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Effects of water table on cellulose and lignin degradation of *Carex cinerascens* in a large seasonal floodplain

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ABSTRACT

Water table affects litter decomposition in wetlands, but its effects on the degradation of cellulose and lignin are poorly understood. We performed a decomposition experiment in Poyang Lake Wetland, to determine how water table affected the degradation of cellulose and lignin. After 60 days of decomposition at a site with a relatively highly water table, 46.19% of initial cellulose and 41.95% of initial lignin remained. Decay rates of both cellulose and lignin increased as the depth of the water table increased. Principle component analysis showed that the decay rates of cellulose and lignin increased with increasing soil pH, but decreased with increasing contents of clay and fungi: bacteria ratio. The path model accounted for 66% and 79% of the variation in cellulose and lignin decay rates, respectively, and considered the effects of interactions between the water table and related factors. The cellulose decay rate was affected by the water table with a direct coefficient of 0.47, and an indirect coefficient of 0.65, but the lignin decay rate was indirectly affected by water table (coefficient, 1.25) and directly affected by soil property (coefficient, 0.67). Thus, the water table affected the decomposition of cellulose and lignin via different mechanisms.

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Decay rate; path model; lignin degradation; cellulose degradation; Poyang Lake Wetland; simple exponential model

Introduction

Wetlands are ecosystems between aquatic and terrestrial ecosystems that are distinguished by special hydrological cycles, either at the surface or below ground (Shaffer et al. 2016). The decomposition of plant residues, a natural and critical process for wetland ecosystem function is essential to nutrient cycling (Mitsch and Gosselink 2000; Wu et al. 2017). This process is regulated by the relationship between leaf litter biochemical quality, site environment (mean annual temperature, mean annual precipitation, annual evapotranspiration), and decomposer community composition (Tang et al. 2014; Charman et al. 2015; Waddington et al. 2015; Liu et al. 2017). Cellulose and lignin are major components of plant residues in wetlands because of their slow decomposition rates under anoxic conditions (Williams and Yavitt 2003). Both cellulose and lignin can serve as indicators of the effects of anaerobic decay.

In terrestrial ecosystems, the soil micro-environment (for instance, the salinity gradient and microbial community types) is the main factor determining cellulose and lignin decomposition rates (Haraguchi et al. 2003). However, at the terrestrial–aquatic interface, especially in typical floodplain

wetlands, the height of the water table affects the community composition of soil microbes and their metabolic activity (Rice et al. 2006). This has important consequences for organic matter decomposition, accumulation, and transformation (Gerull et al. 2011). Environments with drying and rewetting cycles considerably accelerate leaf litter degradation (Abbott et al. 2013; Shi and Marschner 2014). Fluctuations in the depth of the water table affect the physical and chemical characteristics of the wetland soil, and affect the decomposition of plant residues via changes in the soil redox potential, pH, and nutrient contents (Abbott et al. 2013; Shi and Marschner 2014). Schellekens et al. (2015) reported that waterlogging and soil pH significantly affect cellulose and lignin decay processes. Alternate wet and dry periods and the relatively highly water table in wetlands results in a long-term imbalance between leaf litter production and decomposition (Schulze and Freibauer 2005). For example, in sphagnum peatlands, the lower water table restrained leaf litter decomposition by decreasing the activity of several enzymes, including glucosidase, chitinase, and phosphatase (Wiedermann et al. 2017). However, Trinder et al. (2008) reported that a high water table significantly inhibited C losses.

Researchers tend to over- or underestimate the rates of decay and nutrient return because they disregard variations in the height of the water table. Many studies have focused on the role of biotic factors (microorganisms), chemical factors, and physical conditions on the rate of organic matter decomposition in wetland ecosystems (Merovich 2014; Schellekens et al. 2015). Because of a lack of relevant data, it is difficult to quantify the effects of the water table and related micro-environmental factors on the decay rates of plant materials in wetland ecosystems. Hence, it is important to conduct field decomposition experiments to understand the mechanisms of cellulose and lignin decomposition in wetlands.

The water table zone is a comprehensive expression of fluctuations in water availability and microtopography; therefore, it represents the environmental changes driven by the hydrological regime. It is therefore necessary to study litter decay rates variations among different water table zones in wetland ecosystems. This study was designed to construct a comprehensive database of the decay rates of cellulose and lignin, as estimated by incubation of leaf litterbags in Poyang Lake, the largest seasonal floodplain wetland in China. We investigated the effects of the water table on the decay rates of cellulose and lignin at the experimental plot scale. The aim of this study was to quantify the direct and indirect effects (via soil physical, chemical and biological factors) of the water table on the cellulose and lignin decay rates. We hypothesized that both cellulose and lignin begin to degrade in the early period (0–60 d) of leaf litter decomposition, and that the decay rate of each component varies depending on the water table and the related environmental factors. These results will provide insights into C and nutrient cycling and will be useful for environmental impact assessments in land–lake ecosystems.

Materials and methods

Study area

The Poyang Lake Wetland (28°22′–29°45′N, 115°47′–116°45′E) is located in the middle of the Yangtze River basin in northern Jiangxi Province, China. The lake catchment is in a subtropical wet climate zone with an annual mean precipitation of 1680 mm that mainly falls between April and June, and an annual mean temperature of 17.5°C. The bottomlands are almost submerged during the wet season under seasonal changes in hydrology. However, after October, these submerged areas gradually become exposed. Because of the fluctuating water level, the plant communities form a typical ringed pattern along an elevation gradient. The dominant plant species in the Poyang Lake Wetland are *Carex cinerascens*, *Phragmites australis* and *Triarrhena sacchariflora* (Wang et al. 2013).

For this study, Baisha Lake, one of the shallow lakes in the Poyang Lake Wetland, was selected to perform the decomposition simulation field experiment. Our research focused on the dominant leaf litter type, *C. cinerascens*, in four zones spanning the water table zones in a total area of 200 m ×

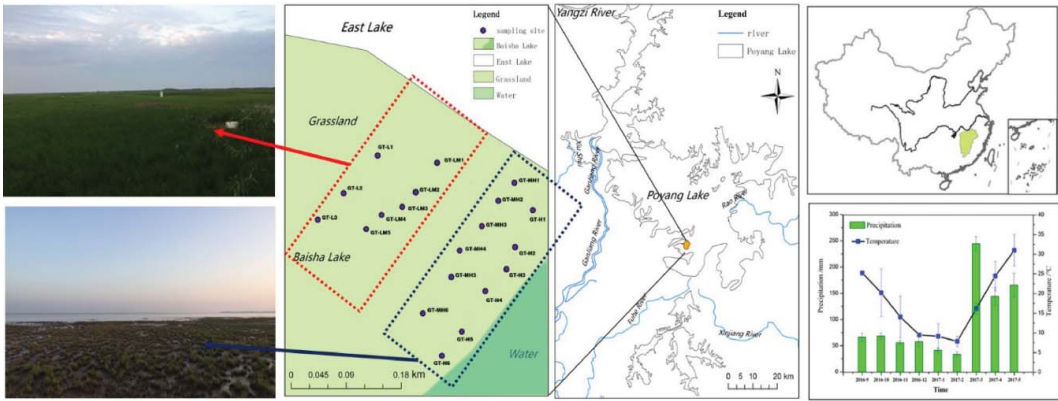


Figure 1. Location of sampling sites in Poyang Lake Wetland, China.

