



A Warm Tea: The Role of Temperature and Hydroperiod on Litter Decomposition in Temporary Wetlands

Candela Madaschi* and Verónica Díaz-Villanueva

Laboratory of Limnology, INIBIOMA, CONICET-Universidad Nacional del Comahue, Quintral, 1250 Bariloche, Argentina

ABSTRACT

Increasing global temperature and changes in the precipitation regime affect the global carbon cycle by altering the process of organic matter decomposition. Temporary aquatic systems are especially susceptible to climate change. We hypothesized that water availability and temperature affect the early and late stages of decomposition of litter differently and determine the decomposition rates according to litter type. We conducted two decomposition experiments using green (*Camellia sinensis* L.) and mint (*Mentha piperita* L.) tea in commercial bags. In the laboratory experiment, we incubated the bags at two contrasting temperatures (4 and 15°C) and in three simulated hydroperiods (M: moist, MS: submerged after 14 days, S: submerged). A field experiment was carried out in winter and spring in nine temporary wetlands (meadows) along a precipitation gradient (from forest to steppe ecosystems) in the Argentinean Patagonia. Water stimulated the leaching of soluble

substances in the S treatment and was the conducting factor in early decomposition stages. Temperature stimulated tea decomposition in advanced stages, and both water and temperature exerted a different response depending on the litter type. In the field experiment, mass loss in meadows was determined by the hydroperiod condition, both in winter and spring. Detritus type was the controlling factor in steppe meadows, but on forest meadows water level stimulated both litter types, and temperature increased decomposition. Under the expected increase of temperature and decrease of precipitations in future climate scenarios, organic matter accumulation would increase in steppe meadows and decomposition would be higher in forest meadows.

Key words: Climate change; Patagonia; Temporary wetlands; Meadows; Tea decomposition; Precipitation gradient.

HIGHLIGHTS

- Hydroperiod was the conducting factor of litter mass loss
- Litter with small chemical differences can decompose differentially.
- Differences between wet and dry biomes were greater in spring

Received 22 April 2021; accepted 4 November 2021

Supplementary Information: The online version contains supplementary material available at <https://doi.org/10.1007/s10021-021-00724-7>.

Author contributions This study was conceived and designed by VDV and CM. Laboratory and field experiments were carried out by VDV and CM. Data were analyzed by CM and VDV and CM wrote the paper.

*Corresponding author; e-mail: candelamadaschi@comahue-conicet.gob.ar

INTRODUCTION

Climate change modifies the functioning of biological systems by altering global temperature and rainfall regimes. In the last century, global surface temperature has risen 0.6°C, and a further increase between 1.1 and 6.4°C is expected for the next century (IPCC 2007). This temperature increase entails an increment in water temperature which affects ecosystem functioning and biological processes (Brown and others 2004). In addition, climate change predictions also involve increases in inter- and intra-annual variability of precipitation regimes, with higher risk of extreme rain and drought events (IPCC 2007). These two factors, temperature and precipitation regime, are regulators of detritus decomposition. As litter decomposition contributes to 70% of the total C annual flux (Coûteaux and others 1995), any alteration introduced by climate change will have consequences on the global C cycle. In terrestrial systems, precipitation may inhibit decomposition (Didion and others 2016; Althuizen and others 2018; Djukic and others 2018), but in aquatic systems, where decomposition is faster (Molles and others 1995; Langhans and others 2008; Leberfinger and others 2010; Abril and others 2016; Tiegs and others 2019), changes in water fluxes and/or water levels will have a strong impact on decomposition dynamics.

In temporary wetlands, like meadows, intermittent rivers or floodplains, decomposition rates are slower than in permanent systems (Langhans and Tockner 2006; Datry and others 2011, 2018; Palmia and others 2019). This is attributed to three factors: lower processing efficiency during drought events (Pinna and Basset 2004; Abril and others 2016), less detritivore abundance during the beginning of the rewetting (Mariluan and others 2015), and lower shredder processing efficiency (Leberfinger and others 2010). In these systems, the dynamic of decomposition is affected by the hydrological condition of the wetland (Battle and Golladay 2001; de Neiff and others 2006). Moreover, the duration of the inundation is a key factor in litter decomposition (Anderson and Smith 2002; Minden and Kleyer 2015; Xie and others 2019). Temporary wetlands are characterized by wet-dry cycles, where litter mass loss accelerates upon rewetting (Glazebrook and Robertson 1999; Langhans and Tockner 2006). Water stimulates the leaching and fragmentation of detritus soluble compounds and sustains a higher microbial metabolism than terrestrial systems (Webster and Benfield 1986; Molles and others 1995; Minden and Kleyer 2015).

Studies on the effect of an increase in water temperature had contrasting results. On the one hand, higher water temperatures accelerate litter decomposition rates (Dang and others 2009; Geraldes and others 2012; Martínez and others 2014) through leaching and by stimulating the metabolic activity of hyphomycetes (Ferreira and Chauvet 2011). Similarly, an increase in water temperature could accelerate the decay of recalcitrant compounds, since these substances need a high activation energy for its decomposition due to the metabolic cost of degrading substances like lignin and cellulose (Follstad Shah and others 2017). Also, an increase in temperature affects the enzymatic latch mechanism, by removing the inhibitory effects of dissolved phenolics, thus increasing the hydrolysis of organic matter (Pinsonneault and others 2016). On the contrary, high water temperature increases carbon-to-nutrient content in leaves, altering the litter quality and slowing decomposition rates (Graça and Poquet 2014). Also, higher water temperature leads to the depletion of dissolved O₂ (Gonçalves and others 2013; Iñiguez-Armijos and others 2016), leading to anaerobic conditions, which inhibits microorganism activities and decelerates leaf litter decomposition rates (Webster and Benfield 1986; Medeiros and others 2009; Pettit and others 2012).

Globally, leaf litter quality is the conducting factor of decomposition, for both terrestrial (Cornwell and others 2008; Zhang and others 2008; Djukic and others 2018) and aquatic systems (Bruder and others 2014; García-Palacios and others 2016; Follstad Shah and others 2017; Zhang and others 2019). But at the site level, early decomposition is controlled by the interaction between abiotic factors and detritus quality, and in later stages the process is dominated by leaf litter quality (Yue and others 2018; Xie and others 2019). Litter quality is related to the chemical composition of the leaf, which varies in their susceptibility to decomposition, ranging from labile (carbohydrates, organic acids and proteins) to relatively recalcitrant compounds (lignin, tannins and the cuticular matrix) (Boerjan and others 2003; Lorenz and others 2007). These structural and recalcitrant substances lead to a slower microbial degradation (Hättenschwiler and Jørgensen 2010). Zhang and others (2008) found that the variables that determine litter decomposition across biomes are the C:N ratio and the total nutrient content of leaves. In aquatic systems, macrophyte litter quality is one of the main drivers of decomposition (Riutta and others 2012; Li and others 2013; Paccagnella and others 2020) as it influences the type and concentration of

decomposers (Battle and Golladay 2001). Similarly, in temporary systems, recalcitrant detritus decomposes more slowly than labile leaf litter due to a higher resistance to physical abrasion and a lower nutrient content (Xie and others 2019).

