decomposition processes, leading to a greater difference in decomposition rates between ecosystem types at high MAT sites than at low MAT sites (Zhang et al. 2008).

Another explanation might be related to C decomposition kinetics. Litters from wetlands have initially less C and lignin contents than those from upland ecosystems. Similarly, Fierer et al. (2005) observed that the sensitivity of decay to temperature increased as initial litter organic C content declined. Enzymatic reactions required to metabolize structurally complex, low-quality C substrates should have a higher net activation energy than reactions metabolizing C substrates that are structurally simpler and with higher quality (Bosatta and Ågren 1999). The temperature sensitivity of microbial decomposition tended to be inversely related to the initial litter carbon quality, which in turn regulates the temperature sensitivity of litter decomposition (Bosatta and Ågren 1999).

Conclusions

Our analyses show that litter decays faster in wetlands than in upland ecosystems on average in China, which is related to climate conditions and initial litter quality. However, the responses of litter decomposition rate to climate variables and initial litter N content were more rapid in wetlands than in upland ecosystems.

Spatial geographical modeling should be used to link the decomposition rate to MAT and MAP and initial litter quality simultaneously. Also, multilinear or non-linear regression should be tested to improve the modeling of decomposition rate at large geographical scales. A more thorough understanding of the factors that control litter decomposition in wetlands will improve our ability to model global C dynamics and predict the effects of future climate and other global changes on biogeochemical cycles. Future studies should incorporate analyses of soil microbial communities and fungal colonization to improve our understanding of how organisms influence rates of litter decay in wetlands at local, regional, and global scales.

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