300 m, in the northwest of lake beach (Figure 1). In these zones, the height of the water table ranged from low to high, as follows: -25 to -50 cm (GT-L), -15 to -25 cm (GT-LM), -5 to -15 cm (GT-MH) and 5 to -5 cm (GT-H) (Zhang et al. 2018). Basic information for each water table zone is shown in Table 1. The water table was relatively stable in the dry season between the end of October and the beginning of March. During the experimental period, most water table zones in GT-L, GT-LM, and GT-MH became exposed and dried, while the moisture zone in GT-H remained submerged until mid-November and usually in alternate state of dry-wet. Three to six subplots were established for each water table zone (as soil factors in a relatively higher water table zone is stable, we only set 3 subplots in GT-L, set 5 subplots in GT-LM, and set 6 subplots in both GT-MH and GT-H).

Decomposition assay

The decomposition potential in plots along the water table zones was determined using a leaf litter-bag experiment, as described by Rejmánková and Houdková (2006). Mature *C. cinerascens* leaf litter was collected from a high elevation meadow in the Poyang Lake wetland. To avoid confounding influences on leaf litter decomposition processes, leaf litter was cut into 1-cm-long sections and pre-treated by washing with deionized water to remove surface impurities. We measured total C, total N, cellulose and lignin content in ten samples from the mixed leaf litter for initial component values. The components of the initial *C. cinerascens* litter (C, N, cellulose and lignin content) are presented in Table 2. First, 5 g air-dried *C. cinerascens* leaves were placed in each leaf litterbag. The leaf litterbags were made of Nytex mesh (size 80 mm), which minimized root in-growth and the influence of invertebrates. The bags were placed on the lakeshore on 15 October 2016 and were loosely attached to stakes with nylon cord to maintain their position near the sediment surface. Three replicate bags were collected from each plot on days 15, 30, 60, 90, 120, and 150. The experiment was terminated in April 2017 when the lake shore began to be submerged under water. A PVC tube (diameter,

Table 1. Basic information for experimental gradient zones.

Zones	Plant biomass (g m^{-2})	Mean height (cm)	Vegetation coverage (%)	Soil temperature ($^{\circ}\text{C}$)	Mean water table (cm)
GT-A	153.33 \pm 67.39	40.25 \pm 7.70	51	25.33 \pm 0.58	-(33.47 \pm 7.97)
GT-B	171.46 \pm 88.49	29.55 \pm 2.36	63	25.80 \pm 1.30	-(21.54 \pm 3.18)
GT-C	70.05 \pm 14.13	27.48 \pm 3.70	42	24.67 \pm 0.82	-(7.14 \pm 4.20)
GT-D	50.87 \pm 19.19	12.88 \pm 9.02	17	24.33 \pm 0.52	-(0.70 \pm 2.66)

Table 2. Abundances of C, N, cellulose and lignin in initial *Carex cinerascens* litter.

Plant litter	C (%)	N (%)	Cellulose (%)	Lignin (%)
<i>Carex cinerascens</i>	42.83	2.21	16.85	11.96

2.5 cm) was inserted beside the experimental plot to a depth of about 0.7 m deep to measure the height of the water table in each plot.

Previous studies (Gulis and Suberkropp 2003; Rejmánková and Sirova 2007) have reported that the effects of microbes on leaf litter decomposition increase rapidly in the first 30 days and remain stable for the next 200 days. On the basis of those results, we decided to use the decay rates of the first 60 days to indicate the decomposition level of cellulose and lignin along the water table zones. At each sampling time, leaf litter was removed from the leaf litterbag and a composite subsample from all three replicates was dried, weighed, and ground for further analyses. Leaf litter C and nitrogen (N) contents were determined using an element analyser (Elementar, Vario Max CN, Hanau, Germany). Cellulose and lignin contents were determined using the method of Ziegler et al. (1986).

Soil samples and measurement of physical and chemical properties

Soil samples were collected by a 20-mm diameter stainless steel soil augur. Samples were collected to a depth of 20cm from three subplots at each experimental site to analyse site micro-ecological environment. For each subplot, soil samples were mixed into one composite sample and stored at 4°C in a polyethylene sealed bag until analysis. After carefully removing fine roots and other organic detritus, each soil sample was divided into two parts. One part was stored at 4°C for microbial assays, and the other part was air-dried for analyses of soil chemical properties. Soil organic C (SOC) and total N (TN) were determined using an element analyser (Elementar, Vario Max CN). Soil total phosphorus (TP) was determined by ashing followed by an automated colorimetric procedure (U.S. Environmental Protection Agency 1993, Method 365.1). Soil moisture content was determined by the oven drying method (weighing before and after drying at 105°C for 72 h). Soil particle fractions were analysed with a Longbench Mastersizer 2000 instrument (Malvern Instruments, Malvern, England). Soil pH was determined using a pH meter (Sartorius, Germany).

Microbial community structure

The microbial community composition was evaluated by phospholipid fatty acids (PLFA) analysis as described by Frostegård and Bååth (1996). Fatty acids were extracted from fresh soil (equivalent to 8 g dry weight) using a one-phase extraction mixture (chloroform: methanol: phosphate buffer = 1: 2: 0.8, v/v/v). Fatty acid methyl esters (FAMES) were analyzed and quantified by gas chromatography–mass spectrometry (GC-MS) with a TRACE GC Ultra ISQ MS instrument (Thermo Scientific, Interscience, Louvain-la-Neuve, Belgium). The individual compounds were identified by comparing their relative retention times with those of 37 commercially available FAMES (FAME 37 47885-U, Supelco, Inc., Bellefonte, PA, USA) and a mixture of 26 bacterial FAMES (BAME 26 47080-U, Supelco, Inc.). The individual compounds were quantified by comparison with an internal standard.

Many studies have used PLFAs as biomarkers for different groups of microorganisms. In this study, we distinguished four microbial groups: Gram-positive (G+) bacteria (i13:0, i14:0, i15:0, i16:0, i17:0, a15:0, a16:0, a17:0, i15:1), Gram-negative (G–) bacteria (12:0,14:0, 15:0, 14:1 ω 5c,15:1 ω 6c, 16:1 ω 9c, cy17:0, cy19:0, 16:1 2OH, i15:0 3OH,i17:0 3OH), fungi (16:1 ω 5c, 18:3 ω 6c, 18:1 ω 9c), and actinomycetes (10Me17:0, 10Me18:0) (Frostegård and Bååth 1996; Frostegård et al. 2011; Bossio 1998; Sun et al. 2011; Wang et al. 2016).

Data analysis

Using *C. cinerascens* residues with the same surface area as the decomposition substrate allowed us to determine the effects of environmental factors on the decomposition rates of cellulose and lignin, since the effect of leaf litter quality had been eliminated. The differences in soil physical and chemical properties, abundance of soil microbial groups, proportions of initial cellulose and lignin, and carbon and nitrogen contents across the water table zones were analysed by one-way analysis of variance (ANOVA) combined with Dunnett's T3 post-hoc pairwise comparisons ($\alpha = 0.05$). We used a general linear model to test how the water table (factors), decomposition days (covariable), and their interaction affected the decay rates of cellulose and lignin across the 180-day experiment.

The decay rates of cellulose and lignin in the first 60 days (k_{60}) were calculated using the following simple exponential model (Olson 1963; Zhang et al. 2008):

$$\ln \frac{M_t}{M_0} = -k_{60}t$$

where M_0 is the initial mass and M_t is the remaining mass at time t .