In Patagonia, there are some particular temporary aquatic ecosystems that resemble wet meadows, locally called *mallines*, which are characterized by seasonally flooded areas. Water inputs in these shallow wetlands derive from precipitation, surface run-off, groundwater, fluxes from deeper water bodies (as lakes and rivers) and, to a lesser extent, high mountain snowmelt (Irisarri and others 2012). Meadows hydrological characteristics depend mainly on the precipitation regime, which determines the period when water is available (hydroperiod). The hydroperiod of meadows extends from autumn to early summer. These aquatic systems are under threat because of cattle grazing, human development and climate change (Chimner and others 2011). As conditions in Patagonia are expected to become warmer and drier (Nuñez and others 2009; Magrin and others 2014), meadow water imbalance will be strongly affected, thus altering ecological and biological processes (Chimner and others 2011). As a result, Crego and others (2014) predicted a decline on meadow surfaces in Northwest Patagonia by the middle of the century.

The aim of the present study was to determine the effect of hydroperiod and temperature in decomposition rates of two litter types. We hypothesized that water availability and temperature affect the early and late stages of litter decomposition differently and determine the decomposition rates according to the litter type. To test these hypotheses, we carried out two experiments, one in the laboratory and one in the field. We used the tea bag methodology proposed by Keuskamp and others (2013) for the TeaComposition Initiative, which uses tea bags as standard litters allowing global and long-term comparisons on litter decomposition measurements across broad spatial scales. The predictions associated with the hypotheses are that detritus under submerged and increased temperature conditions would decompose faster than under moist and low-temperature conditions, according to litter type, and that longer hydroperiods would determine higher decomposition rates at higher temperatures but not at lower ones.

METHODS

Study Area

This study was carried out in the Nahuel Huapi National Park, in northern Argentinean Patagonia (between 40°20' S–41°35' S and 71°02' W–71°56' W, Figure 1). This temperate-cold region is characterized by a West–East precipitation gradient, with records from 2500 annual mm in the Andean mountains to 250 annual mm in the steppe grassland in a 100 km transect (Jobbágy and others 1995). Patagonian meadows hydroperiod (the duration of the wet season, when water is available) starts with the autumn rains (May) and lasts until early summer (December) (Chimner and others 2011).

We selected nine meadows along a West–East transect which correspond to the precipitation gradient (Figure 1). Annual precipitation for 2019 was of 1135 mm in the West of the precipitation gradient and 483 mm in the East of the gradient (data from the meteorological stations of IN-IBIOMA). Meadows in the West part of the gradient correspond to a forest biome, while meadows in the East part of the transect are in the steppe. These sites were chosen for their low to medium land use history (cattle) with the exception of Fantasma meadow, which is in a protected suburban zone, but with low building density (Cuassolo and Díaz-Villanueva 2019). Some of these meadows have small permanent water eyes, but the overall characteristic is the dry soil during summer–early autumn. The precipitation gradient generates a gradient in the duration of the hydroperiod of meadows. In late spring, the meadows in the steppe begin to drain water toward lower topographic zones (Buono and others 2010), but in forest meadows surface water may persist until early summer, as a result of the accumulation of winter precipitations and the snowmelt.

As there is a high volume of water available for the flora, the vegetation of meadows is particular: it is characterized by the presence of species from the Cyperaceae, Juncaceae and Gramineae families (Kandus and others 2008). All the sites have a similar floristic composition, with species such as *Eleocharis pachycarpa*, *Carex aematorrhyncha*, *Juncus balticus* and *Schoenoplectus californicus* var. *spoliatus* being the most common in forest meadows (Cuassolo and Díaz-Villanueva 2019). To test the effect of temperature and hydroperiod in decomposition we used a modified procedure from that proposed by Keuskamp and others (2013) both in the field and in the laboratory experiments. The

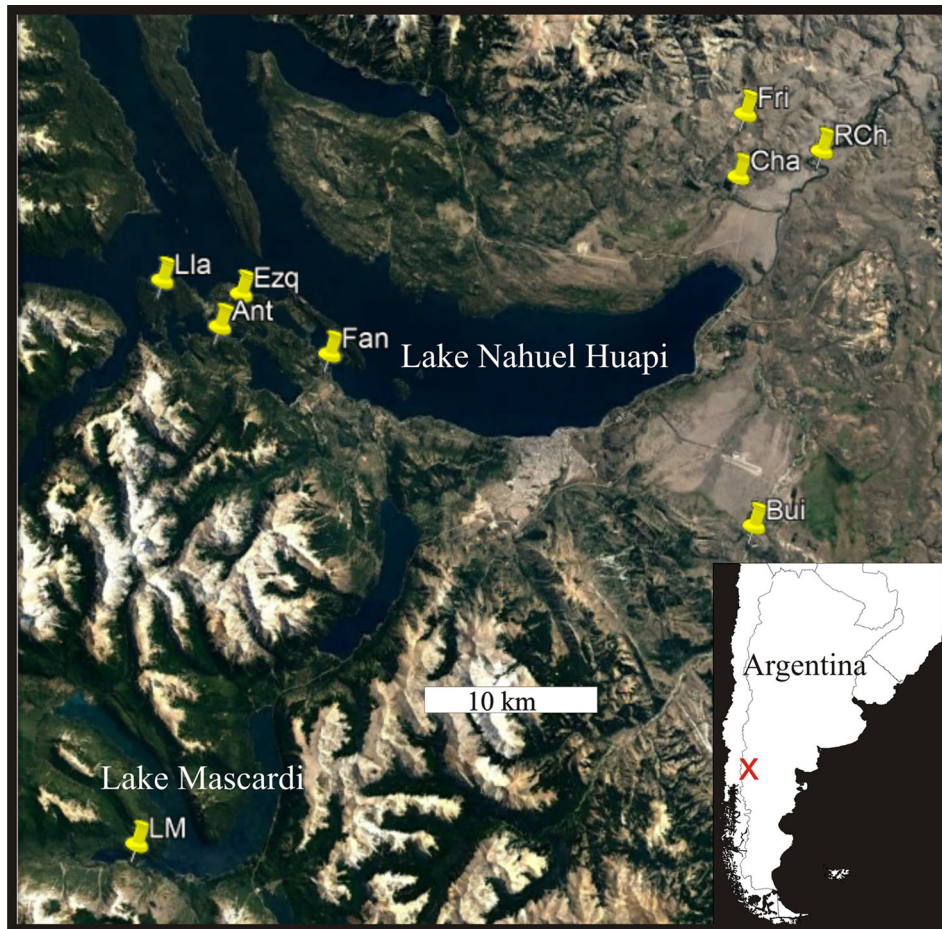


Figure 1. Location of meadows along the precipitation gradient in northern Patagonia (Argentina). Meadows in the West part of the gradient correspond to the forest biome, while meadows in the East part of the transect are in the steppe. Meadows from West to East: LM: Los Moscos, Lla: Llao Llao, Ant: Antaño, Ezq: Ezquerria, Fan: Fantasma, Bui: Buitrera, Cha: Chacabuco, Fri: Frizón, and RCh: Rincón Chico.

authors used green tea (*Camellia sinensis* L.) and rooibos tea (*Aspalathus linearis* L.) from the commercial Lipton brand, as dead plant material. Instead of rooibos, we used peppermint infusion (Taragüi brand) as we wanted to introduce a modification suitable to an aquatic environment, and peppermint (*Mentha piperita* L.) commonly grows in wet soils including the environments of the present study (Cuassolo and Díaz-Villanueva 2019).

Detritus Characteristics

We measured initial phosphorous (P), nitrogen (N) and carbon (C) content of green tea and mint tea. To obtain the initial P content, subsamples of the tea bags content ($N = 3$) were dried for 48 h at 60°C and weighed (~ 10 mg) and then combusted at 450°C. The ashes were suspended in MilliQ water, followed by the ascorbate-reduced-molyb-

denum method (APHA 2005). Another set of subsamples ($N = 3$) was used to measure N and C contents, using a CN analyzer (Thermo Finnigan Flash EA 1112) after drying the material for 48 h at 60°C and weighing it. Based on these results, molar C:N, C:P and N:P ratios were calculated.

To measure the loss of soluble organic C and P in the first 48 h (leachates), we carried out a leaching incubation assay. Leachates were obtained in acid-washed flasks with 100 ml MilliQ water and 1 g of detritus, incubated in the dark at 4°C for 48 h. Afterward, the suspension was filtered through GF/F filters. We measured dissolved organic carbon (DOC) with a high-temperature combustion analyzer (Shimadzu TOC V-CSH) and soluble reactive phosphorus (SRP) spectrophotometrically, with the ascorbate-reduced-molybdenum method (APHA 2005).

Microcosm Assay

In the laboratory experiment, we selected two incubation temperatures and three different hydroperiods. Tea bags of each species were placed inside plastic trays and collected after 2, 7, 14, 28, 56 and 112 days ($N = 5$ for each extraction date). The bottom of each tray was filled with gravel (Perlita, Lombriquen) and watered with filtered (55 μm pore size) water from the meadow Fantasma (Table S1) according to the simulated hydroperiod. We selected incubation temperature as: T1: the natural scenario in the Fantasma meadow (4°C), and T2: the lowest temperature in the experiment proposed by Keuskamp and others (15°C), which coincided with the highest temperature found in one of the selected meadows. The three simulated hydroperiods were: M: tea bags were moist during all the experiment ($90.5 \pm 0.5\%$ of water content), but never submerged; MS: submerged after 14 days, in which the tea bags were on moist substrate; and S: submerged through the entire experiment duration. Water was changed or refilled every 48–72 h to ensure the same nutrient concentrations and oxygenation throughout the experiment.

At each extraction date, tea bags were collected and oven-dried (60°C, 48 h) to determine dry mass of detritus (bag content). Then, detritus was incinerated (450°C) to obtain the ash-free dry mass (AFDM). Remaining AFDM was used as the response variable. The envelope and thread of the tea bags were excluded to obtain only the mass loss of the crushed tea leaves.

Field Assay

The field experiment was carried out for 90 days during June–September (winter treatment) and August–November (spring treatment). Temperature during the experiment was recorded with data loggers (HOBO, Pendant, UA-001-08) located at each site. As the accumulation of water in the meadows stabilizes during the spring, water level in each site was recorded in November with a tape measure. In some meadows, there was no water column, but soils were saturated (Table S1).

Soil samples from each site were collected in February, when soils were dried-out, to measure soil organic matter content, humidity percentage, conductivity and pH. Samples were taken from the top soil layer (0–25 cm depth) in hermetic bags and transported to the laboratory for analysis. Sub-samples from each soil were immediately weighed (WW) and oven-dried (at 105°C) for 48 h (DW) (5

analytical replicates for each soil sample) (Reynolds 1970) to obtain soil water content as the difference between WW and DW. Organic matter content was estimated as the ash-free dry mass (AFDM) after calcination at 550°C for 4 h. The rest of the soil samples were air-dried for 48 h, sieved through a 4-mm mesh and stored for further analyses. Electrical conductivity and pH were measured on a water:soil suspension (1:10) with a conductimeter (YSI 85) and a pH-meter (Hanna, HI8424).

Tea bags ($N = 5$ of each species) were placed inside litter bags (1 mm pore size) to prevent the loss of material by animals (mainly rodents). All litter bags were tied to a nylon thread, attached to a metal rod and placed on the shore of each meadow. We preferred shores since they are of easy access once the meadow is flooded and shows differences in flooded periods according to the hydroperiod of each meadow. The litter bags were collected after 90 days and carried inside hermetic bags to the laboratory. All tea bags were rinsed with distilled water to remove any sediment or particle present and were oven-dried to constant weight (60°C, 48 h). As in the laboratory assay, detritus (without the bag and the thread) was incinerated to obtain the AFDM and calculate mass loss as the response variable.

Data Analysis

Initial nutrient concentrations for both tea species were compared with t tests. In the laboratory experiment, as treatment MS had two different conditions (from t_0 to t_{14} , tea bags were under moist conditions, and from t_{14} to t_{112} , tea bags were submerged) we adjusted a double exponential decay rate model (Wider and Lang 1982) for each treatment, as follows:

$$M_t = a * e^{-k_1 * t} + b * e^{-k_2 * t}$$

where M_t is the percent AFDM remaining at time “ t ,” a is the ash-free mass from t_0 , k_1 is the decomposition rate during this time period, b is the ash-free mass from t_{14} , and k_2 is the decomposition rate from day 14 to day 112. In each nonlinear regression, a and b parameters were constrained to the AFDM data for each time period. Each decay model was fitted using weighted (WLS) nonlinear regression of the remaining AFDM over time, via the *nls* function from the stats package.

To compare the k_1 and k_2 decomposition rates among the different hydroperiod and temperature treatments and between litter type, we fit models through generalized least squares (GLS). This approach allowed us to fit different variance compo-

nents per time. Hydroperiod, temperature and detritus species were the fixed factors and time was the covariate. The response variable was the percent of AFDM remaining. We used *gls* function from package *nlme* (Pinheiro and others 2017) and *Anova* function from package *car* (Fox and others 2012), which allowed us to use type III sums of squares. Model assumptions were visually explored. Multiple comparisons for both *ks* were made using *emmeans* package (Lenth and Lenth 2018), with Tukey as P-adjustment method.

We ran a linear regression to assess whether longitude was a reliable estimator of hydroperiod and whether winter and spring temperatures followed a longitudinal pattern. In the first case, we used water height as the response variable and in the second case the temperatures of each season. In both cases, longitude was the regressive variable (R^2_{adj} : 50.7%, $P < 0.05$). Also, we compared the mean winter and spring site temperature with a two-way ANOVA, using the function *lm* from base package *stats* and the *Anova* from package *car*. Biome and season were the fixed effects and mean meadow temperature, the response variable. Multiple comparisons were made using the *emmeans* package, with Tukey as P-adjustment method.