Principal component analysis (PCA) was conducted to identify the main components by describing their variability in the studied plots and objectively separating the environmental gradients based on soil physical, soil chemical, and microbiological variables. The correlation coefficients between decay rates and the environmental variables were calculated using a linear regression model.

A path analysis was conducted to explore how soil physical, soil chemical, and microbiological factors control leaf litter decomposition across the water table zones. This was made by constructing structural equation models, known as the path models, based on the conceptual model shown in Figure 2. Structural equation modelling (SEM) is an advanced multivariate statistical technique that allows for hypotheses testing of complex path-relation networks (Grace et al. 2007). Path models were established and separately tested based on hypothetical connections between water table condition and the soil environmental factors and the decay rates of both cellulose and lignin. The goodness-of-fit of the model was determined by χ^2 test ($P > 0.05$). To obtain the most parsimonious model, the primary principal component scores of the soil physical, chemical, and microbiological variables were used to indicate the overall trend in soil properties and microbial abundance. The final model eliminated the nonsignificant indicators and pathways. The proportion of total variance explained by the model was represented by R^2 values (Grace et al. 2007).

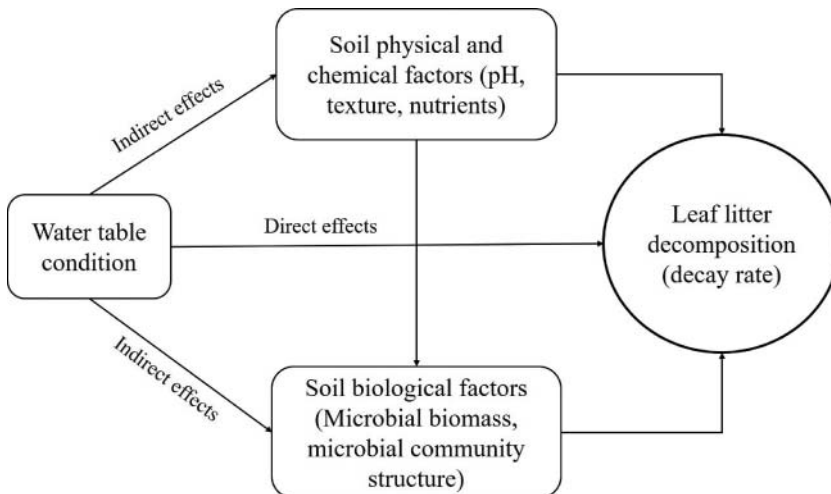


Figure 2. A conceptual model illustrating the interactions between water table conditions and soil physical, chemical and biological factors, and regulations of decay rates.

All statistical analyses were performed with R language V3.4.0 (R Development Core Team 2013). Maps of the spatial distribution of remaining cellulose and lignin were drawn using ArcMap 10.1 with the Kriging interpolation method.

Results

Decay rates of cellulose and lignin along the water table zones

The decay rates of both cellulose and lignin were significantly affected by the water table and the decomposition days (Table 3, $P < 0.05$). The spatial distribution map of cellulose and lignin remaining (Figure 3) shows the degradation pattern of cellulose and lignin according to variance in the water table. During the 150-day decomposition experiment, the amount of cellulose and lignin remaining was significantly lower in GT-H than in GT-L, GT-LM, and GT-MH (Figure 4(a,b); $P < 0.05$). Compared with GT-L, GT-H showed faster and more complete degradation of cellulose and lignin. After 15, 30, and 60 days of decomposition, the proportion of cellulose remaining was 14.69%, 20.84%, and 19.44% lower, respectively, in GT-H than in GT-L (Figure 4(a); $P < 0.05$). Similarly, after 30 and 60 days of decomposition, the proportion of lignin remaining was 27.21% and 33.36% lower, respectively, in GT-H than in GT-L (Figure 4(b); $P < 0.05$). Using the simple exponential decay model to fit the decomposition dynamic of cellulose and lignin, GT-H reached the maximum loss in the shortest time (Table 4; $P < 0.05$).

The dynamic changes in the decay rate of cellulose across the water table zones are shown in Figure 4(c). The decay rate increased in the first 30 days, and reached a climax in the next 30 days, and then began to decline after 60 days. During the first 90 days, the decay rate of cellulose was higher at GT-H than at other sites (Figure 4(c); $P < 0.05$). The decay rate of lignin in GT-L and GT-LM increased in the first 15 days and then began to decrease (Figure 4(d)). In GT-MH and GT-H, the decay rate of lignin increased in the first 30 days and then began to decrease. In GT-H, the lignin decay rate was significantly lower than at the other sites in the first 15 days (Figure 4(d);

Table 3. Results of general linear model showing effects of water table, decomposition period, and their interaction on decay rates of lignin and cellulose during 150-day experiment.

Factor	df ^a	Cellulose		Lignin	
		F-value	P-value	F-value	P-value
Water table	3	13.66	<0.00	44.21	<0.00
Period	4	87.10	<0.00	60.10	<0.00
Water table × period	12	3.58	<0.00	3.11	<0.00

^adf: degrees of freedom.

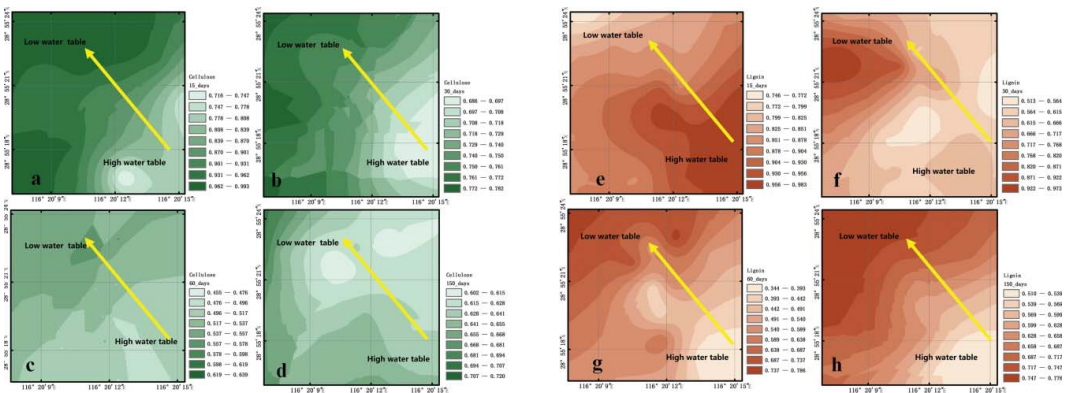


Figure 3. Spatial distribution of cellulose and lignin remaining at various times during decomposition period: (a & e): 15 days; (b & f): 30 days; (c & g): 60 days; and (d & h): 150 days. Yellow arrow indicates the direction of water table from high to low.