We modeled the effect of hydroperiod and temperature on litter mass loss with a linear mixed effects model. Longitude coordinates (as hydroperiod estimator), spring temperature and detritus species were set as fixed factors, and site as a random one. The proportion of detritus mass loss ($\frac{\text{initial mass} - \text{final mass}}{\text{initial mass}}$) for each meadow was the response variable. We only used values from the spring experiment for this analysis since the tea bags were lost in four of the nine meadows in the winter experiment. As the interaction between detritus type, longitude coordinate and mean site temperature was significant, we tested the effect of the covariates for each tea type fitting separate mixed models. The relationship between detritus mass loss and temperature was nonlinear, so we modeled the effect of temperature using a cubic spline (function *ns*, package *Splines*) (Bates and others 2011). Assumptions were inspected visually and variance components were determined using the *r2beta* function of package *r2glmm* (Jaeger 2017). All linear mixed effect models were fitted using *lmer* function from package *lme4* (Bates and others 2007), and package *lmerTest* was used to obtain ANOVA tables with type III sums of square (Kuznetsova and others 2017).

To assess the difference in litter mass loss between seasons, we compared winter and spring tea

mass losses for the five meadows where tea bags were found in winter (Llao Llao, Ezquerria, Fantasma, Frizón and Rincón Chico). Meadows were divided according to their biome (forest or steppe). We ran a randomized block ANOVA per litter species, with two factors (season and biome) and meadows as blocks. We used *aov* function, and multiple comparisons between season and biome type were made with Tukey as P-adjustment method. All statistical analyses were performed using R statistical software (v. 4.0.0, (R Core Team 2013)), and all graphics were done in SigmaPlot software (v. 14. 0. 0. 124).

RESULTS

Detritus Characteristics

Initial nutrient content was similar between green tea and mint (Table 1). However, differences were found in total C content and hence in C:P and N:P ratios, both higher in green than in mint tea (Table 1). Both detritus species released different amounts of C and P in leachates. While DOC was higher in green tea leachates than in mint, SRP was higher in mint leachates (Table 1).

Microcosm Assay

Mass loss due to leaching in the S treatment was higher for green tea ($28 \pm 1\%$) than for mint ($23 \pm 1\%$), without differences in temperatures. On the contrary, mass loss in the M and MS treatments was 5 ± 3 and $7 \pm 1\%$ (T1 and T2, respectively), without differences between litter type (Table S2, three-way ANOVA, interaction hydroperiod \times species $P < 0.05$).

By the end of the laboratory experiment, both species reached less than 50% of remaining AFDM in all treatments, except in the M treatment at T1 (Figure 2). Curve fitting per detritus species for the double exponential decomposition model produced good fits ($R^2_{\text{adj}} > 90\%$, for all cases). Differences in leaching among treatments were reflected in the decomposition rates during the first 14 days (k_1), which differed among the hydroperiod treatments for both species without a significant effect caused by temperature (Table 2). Detritus decay rates at S treatments were faster than the rates for the M and MS treatments (Tukey, $P < 0.05$ for each pairwise comparison per specie; Figure 3A).

On the other hand, the effect of the hydroperiod on the long-term decomposition rates (k_2) depended on the incubation temperature and on detritus species (Table 2). Particularly, green tea decomposition rate at the lowest temperature (T1)

Table 1. Chemical Characteristics and Elemental Ratios of Selected Tea Species

	Green	Mint	P-value
Total C ($\mu\text{g mg}^{-1}$)	468 (± 5)	414 (± 9)	< 0.05
Total N ($\mu\text{g mg}^{-1}$)	34 (± 1)	34 (± 1)	No
Total P ($\mu\text{g mg}^{-1}$)	1.47 (± 0.25)	1.92 (± 0.13)	No
C:N	16.0 (± 0.4)	14.3 (± 0.2)	No
C:P	819 (± 9)	556 (± 12)	< 0.05
N:P	51 (± 2)	39 (± 1)	< 0.05
DOC ($\mu\text{g mg}^{-1}$)	2.22 (± 0.07)	1.41 (± 0.04)	< 0.001
SRP ($\mu\text{g mg}^{-1}$)	0.294 (± 0.042)	0.460 (± 0.032)	< 0.05

Elemental composition (carbon, nitrogen and phosphorus content) and molar ratios of green tea and mint, and dissolved organic carbon (DOC) and soluble reactive phosphorus (SRP) in leachates of green tea and mint (mean \pm standard error). Comparisons between species were made with *t* tests.

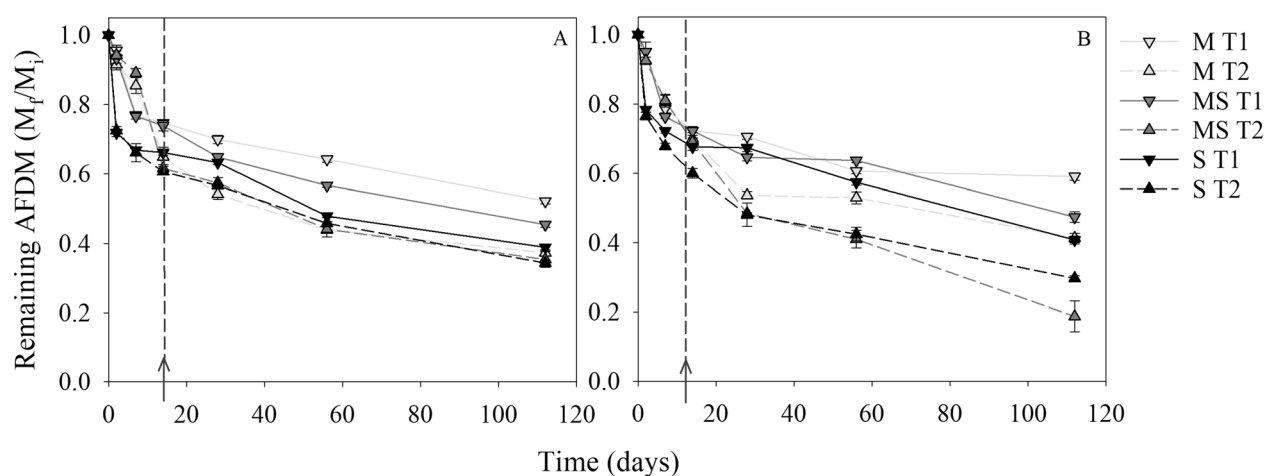


Figure 2. Remaining mass (ash-free dry mass) expressed as the proportion of final (M_f) to initial (M_i) mass of green (**A**) and mint (**B**) tea on each sampling date in moist (M), mixed (MS) and submerged (S) treatments at 4°C (T1) and 15°C (T2). The arrow on the *x*-axis indicates the date (14 days) in which MS treatment was submerged. Error bars are standard errors.

for the M treatment was the slowest decay rate, and it differed from the rest (Tukey, for each pairwise comparison, $P < 0.05$, Figure 3B). On the contrary, decomposition rates for mint tea were similar among hydroperiods at T1 and were slower than the rates found at T2 (Tukey, for each pairwise comparison, $P < 0.05$, Figure 3B).

When tea bags were submerged (MS and S treatments) at low temperatures (T1), green tea k_2 decomposition rates were higher than mint decay rates (Tukey, $P < 0.01$). On the contrary, at higher temperatures (T2) mint decay rates (k_2) were higher than green tea decomposition rates (Tukey, $P < 0.01$, Figure 3c) among all hydroperiods.