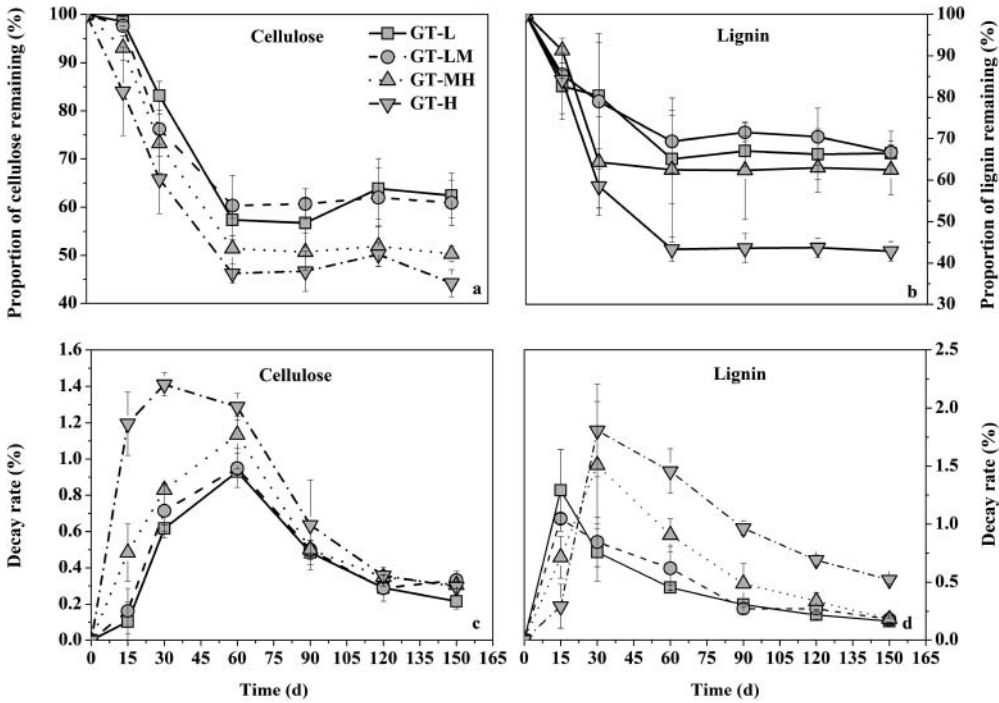


Figure 4. Proportion of initial cellulose and lignin remaining of leaf litter in litter bags (a & b), and variation in cellulose and lignin decay rates (c & d) during 150-day decomposition experiment along water table zones. Values shown are mean \pm SE.

$P < 0.05$) and significantly higher than that at other sites during the later decomposition period (Figure 4(d); $P < 0.05$).

Effects of soil environmental factors on decay rates of cellulose and lignin

All soil property indicators except soil temperature, TN, and TP showed significant differences across the water table zones (Table 5). Compared with sites with lower water tables, the site with the highest water table, GT-H, was characterized by significantly higher pH, moisture, and sand, and lower silt, clay, and SOC (Table 5, $P < 0.05$). As the height of the water table increased, the soil pH increased from 4.62 (in GT-L) to 5.05 (in GT-H), and soil moisture increased from 30.80% to 52.56% (Table 5, $P < 0.05$). Compared with GT-L, GT-MH and GT-H had 5.61% and 7.59% lower soil silt content, respectively, and 15.35% and 52.82% lower soil clay content, respectively (Table 5, $P < 0.05$). However, the sand content in GT-MH and GT-H was 3.35-fold and 4.28-fold higher, respectively, than that in GT-L (Table 5, $P < 0.05$). In GT-H, there were low soil TOC and TN contents, and high leaching of TP (Table 5). Compared with GT-L, GT-H had 53.49% lower SOC, 40.21% lower TN, and 26.09% lower TP (Table 5, $P < 0.05$).

Table 4. Decay rates of cellulose and lignin in first 60 days, as calculated using exponential decay model. Values followed by different letters are significantly different (Dunnett’s T3 post-hoc pairwise comparisons, $P < 0.05$).

zones	Cellulose				Lignin			
	$k_{60}(\%)^a$	R^2	$t_{50}(\text{d})^b$	$t_{99}(\text{d})^c$	$k_{60}(\%)^a$	R^2	$t_{50}(\text{d})^b$	$t_{99}(\text{d})^c$
GT-L	1.00 \pm 0.08 ^{bc}	0.93 \pm 0.01 ^a	69.77 \pm 7.01 ^{bc}	503.37 \pm 50.59 ^{bc}	0.40 \pm 0.07 ^b	0.89 \pm 0.09 ^a	192.50 \pm 42.87 ^c	1388.43 \pm 276.29 ^b
GT-LM	0.92 \pm 0.15 ^c	0.93 \pm 0.02 ^a	77.06 \pm 13.59 ^c	555.99 \pm 98.09 ^c	0.60 \pm 0.08 ^b	0.79 \pm 0.04 ^a	127.05 \pm 38.31 ^c	916.67 \pm 250.26 ^b
GT-MH	1.32 \pm 0.13 ^{ab}	0.95 \pm 0.02 ^a	53.10 \pm 5.63 ^{ab}	383.14 \pm 40.65 ^{ab}	0.97 \pm 0.12 ^b	0.85 \pm 0.11 ^a	74.46 \pm 45.50 ^b	537.30 \pm 335.08 ^b
GT-H	1.44 \pm 0.21 ^a	0.96 \pm 0.02 ^a	48.76 \pm 5.84 ^a	351.82 \pm 42.16 ^a	1.45 \pm 0.15 ^a	0.94 \pm 0.05 ^a	48.26 \pm 5.41 ^a	348.21 \pm 39.03 ^a

^a k_{60} : Decay rate in first 60 d; ^b t_{50} : Time for proportion of initial cellulose or lignin to reach 50%, $t_{50} = 0.693/k$; ^c t_{99} : Time for proportion of initial cellulose or lignin to reach the minimum, $t_{99} = 5/k$.

Table 5. Descriptive statistics of soil physical, chemical and microbial indicators along the water table gradient. Values shown are mean ± standard deviation. Different letters indicate significant differences (Dunnett’s T3 post-hoc pairwise comparisons) among four water table gradients (** $P < 0.001$; * $0.001 < P < 0.01$; * $0.01 < P < 0.05$; ns, not significant at $P \geq 0.05$).

		Water table gradient				F-value
Variables		GT-A	GT-B	GT-C	GT-D	
Physical and chemical properties	Temperature	25.33±0.58 ^a	25.80±1.30 ^a	24.67±0.82 ^a	24.33±0.52 ^a	3.0 ns
	Soil pH	4.62±0.11 ^a	4.68±0.05 ^a	4.86±0.07 ^b	5.05±0.05 ^c	37.51***
	Moisture (%)	30.80±1.61 ^a	31.36±2.82 ^a	33.93±6.24 ^a	52.56±10.20 ^b	4.16*
	Sand (%)	3.44±1.36 ^a	6.77±1.68 ^a	11.53±2.92 ^b	14.74±3.45 ^b	12.65***
	Silt (%)	78.74±0.88 ^c	76.70±1.49 ^b	74.33±1.38 ^a	73.19±1.41 ^a	13.91***
	Clay (%)	17.30±1.12 ^c	16.45±0.74 ^c	14.65±1.84 ^b	11.32±0.79 ^a	22.28***
	SOC (g kg ⁻¹)	10.32±3.12 ^b	9.73±1.85 ^b	6.19±1.23 ^a	4.80±0.60 ^a	8.76**
	TN (g kg ⁻¹)	0.97±0.08 ^a	0.98±0.19 ^a	0.66±0.03 ^a	0.58±0.17 ^a	2.71ns
Microbial properties (ng·g ⁻¹)	TP (mg kg ⁻¹)	328.50±44.09 ^b	321.13±32.41 ^b	297.10±71.71 ^b	242.80±60.64 ^a	2.34ns
	Bacteria	1920.3±455.35 ^a	2434.42±319.68 ^a	2245.46±702.56 ^a	4171.69±610.48 ^b	17.53***
	Fungi	312.05±39.98 ^a	388.09±112.50 ^b	323.97±152.06 ^{ab}	398.20±77.30 ^b	19.80***
	Actinomycetes	140.93±34.12 ^a	185.62±24.62 ^b	224.67±40.87 ^{bc}	246.48±20.35 ^c	9.33**
	G (+) Bacteria	929.92±217.48 ^a	1108.19±76.65 ^b	1149.30±325.37 ^{ab}	1932.81±197.93 ^b	19.61***
	G (-) Bacteria	435.01±59.75 ^a	547.49±95.58 ^a	504.43±243.80 ^a	1336.26±120.73 ^b	46.71***
	Total PLFAs	2416.93±527.36 ^a	3008.14±447.18 ^a	2867.90±869.20 ^a	4997.95±654.36 ^b	15.75***