Field Assay

Water level was higher in meadows in the West and it decreased toward the East. We found a linear

relationship between water level and the longitudinal gradient (R^2_{adj} : 50.7%, $P < 0.05$, Figure 4). However, Lao Lao meadow was very shallow (10 cm, Table S1), despite being located in the western region of the gradient. Alternatively, there was not a winter and spring temperature gradient along the transect (R^2_{adj} winter: 0.12, $P > 0.05$; R^2_{adj} spring: 0.14, $P > 0.05$). Mean temperature in the forest meadows was $3.24 \pm 0.19^\circ\text{C}$ and $8.01 \pm 0.21^\circ\text{C}$ in winter and spring, respectively, while in steppe meadows it was $3.14 \pm 0.28^\circ\text{C}$ and $8.14 \pm 0.35^\circ\text{C}$. Meadow temperature differed between seasons ($F = 531$, $P < 0.001$), with lower temperatures in winter (Tukey, $P < 0.001$), but not between biomes ($F = 0.09$, $P > 0.05$). Despite the lack of a gradient in temperature, there were differences among meadows, with higher temperature in the Fantasma meadow (Forest) and Chacabuco meadow (steppe) (Figure 4, Table S1).

Table 2. Effect of Temperature, Hydroperiod and Detritus Species on Tea Decomposition

	k_1	
	χ^2	<i>P</i> -value
Intercept	3776	< 0.001
Hydroperiod	10.4	0.005
Temperature	3.43	0.063
Time	632	< 0.001
Species	0.023	0.880
Hydroperiod*Temperature	6.36	0.051
Hydroperiod *Species	3.40	0.182
Temperature*Species	3.02	0.082
Hydroperiod*Temperature*Species	2.93	0.231
	k_2	
	χ^2	<i>P</i> -value
Intercept	3749	< 0.001
Hydroperiod	2.66	0.264
Temperature	109	< 0.001
Species	1.33	0.248
Time	641	< 0.001
Hydroperiod*Temperature	7.08	0.029
Hydroperiod*Species	5.61	0.060
Temperature*Species	11.6	0.001
Hydroperiod*Temperature*Species	8.86	0.012

Results from the GLS model on the effects of temperature, hydroperiod and detritus species on green tea and mint k_1 and k_2 decomposition rates. Pseudo- $R^2_{k_1}$ = 76.9%, pseudo- $R^2_{k_2}$ = 83.4%.

The fixed effects of the linear mixed effects model explained 85.2% of the variance (R^2_{marginal}), and the entire model explained 96.3% of the variance ($R^2_{\text{conditional}}$). Detritus mass loss depended on both spring temperature and longitude variables, as well as tea type ($F = 24.3$, $P < 0.001$, Figure 5A, B). However, individual models for each tea type showed that longitude was the main driver of litter mass loss (green tea: $F = 21.4$, $P = 0.005$; mint tea: $F = 41.2$, $P = 0.001$) and explained 66.3 and 81.7% of the total variance for green and mint tea, respectively. Both detritus types exhibited the same response: a decrease in mass loss from West to East in the precipitation gradient (β -coefficient_{green tea} = -1.12 , β -coefficient_{mint tea} = -1.74 ; Figure 5A). Detritus mass loss was close to 100% in forest meadows (green tea: $92\% \pm 3$, mint tea: $97\% \pm 1$) and decreased to $40\% \pm 2$ for green tea and to $29\% \pm 2$ for mint tea, toward the East of the precipitation gradient. Overall, green tea mass loss was higher than mint mass loss. Green tea lost 25 and 29% more mass than mint tea for meadows allocated in the center and east of the precipitation

gradient, respectively (Figure 5A). Although tea mass loss did not depend on spring site temperature (green tea: $F = 0.09$, $P > 0.05$; mint tea: $F = 3.43$, $P > 0.05$; Figure 5B), there seems to be a bell-shaped mass loss response to temperature variations in meadows. Green and mint tea mass loss was higher in the range of 7.2 to 8°C (Figure 5B) (Table 3).

Comparing detritus mass loss between winter and spring, considering the two biomes (forest vs steppe), we found that differences between the two depended on the season and on the detritus species (Table 4). In forest meadows, green tea and mint mass loss were higher in spring than in winter (Tukey, $P < 0.001$ for both cases) and higher than in steppe meadows (Tukey, $P < 0.001$ in all cases). In steppe meadows, green tea and mint mass loss were similar between winter and spring (Tukey, $P > 0.05$ for both cases, Figure 6).

DISCUSSION

Our results showed that the effects of temperature and hydroperiod change throughout the decomposition process and these effects are different based on litter type, which confirms our hypotheses. The results, both from the laboratory and field experiments, highlighted the key role of water availability in the litter decomposition process.

Role of Temperature and Hydroperiod on Litter Decomposition

The laboratory experiment proved that in the early stages of litter decomposition (k_1), mass loss depends upon the aquatic condition and not on temperature or litter type. The k_1 decay rates for the S treatment, independently of temperature, were on average 5.6- and 3.6-fold faster than the rates found for the M and MS treatments, for green and mint tea, respectively (Figure 3A). This result agrees with Djukic and others (2018) who observed an effect of precipitation on the early stage of green tea mass loss, while temperature did not show any significant effect. In aquatic systems, detritus mass loss and decomposition rates are affected by the continuous exposure to water, which enhances the leaching of soluble compounds, thus accelerating the decomposition rates of labile detritus (Bottino and others 2016; Yajun and others 2016; Petraglia and others 2019). In this regard, Seelen and others (2019) highlighted the importance of measuring tea leachates when assessing aquatic decomposition rates. They found a 28% green tea mass loss after 3 h in the pelagic zone of a lake, where