In terms of soil microbial properties, GT-H was characterized by significantly higher abundance of total bacteria, G+ bacteria, G- bacteria, fungi, actinomycetes, and total PLFAs (Table 5; $P < 0.05$). Compared with GT-L, GT-H showed 106.79% higher total PLFAs, 117.24% higher abundance of bacteria, and 74.89% higher abundance of actinomycetes. From GT-L to GT-H, the abundance of G- bacteria increased 1.92-fold more than that of G+ bacteria. In GT-L, GT-LM, GT-MH, and GT-H, bacteria accounted for 79.45%, 80.93%, 78.30%, 83.47% of the total PLFAs; fungi accounted for 12.91%, 12.90%, 11.30%, 7.98%; and actinomycetes accounted for 5.83%, 6.17%, 7.83%, 4.93%, respectively.

Soil environmental variables were synthesized into two PCs that together accounted for 99.99% of the variation in those properties (Figure 5). The first PC accounted for 94.71% of the variation in these variables; soil pH, F: B and clay content had roughly equal loadings. The second PC only

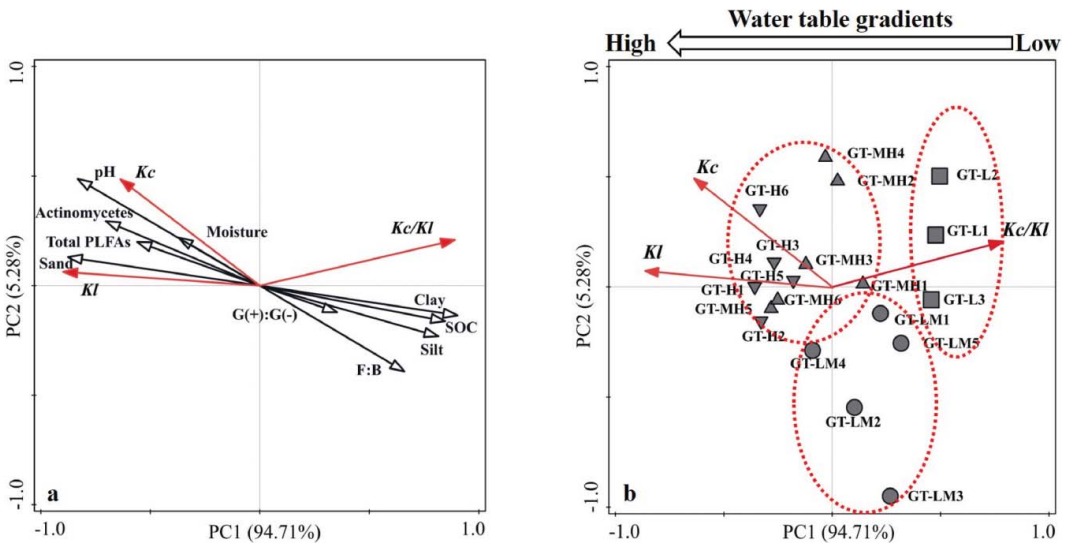


Figure 5. Principal component analysis of soil variables and their relationships with decay rate of cellulose and lignin. Experimental plots were separated into three groups (red dotted circles). Green and black arrows indicate soil variables; the red arrow indicates decay rate of cellulose (Kc) and lignin (Kl).

accounted for 5.28% of the variation in these variables. The decay rates of cellulose and lignin were significantly positively correlated with soil pH (Figure 5(a); $P < 0.001$, $F = 30.43$ and $P < 0.001$, $F = 33.22$, respectively), and negatively and significantly correlated with clay content (Figure 5(a); $P < 0.001$, $F = 14.90$ and $P < 0.001$, $F = 52.04$, respectively). The decay rates of both cellulose and lignin were negatively correlated with the F: B ratio (Figure 5(a); $P < 0.001$, $F = 18.60$ and $P < 0.001$, $F = 12.75$, respectively). Distribution pattern of the experimental sites and its relationship with decay rates of cellulose (Kc) and lignin (Kl) as well as Kc/Kl was presented in Figure 4(b).

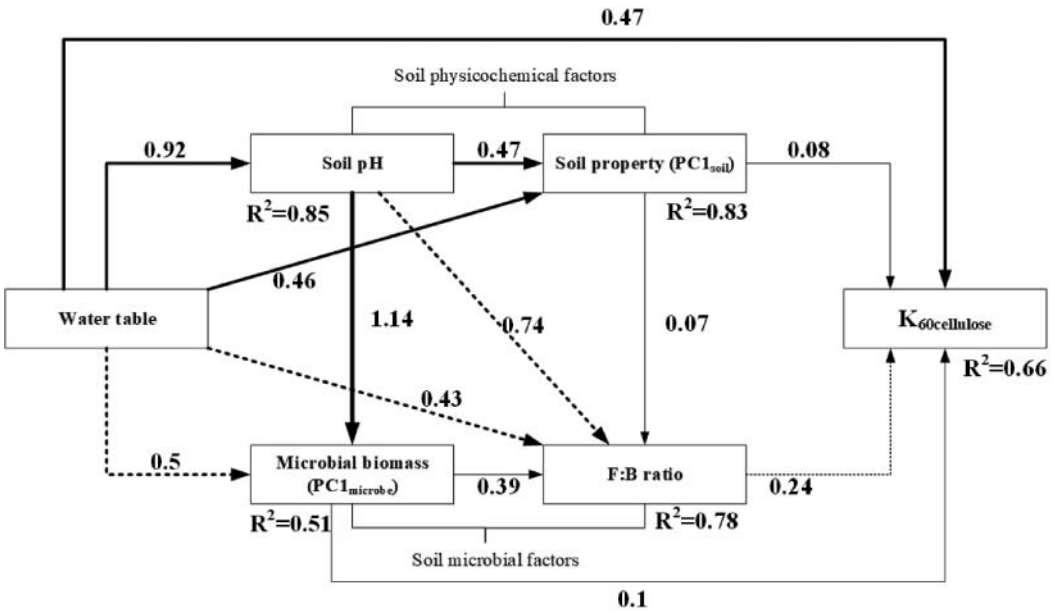
Path models of decay rates

Path models were constructed to examine the direct and indirect effects of the water table on the decay rate of cellulose ($\chi^2 = 1.96$, $P = 0.37$) and lignin ($\chi^2 = 0.62$, $P = 0.74$) in the first 60 days of the experiment (Figure 6). The results of statistical comparisons among the measured soil variables showed that there were significant differences among soils at different sites in SOC, TN, clay, silt, sand, G+, G-, total bacteria, fungi, actinomycetes, and total PLFAs. Because soil pH and the F: B ratios were significantly correlated with the decay rate of both lignin and cellulose, these two indicators were selected as independent factors in this model. The 11 parameters above except for soil pH were chosen for the PCA to reduce the redundancy indicators for the path analysis (Table 6). We acquired the principal component scores for each studied plot for the soil physical, chemical, and microbiological properties. The first PC of soil physical and chemical factors explained 80.0% of variation, and SOC and sand were the highly weighted variables. The first PC of soil microbiological factors explained 78.3% of variation, and bacterial abundance and total PLFAs were the highly weighted variables.