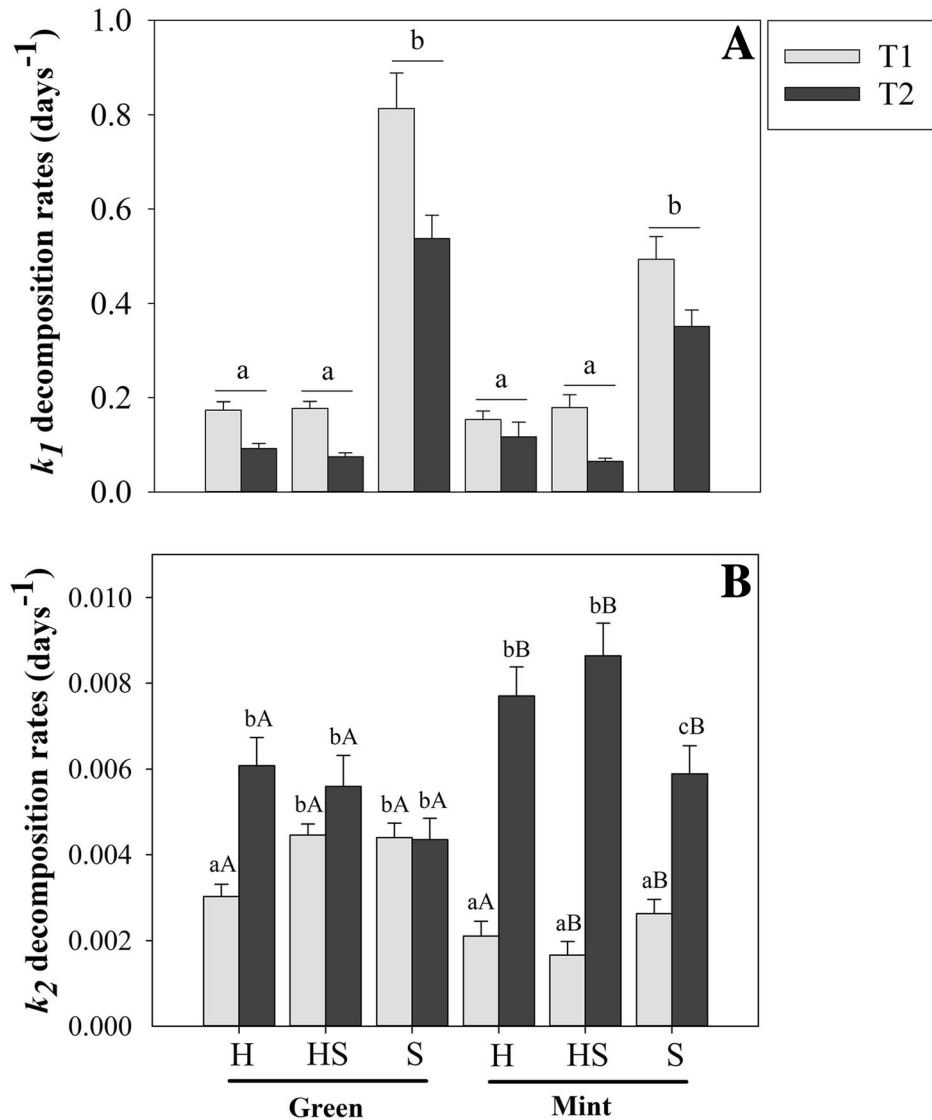


Figure 3. Green and mint tea k_1 (A) and k_2 (B) decomposition rates (\pm SE) for each hydroperiod (M, MS, S) and temperature (T1, T2) combination. Lower case letters indicate significant differences among treatments, and upper case letters indicate significant differences between detritus species within the same treatment (Tukey, $P < 0.05$).

temperatures ranged from 9.5 to 14°C. Furthermore, green tea mass loss was higher in the water column than in the littoral zone. In our experiment, green tea also lost 28% of its initial mass, while mint tea lost 23% after 48 h in the S treatment, while only 5–7% of tea mass was lost in the M and MS condition. These high values of litter mass loss by leaching in the tea bags could not be expected in leaf litter of higher particle size, since small particles, with high area-to-mass ratios, leach more because of high surface exposure (Zukswert and Prescott 2017; Dossou-Yovo and others 2021). However, the difference in detritus mass loss between submerged and not submerged substrates

may also be expected to occur in large particulate litter.

On the other hand, the decomposition rates of the recalcitrant fraction of litter (k_2) depended on litter quality, water condition and, in most cases, temperature. MS treatment showed that upon immersion, litter decomposition is stimulated. This result agrees with in situ experiments on submerged leaf litter (Langhans and Tockner 2006; Abril and others 2016) and in microcosm experiments (Palmia and others 2019). Likewise, decomposition was faster with higher temperatures, with the exception of green tea under submerged conditions (MS and S treatments). This

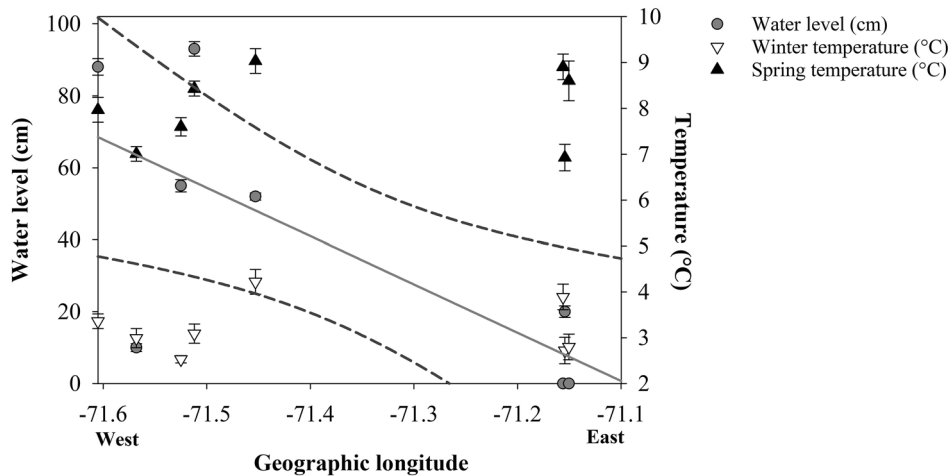


Figure 4. Relationship between meadow water height and mean winter and spring temperature (\pm SE) with site coordinate. The linear relationship between longitude and water height was obtained from a regression analysis (R^2_{adj} : 50.7%, $P < 0.05$). Dotted lines show the 95% confidence interval.

result was predicted and coincides with previous studies (Keuskamp and others 2013; Didion and others 2016; Helsen and others 2018; Mori and others 2021) for green tea in moist conditions. On the other hand, mint tea decomposition was stimulated by the increase in the incubation temperature, independently of the hydroperiod condition.

In the spring field experiment, detritus mass loss was explained mainly by site humidity, estimated by geographic longitude. Detritus mass loss decreased from meadows with available water (> 10 cm above soil surface) to dryer sites, with moist soil. Sarneel and others (2020) also found that under cold temperatures (like our field temperature), tea decomposition rates increased in wetter meadows. They also demonstrated that differences between litter species were higher at drier conditions, which agrees with the different mass loss found between tea types in steppe meadows (Figure 5A). Yajun and others (2016) and Petraglia and others (2019) showed that an increase in water availability increases the synergistic interaction between soil water content and litter type, since, as has been mentioned before, water enhances the leaching of soluble compounds. Our field experiment supports the initial results from the laboratory assay, where the hydroperiod was the conducting factor of decomposition. Tea mass loss in meadows with wetter conditions (that is, where detritus was submerged) was stimulated, while in meadows with moist soil, tea mass loss was on average 1.9 (green tea) and 2.6 (mint tea) fold lower.

Although the effect of temperature in the field experiment in spring could not be verified, because

of the straight range of temperatures found in the W-E transect, the comparison between spring and winter experiments showed that differences between wet (forest meadows) and dry (steppe meadows) biomes are greater in spring, with higher temperatures (Figure 6). This confirms our hypothesis and also the second prediction proposed by Djukic and others (2018) in which differences in wet and dry biomes are evident in warmer climates. These results were also confirmed in peatlands (MacDonald and others 2018) and wetlands (Petraglia and others 2019), where tea decomposition was higher with high soil water content and high temperature. Here we confirmed these differences in a very small geographic scale (37 km distance). Tea mass loss in forest meadows, in spring, was $37 \pm 2\%$ and $39 \pm 0.4\%$ higher than the green and mint tea mass lost, respectively, in the steppe meadows (averaged over seasons), which agrees with the results found by Zhang and others (2008) that decomposition is usually higher in forested than in nonforested systems. Forest microbial communities were found to be more capable of respiring C-based substrates than grassland microbes (Baldrian and others 2012; Ochoa-Hueso and others 2019).