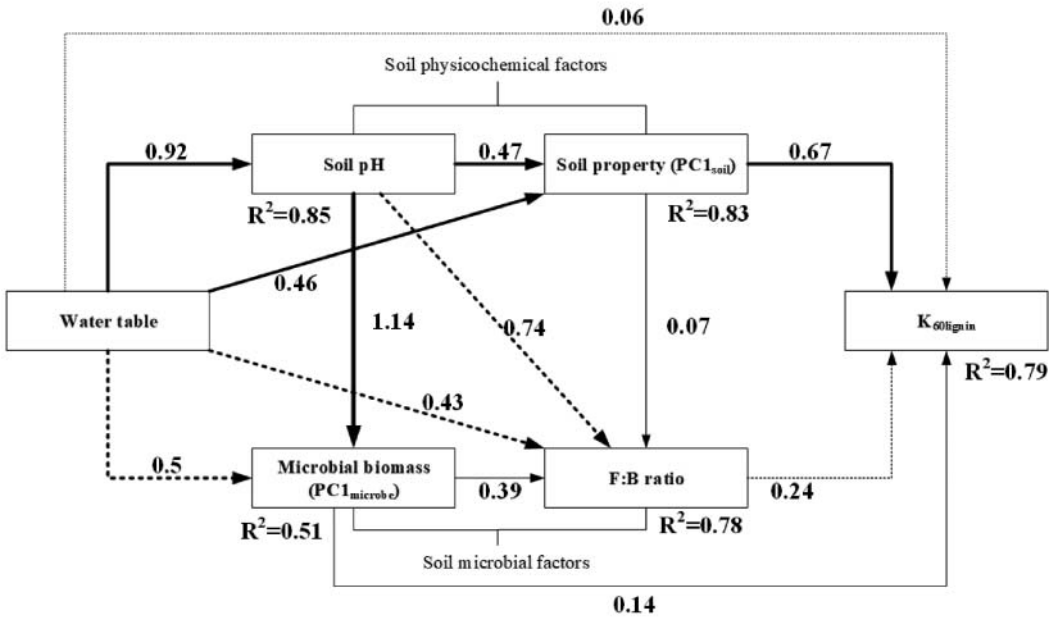
All of the variables in the model could be explained directly or indirectly by the water table with all contribution rates greater than 0.5 ($R^2 > 0.5$). The path models accounted for 66.0% and 79.0% of the variance in the decay rate of cellulose and lignin, respectively. The water table influenced cellulose decomposition mainly by its direct effects (path coefficient, 0.47). The decay rate of cellulose was also controlled by the F: B ratio (path coefficient, 0.24) and microbial abundance (path coefficient, 0.1). The decay rate of lignin was strongly indirectly controlled by the water table. Soil property had strong positive effects on the lignin decay rate (path coefficient, 0.67). Considering the indirect effects, the water table controlled soil pH (path coefficient, 0.92), which imposed strong positive effects on both microbial abundance and soil property (path coefficient of 1.14 and 0.47, respectively). The F: B ratio was negatively regulated by water table and soil pH (path coefficient of 0.43 and 0.74, respectively), and positively by the direct effect of microbial abundance (path coefficient, 0.39).

Discussion

The decomposition pattern in wetland ecosystems is remarkably different from that observed in terrestrial ecosystems. Our results showed that 30%–50% of cellulose and 20%–50% of lignin degraded in the first 60 d of the leaf litter decomposition duration (Figure 2), indicating that the degradation of lignin and cellulose occurs faster, and to a greater extent, in this wetland ecosystem than in terrestrial ecosystems (Dignac et al. 2010; Berg and Mc Clougherty 2014). Time and water table were the main factors affecting these decomposition processes (Table 3). We observed statistically significant differences in the proportion of cellulose and lignin remaining of leaf litter across the water table zones (sites GT-L to GT-H) during the 150-day field incubation experiment. Compared with the highest water table, a high water table in an alternating dry–wet environment promoted cellulose and lignin degradation, and decreased the time for decomposition to reach a steady state (Table 4; Figures 3 and 4). This indicated that a higher water table zone and intermittent submergence accelerate litter decomposition through higher microbial metabolism and greater leaching losses (Battle and Golladay 2001).



(A) Path analysis shows effects on decay rate of cellulose ($K_{60\text{cellulose}}$)



(B) Path analysis shows effects on decay rate of lignin ($K_{60\text{lignin}}$)

Figure 6. Path model structure showing direct and indirect effects of various factors on decay rate of cellulose (A) and lignin (B) in the wetland. Solid arrows indicate positive effects and dashed arrows indicate negative effects. Arrow widths are proportional to standardized direct effects; R^2 values represent total variance explained by all predictors pointing to that variable.

Table 6. Results of principal component analysis (PCA) of statistically significant soil indicators: (a) PCA for soil physical and chemical factors and (b) PCA for soil microbial factors. Factor loadings in bold are considered highly weighted.

(a) Soil physical and chemical factors			(b) Soil microbial factors		
Variable	PC1	PC2	Variable	PC1	PC2
SOC	-1.22	-0.37	G+	1.30	-0.07
TN	-1.06	-0.75	G-	1.28	-0.06
Clay	-1.19	0.23	Bacteria	1.31	0.02
Silt	-1.20	0.16	Fungi	0.84	0.91
Sand	1.22	0.00	Actinomycetes	0.91	-0.74
			Total PLFAs	1.32	0.04

In this study, the decay rates increased rapidly during the initial incubation period and then declined gradually over time (Figure 4). Lignin has traditionally been considered as a recalcitrant compound that prevents the biotic breakdown of organic matter (Williams and Yavitt 2003). Analyses have suggested that the labile compounds (e.g. water-soluble constituents) are the predominant factors regulating the loss of leaf litter mass, while lignin is preserved (Berg and McClaugherty 2014). However, recent studies on soil systems indicate that lignin is considerably more bioavailable and decomposable than was previously thought. For example, strong lignin degradation occurred in the first 41 days of leaf litter decomposition in a forest river, suggesting that the traditional view of lignin dynamics during leaf litter decomposition should be revised (Klotzbücher et al. 2011). Consistent with these findings, our study showed that substantial lignin degradation occurred in the first 60 days. Therefore, compared with terrestrial ecosystems, the wetland ecosystem shows much earlier and stronger degradation of lignin.

Studies have reported that the composition of the microbial community may be important to predict nutrient fluxes from leaf litter decomposition (Balsler and Firestone 2005). Changes in the soil microbial community composition are likely to result in a shift in the function of microbial communities, thus altering soil biological and physiochemical processes (Waldrop and Firestone 2006). Foulquier et al. (2013) reported that a higher water table zone provides an appropriate environment for degradation, that is, suitable microbial community, soil pH, and soil texture to promote the bioavailability and turnover of organic C. In this study, as the raise of water table zone can lead to significant increases in the abundance of total PLFAs, bacteria, and actinomycetes, indicating that the alternating dry-wet environment favoured the growth of bacteria and actinomycetes (Table 5). This is consistent with several reports that variations in the hydrological regime can drive long-lasting transformation of the composition of the soil microbial community (Mentzer et al. 2006; Foulquier et al. 2013). Soil pH, moisture, texture are important factors affecting microbial community composition, and they directly control the decomposition of organic matter (Peralta et al. 2014). Our previous study showed that C and N turnover rates were enhanced at a relatively high water table zone (Zhang et al. 2018). A potential mechanism to explain these results is that C availability is one of the main factors affecting cellulose and lignin degradation (Klotzbücher et al. 2011). This phenomenon may indicate that in soils along a water table zone, these values are useful indicators for explaining the rate of cellulose and lignin decomposition. Consistent with previous reports (Jerryvan et al. 2009), our results indicated the importance of the microbial community in sites with a high water table (lower F: B ratio, higher abundance of bacteria) (Table 4). The bacterial decomposition process is generally considered to be faster than the fungal decomposition process in the recycling of C and N (Wardle 2004).

By applying the path model, we examined the direct and indirect effects of these variables on the decay rates of cellulose and lignin. This analysis allowed us to determine whether the micro-environment factors affected the decomposition of cellulose and lignin by similar pathways (Figure 6). The relatively low predictive power overall suggests there are other unaccounted factors influencing the degradation of cellulose and lignin. The unexplained variance may possibly be due to the interference of root exudates of plant under different environmental conditions (Pires et al. 2012) and the interference of soil fauna (Zhang et al. 2016).

Cellulose degrades more rapidly than lignin (Berg and McClaugherty 2014), because lignin decomposition is more complicated than cellulose decomposition. The water table influenced cellulose decomposition mainly through direct effects (coefficient, 0.47), while the water table had no significant direct relationship with the lignin decay rate. Soil property had a major effect on the lignin decay rate (direct path coefficient, 0.67). Many studies have reported that the rate of lignin decay is a linear function of the lignocellulose index ($LCI = \text{lignin} / (\text{lignin} + \text{cellulose})$). Lignin degradation occurs only when the LCI is between 0.4 and 0.7, indicating that decomposition of lignin is not only directly affected by environment conditions, but also by the concentration of cellulose (Herman et al. 2008). We found that LCI values of the *C. cinerascens* residue after 60 days ranged from 0.45 to 0.6. Soil texture and moisture affect oxygen concentrations, which in turn affect the abundance of lignin-degrading microorganisms (Hall et al. 2015). The water table mainly regulates the decomposition process directly through its effects on enzyme activity. The activity of hydrolytic enzymes is higher under a highly water table than under a low water table (Romanowicz et al. 2015). Cellulose was shown to degrade more rapidly in a river bank ecosystem than in a terrestrial ecosystem (Yue et al. 2016). This may help to explain the different pathways by which the water table affected the decay rates of cellulose and lignin. The water table had indirect effects on the decay rates of both cellulose and lignin via its effects on microbial abundance and structure. The water table also affected soil pH, which was the critical link between the water table and soil properties, microbial abundance, and microbial structure, the factors that ultimately controlled decomposition.

Conclusion

Our study revealed variations in the decay rates of cellulose and lignin that were affected indirectly and directly by the water table, and clarified several aspects of cellulose and lignin decomposition. First, it is demonstrated that leaf litter decomposes very rapidly in wetland ecosystems, and Lignin and cellulose were strongly degraded in the first 60 days of the experiment. Second, the water table significantly affected the lignin and cellulose decay rates. It takes less than 1 year for cellulose and lignin degradation to reach a steady state in these conditions. Third, soil pH, clay content, and F: B significantly affected the cellulose and lignin decay rates. Finally, the path model accounted for 66% and 79% of the variation in cellulose and lignin decay rates, respectively, as explained by the combination of the water table and its related soil physical, chemical, and microbiological factors. The water table influences the decay rate of cellulose directly (path coefficient, 0.47) as well as indirectly via its effects on soil properties (path coefficient, 0.07), soil microbial abundance (path coefficient, 0.15) and microbial community structure (path coefficient, 0.43). In contrast, the water table affected the lignin decay rate by indirect effects via soil properties (path coefficient, 0.60), microbial abundance (path coefficient, 0.22), and microbial community structure (path coefficient, 0.43).

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References

- Abbott GD, Swain EY, Muhammad AB, Allton K, Belyea LR, Laing GC, Cowie GL. 2013. Effect of water-table fluctuations on the degradation of sphagnum, phenols in surficial peats. *Geochim Cosmochim Acta*. 106(4):177–191.
- Balser TC, Firestone MK. 2005. Linking microbial community composition and soil processes in a California annual grassland and mixed-conifer forest. *Biogeochemistry*. 73(2):395–415.
- Battle JM, Golladay SW. 2001. Hydroperiod influence on breakdown of leaf litter in cypress-gum wetlands. *Am Midl Nat*. 146(1):128–145.
- Berg B, McClaugherty C. 2014. *Plant litter: decomposition, humus formation, carbon sequestration*. 3rd ed. New York: Springer Berlin Heidelberg.
- Bossio D. 1998. Impacts of carbon and flooding on soil microbial communities: Phospholipid fatty acid profiles and substrate utilization patterns. *Microbial Ecol*. 35(3–4): 265–278.
- Charman DJ, Amesbury MJ, Hinchliffe W, Hughes PDM, Mallon G, Blake WH, Daley TJ, Gallego-Sala AV, Mauquoy D. 2015. Drivers of Holocene peatland carbon accumulation across a climate gradient in northeastern North America. *Quat Sci Rev*. 121:110–119.
- Dignac MF, Rumpel C, Thevenot M. 2010. Fate of lignins in soils: a review. *Soil Biol Biochem*. 42(8):1200–1211.
- Foulquier A, Volat B, Neyra M, Bornette G, Montuelle B. 2013. Long-term impact of hydrological regime on structure and functions of microbial communities in riverine wetland sediments. *FEMS Microbiol Ecol*. 85(2):211–226.