Particularly, steppe meadows were characterized by the absence of a water column and a soil water content of 20 to 50% at the end of the spring (Table S1). The seasonal increase in temperature (spring) did not stimulate litter mass loss and soil moisture seemed to limit litter decomposition in these meadows. This result does not coincide with the tea decomposition process in the M treatment, for the laboratory experiment, where both green

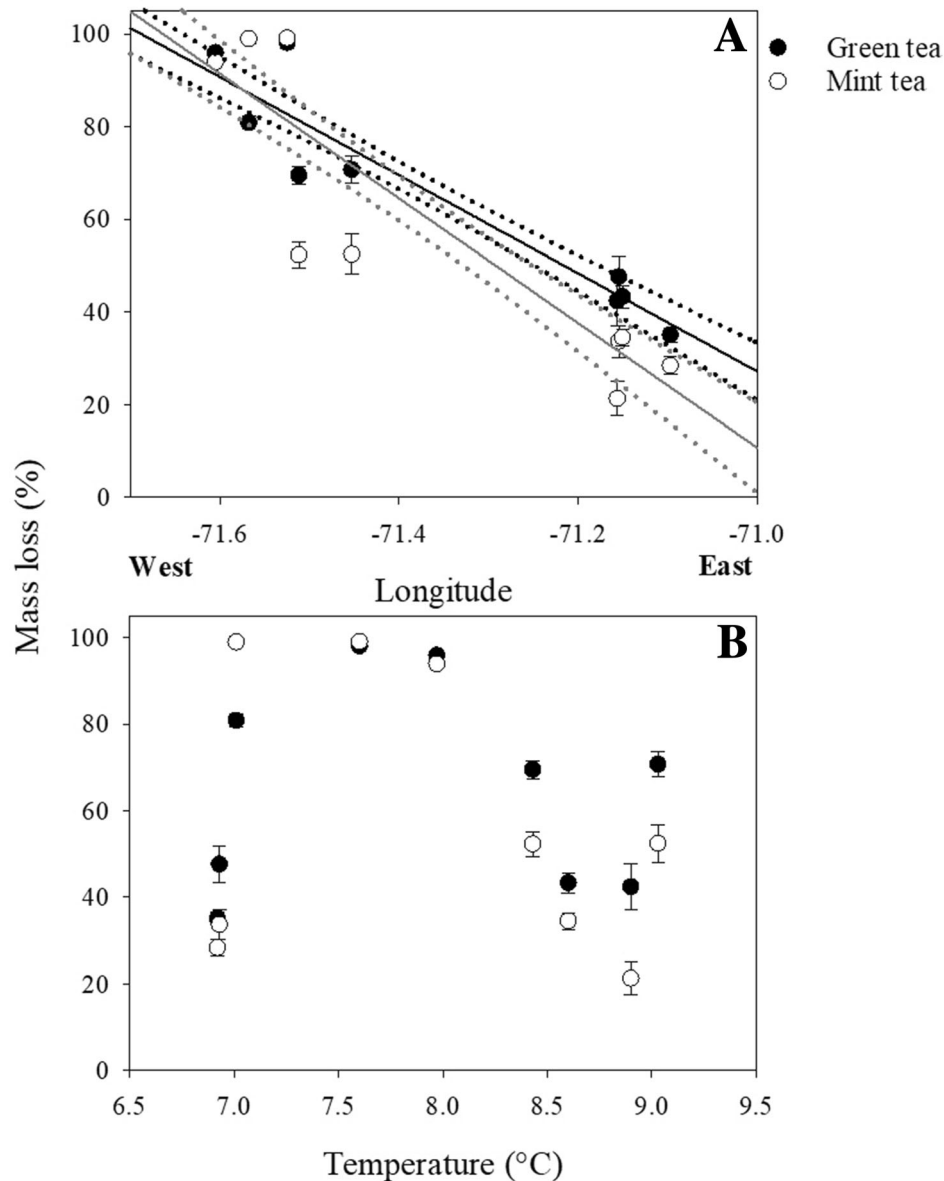


Figure 5. Mass loss of green and mint tea at each meadow: **A** along the longitudinal gradient and **B** at each mean spring temperature. The linear relationship between tea mass loss and longitude was obtained from the minimum adequate model for the significant fixed effects. Dotted lines show the 95% confidence interval. Error bars are standard errors.

and mint tea mass loss was enhanced by an increase in the incubation temperature. This difference could be due to drier conditions in steppe meadows (20–50% soil water content) than in the M treatment (90% perlite water content). On the other hand, in forest meadows, where detritus was submerged, spring temperatures did stimulate detritus mass loss (Figure 6). This increase in seasonal temperature could have stimulated decomposition in submerged conditions due to higher fungal activity (Mora-Gómez and others 2016), promoted litter leaching (Seelen and others 2019)

or enhanced enzymatic activities (Baldrian and others 2012; Pinsonneault and others 2016; Follstad Shah and others 2017) leading to higher litter mass loss.

Differences in Decomposition According to Litter Type

Green and mint tea were quite similar in their nutrient content, which led to similarities in early stages of the decay process (k_1) (Figure 3A). Although the green tea releases more DOC than mint

Table 3. Effect of Hydroperiod and Meadow Temperature on Tea Mass Loss

	F-value	P-value
Species	49.5	< 0.001
Longitude	34.1	0.002
ns (Temperature)	1.43	0.284
Species*Longitude	49.6	< 0.001
Species*ns (Temperature)	24.2	< 0.001
Longitude*ns (Temperature)	1.44	0.282
Species*Longitude*ns (Temperature)	24.3	< 0.001

Parameter	Est. (SE)	F-value	P-value
Green tea ($R^2_m = 80.3\%$, $R^2_c = 94.8\%$.)			
Longitude	- 1.12 (0.24)	21.4	0.006
Ns (Temperature)	12.9 (41.4)	0.09	0.766
Longitude*ns (Temperature)	0.18 (0.58)	0.09	0.765
Mint tea ($R^2_m = 87.4\%$, $R^2_c = 97.8\%$.)			
Longitude	- 1.74 (0.27)	41.2	0.001
Ns (Temperature)	85.8 (46.3)	3.43	0.12
Longitude*ns (Temperature)	1.21 (0.65)	3.46	0.12

Results of the linear mixed effects model of hydroperiod and temperature on tea mass loss at the site level. Longitude was used as an estimator of hydroperiod, and site temperature refers to the mean spring meadow temperature. Meadow was used as a random factor. $R^2_m = 85.2\%$, $R^2_c = 96.3\%$.