- Frostegård A, Bååth E. 1996. The use of phospholipid fatty acid analysis to estimate bacterial and fungal biomass in soil. *Biol Fert Soils*. 22:59–65.
- Frostegård A, Tunlid A, Bååth E. 2011. Use and misuse of plfa measurements in soils. *Soil Biol Biochem*. 43(8):1621–1625.
- Gerull L, Frossard A, Gessner MO, Mutz M. 2011. Variability of heterotrophic metabolism in small stream corridors of an early successional watershed. *J Geophys Res-Biogeosci*. 116(G2):69–69.
- Grace JB, Michael AT, Smith MD, Seabloom E, Andelman SJ, Meche G, Weiher E, Allain L, Jutila H, Sankaran M, et al. 2007. Does species diversity limit productivity in natural grassland communities? *Ecol Lett*. 10(8):680–689.
- Gulis V, Suberkropp K. 2003. Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. *Freshw Biol*. 48(1):123–134.
- Hall SJ, Silver WL, Timokhin VI, Hammel KE. 2015. Lignin decomposition is sustained under fluctuating redox conditions in humid tropical forest soils. *Glob Change Biol*. 21(7):2818–2828.
- Haraguchi A, Hasegawa C, Hirayama A, Kojima H. 2003. Decomposition activity of peat soils in Geogenous Mires in Sakami, central japan. *Eur J Soil Biol*. 39(4):191–196.
- Herman J, Moorhead D, Berg B. 2008. The relationship between rates of lignin and cellulose decay in aboveground forest leaf litter. *Soil Biol Biochem*. 40(10):2620–2626.
- Jerryvan D, Wimam D, Frans K, Petermvan B, Hermana V, Rien A. 2009. Can differences in soil community composition after peat meadow restoration lead to different decomposition and mineralization rates. *Soil Biol Biochem*. 41(8):1717–1725.
- Klotzbücher T, Kaiser K, Guggenberger G, Gatzek C, Kalbitz K. 2011. A new conceptual model for the fate of lignin in decomposing plant litter. *Ecology*. 92:1052–1062.
- Liu G, Sun J, Tian K, Xiao D, Yuan X. 2017. Long-term responses of leaf litter decomposition to temperature, leaf litter quality and leaf litter mixing in plateau wetlands. *Freshw Biol*. 62:178–190.
- Mentzer JL, Goodman RM, Balser TC. 2006. Microbial response over time to hydrologic and fertilization treatments in a simulated wet prairie. *Plant Soil*. 284(1):85–100.
- Merovich G. 2014. Influence of environmental parameters on leaf litter decomposition in wetlands in West Virginia, USA. *J Fresh Water Ecol*. 29(4):535–549.
- Mitsch WJ, Gosselink JE. 2000. *Wetlands*. 3rd ed. New York: John Wiley & Sons; 920 pp.
- Olson JS. 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology*. 44:322–331.
- Peralta AL, Ludmer SJ, Matthews W, Kent AD. 2014. Bacterial community response to changes in soil redox potential along a moisture gradient in restored wetlands. *Ecol Eng*. 73:246–253.
- Pires AC, Cleary DF, Almeida A, Cunha A, Dealtry S, Mendonçahagler LC, Smalla K, Gomes NCM. 2012. Denaturing gradient gel electrophoresis and barcoded pyrosequencing reveal unprecedented archaeal diversity in mangrove sediment and rhizosphere samples. *Appl Environ Microbiol*. 78(16):5520–5528.
- R Development Core Team. 2013. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. [accessed 20.05.13]. <http://www.r-project.org>.
- Rejmánková E, Houdková K. 2006. Wetland macrophyte decomposition under different nutrient conditions: what is more important, leaf litter quality or site quality? *Biogeochemistry*. 80(3):245–262.
- Rejmánková E, Sirová D. 2007. Wetland macrophyte decomposition under different nutrient conditions: relationships between decomposition rate, enzyme activities and microbial biomass. *Soil Biol Biochem*. 39(2):526–538.
- Rice AV, Tsuneda A, Currah RS. 2006. In vitro decomposition of Sphagnum by some microfungi resembles white rot of wood. *FEMS Microbiol Ecol*. 56:372–382.
- Romanowicz KJ, Kane ES, Potvin LR, Daniels AL, Kolka RK, Lilleskov EA. 2015. Understanding drivers of peatland extracellular enzyme activity in the peatcosm experiment: mixed evidence for enzymic latch hypothesis. *Plant Soil*. 397(1):1–16.
- Schellekens J, Buurman P, Kuyper TW, Abbott GD, Pontevedra-Pombal X, Martínez-Cortizas A. 2015. Influence of source vegetation and redox conditions on lignin-based decomposition proxies in graminoid-dominated ombrotrophic peat (Penido Vello, NW Spain). *Geoderma*. 237–238:270–282.
- Schulze ED, Freibauer A. 2005. Carbon unlocked from soils. *Nature*. 437:205–206.
- Shaffer PW, Cole CA, Kentula ME, Brooks RP. 2016. Effects of measurement frequency on water-level summary statistics. *Wetlands*. 20(1):148–161.
- Shi A, Marschner P. 2014. Drying and rewetting frequency influences cumulative respiration and its distribution over time in two soils with contrasting management. *Soil Biol Biochem*. 72:172–179.
- Sun Y, Wu J, Shao Y, Zhou L, Mai B, Lin Y, Fu S. 2011. Responses of soil microbial communities to prescribed burning in two paired vegetation sites in southern china. *Ecol Res*. 26(3):669–677.
- Tang SS, Yang WQ, Yin R, Xiong L, Wang HP, Wang B, Zhang Y, Peng YJ, Chen QS, Zhen ZF. 2014. Spatial characteristics in decomposition rate of foliar leaf litter and controlling factors in chinese forest ecosystems. *Chin J Plant Ecol*. 38(6):529–539. (in Chinese with English abstract).
- Trinder CJ, Johnson D, Artz RRE. 2008. Interactions among fungal community structure, leaf litter decomposition and depth of water table in a cutover peatland. *FEMS Microbiol Ecol*. 64(3):433–448.

- U.S. Environmental Protection Agency. 1993. Methods for the determination of inorganic substances in environmental samples. Cincinnati (OH): Environmental Monitoring Systems Lab.
- Waddington JM, Morris PJ, Kettridge N, Granath G, Thompson DK, Moore PA. 2015. Hydrological feedbacks in northern peatlands. *Ecohydrology*. 8:113–127.
- Waldrop MP, Firestone MK. 2006. Seasonal dynamics of microbial community composition and function in oak canopy and open grassland soils. *Microb Ecol*. 52(3):470.
- Wang X, Helgason B, Westbrook C, Bedard-Haughn A. 2016. Effect of mineral sediments on carbon mineralization, organic matter composition and microbial community dynamics in a mountain peatland. *Soil Biol Biochem*. 103:16–27.
- Wang Y, Yu X, Zhang L, Lei G. 2013. Seasonal variability in baseline $\delta^{15}\text{N}$ and usage as a nutrient indicator in Lake Poyang, China. *J Fresh Water Ecol*. 28(3):365–373.
- Wardle DA. 2004. Communities and ecosystems: linking the aboveground and belowground components. *Austral Ecol*. 29(3):358–359.
- Wiedermann MM, Kane ES, Potvin LR, Lilleskov EA. 2017. Interactive plant functional group and water table effects on decomposition and extracellular enzyme activity in sphagnum, peatlands. *Soil Biol Biochem*. 108:1–8.
- Williams CJ, Yavitt JB. 2003. Botanical composition of peat and degree of peat decomposition in three temperate peatlands. *Ecoscience*. 10:85–95.
- Wu S, He S, Huang J, Gu J, Zhou W, Gao L. 2017. Decomposition of emergent aquatic plant (cattail) leaf litter under different conditions and the influence on water quality. *Water Air Soil Pollut*. 228(2):70.
- Yue K, Peng C, Yang W, Peng Y, Zhang C, Huang C, Wu F. 2016. Degradation of lignin and cellulose during foliar leaf litter decomposition in an alpine forest river. *Ecosphere*. 7(10):e01523.
- Zhang D, Hui D, Luo Y, Zhou G. 2008. Rates of leaf litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *J Plant Ecol*. 1(2):85–93.
- Zhang W, Chao L, Yang Q, Wang Q, Fang Y, Wang S. 2016. Litter quality mediated nitrogen effect on plant litter decomposition regardless of soil fauna presence. *Ecology*. 97(10):2834.
- Zhang G, Yu X, Xu J, Duan H, Zhang Q, Fisher L, Zhang Q, Li Y, Liu Y, Xia S. 2018. Effects of environmental variation on stable isotope abundances during typical seasonal floodplain dry season litter decomposition. *Sc Tot Environ*. 630:1205–1215.
- Ziegler F, Kögel I, Zech W. 1986. Alteration of gymnosperm and angiosperm lignin during decomposition in forest humus layers. *J Plant Nutr Soil Sc*. 149(3):323–331.