Table 4. Effect of Season and Biome on Species Detritus Mass Loss

	Green tea		Mint tea	
	F-value	P-value	F-value	P-value
Season	12.05	0.001	9.98	0.003
Biome	117.94	< 0.001	50.51	< 0.001
Block	2.36	0.086	12.14	< 0.001
Season*biome	20.31	< 0.001	6.36	0.017

Results of the randomized block ANOVA, comparing winter and spring tea mass losses from forest and steppe meadows. Green tea: $R^2_{adj} = 77\%$, mint tea: $R^2_{adj} = 72\%$.

tea, the similarity between the k_1 decomposition rates among litter types could be due to a similar labile component fraction in both teas. However, there were some differences between them in the recalcitrant fraction, which led to different decomposition rates for each litter type. Toward the end of the laboratory experiment, we found that

while green tea k_2 decomposition rates were faster than that of mint tea at 4°C, mint tea rates at 15°C were faster than green tea decay rates (Figure 3B). This result would imply that temperature has an important role in the decomposition of the more recalcitrant fraction of litter and agrees with the higher green tea mass loss found in both steppe and forest meadows under winter temperatures than the fraction lost by mint tea. Among the differences between litter types, a higher concentration of phenols and aromatic substances was reported for mint tea (Trevisan and others 2017) as well as antifungal and antimicrobial activities (Singh and others 2015) which could have delayed decomposition. These results did not coincide with the findings by Suseela and others (2013) that the effect of climate on the decomposition process depends on the proportion of labile compounds on leaf litter, because in our study the effect of temperature and hydroperiod depended more on the recalcitrant fraction in detritus type. Under spring temperatures, green tea mass loss was higher than mint tea mass loss in steppe meadows, but both litter types lost a similar fraction in the forest. Mean spring temperature in meadows ranged from 6.9 ± 0.33 to $9 \pm 0.27^\circ\text{C}$ and was lower than the laboratory incubation temperature (15°C). This could imply that temperatures under 15°C stimulate decomposition when detritus is submerged (forest meadows), independently of litter type, while in water-limited conditions (steppe meadows) litter mass loss could be limited by the labile C fraction in detritus (Hättenschwiler and Jørgensen 2010). Besides, the higher N:P ratio in green tea than in mint tea could have promoted fungal activity, as N:P rates above 50 were found to stimulate fungal metabolisms (Gusewell and Freeman 2005). At higher incubation temperatures (> 15°C) decomposition could be stimulated by the proportion of P released and by low N:P and C:P ratios, compared to those of green tea, which could explain the faster k_2 mint decomposition rates.

CONCLUSIONS

Our experiments showed that water availability plays a key role in the early stage of decomposition, independently of litter species or temperature, by stimulating the leaching of soluble compounds. As the process advances, temperature exerts a different effect depending on litter type and water availability. Rising temperatures, as expected by climate change, could stimulate litter mass loss in forested meadows. However, a reduction in precipitation is also predicted for the Patagonia region

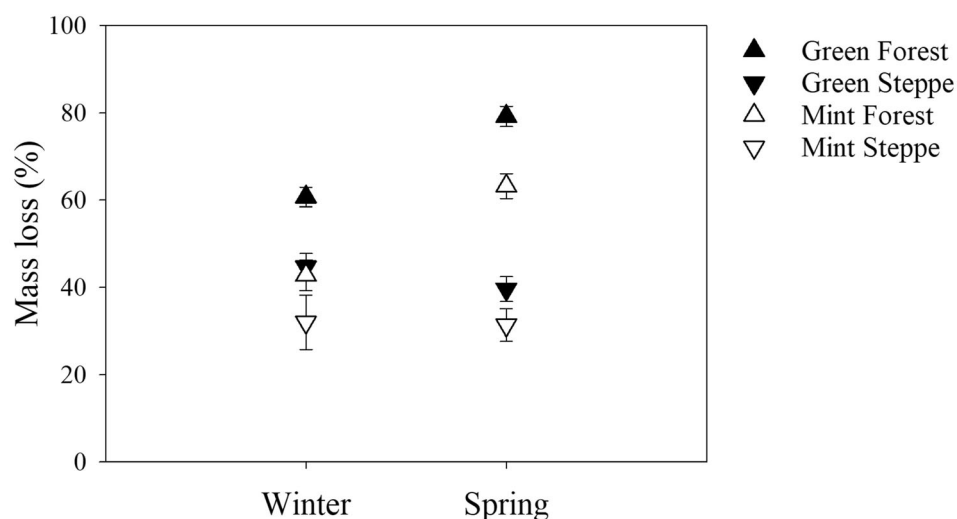


Figure 6. Mass loss of green and mint tea in forest and steppe meadows in the winter and spring experiment. Error bars are standard errors.

(Nuñez and others 2009; Magrin and others 2014), as well as a reduction in water resources (Pessacg and others 2020) so that the period of decomposition could be shortened as meadows hydroperiod is reduced, which could lead to a higher organic matter accumulation in these systems.

On the other hand, an increase in steppe meadows temperature would be insufficient to accelerate decomposition rates if a further reduction in the precipitation regime is to be expected. As soil moisture limited mass loss in steppe meadows, reduction in the frequency of precipitation could lead to a higher accumulation of organic matter in these wetlands. As temperature and hydroperiod affected detritus material differentially, labile litter is expected to be recycled faster than litter with a lower labile C content. This more labile material would decompose faster in steppe meadows, where flooding events are rare. Ecosystems with small-size plants, like forest and steppe meadows, are expected to store more C under climate change (Davidson and Janssens 2006; Kirschbaum 2006; Petraglia and others 2019). Further analysis of decomposition with: (1) a slowly decomposing detritus species that would allow an effective comparison between litter type and an accurate estimation of the C fraction to be sequestered in the wetland, and (2) throughout the different seasons as the majority of studies are carried out in the spring/summer under “favorable” conditions (see Mora-Gómez and others 2016; Djukic and others 2018; Sarneel and others 2020) would be needed to disentangle the mass loss process in these wetlands.

It is known that upon rewetting, respiration increases in both lentic and lotic systems (Marcé and others 2019; Von Schiller and others 2019). In this way, meadow rewetting would increase decomposition rates, thus the respiration rates. Studies in both dry and wet meadow phases are needed to disentangle the organic matter cycle and to assess the CO₂ emission rates from these particular freshwater systems.

ACKNOWLEDGEMENTS

We thank Estancia Fortín Chacabuco for allowing us to carry out the experiments in their steppe meadows and to Ariel Mayoral, Pablo Alvear and Matías Millerón for their support in the field work. Also, we would like to thank Matías Millerón for providing us with meteorological data from IN-IBIOMA stations. Finally, we thank the two reviewers for their valuable comments and suggestions which helped us to improve the manuscript.

FUNDING

Research was carried out with funds from FONCyT (PICT-2018-4385 to V.D-V) and from CONICET (PUE-229-2016-0100008-CO).

DATA AVAILABILITY

The DOI associated with the data is: <https://doi.org/10.17632/9v87x4jmw.3>, and the URL is: <https://data.mendeley.com/drafts/9v87x4jmw>.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

REFERENCES

- Abril M, Muñoz I, Menéndez M. 2016. Heterogeneity in leaf litter decomposition in a temporary Mediterranean stream during flow fragmentation. *Science of the Total Environment* 553:330–339.
- Althuizen IH, Lee H, Sarneel JM, Vandvik V. 2018. Long-term climate regime modulates the impact of short-term climate variability on decomposition in alpine grassland soils. *Ecosystems* 21:1580–1592.
- Anderson JT, Smith LM. 2002. The effect of flooding regimes on decomposition of *Polygonum pensylvanicum* in playa wetlands (Southern Great Plains, USA). *Aquatic Botany* 74:97–108.
- APHA. 2005. Standard methods for the examination of water and wastewater.
- Baldrian P, Kolařík M, Stursová M, Kopecký J, Valášková V, Větrovský T, Zifčáková L, Snajdr J, Řídl J, Vlček C, Voříšková J. 2012. Active and total microbial communities in forest soil are largely different and highly stratified during decomposition. *The ISME Journal* 6:248–258.
- Bates D, Sarkar D, Bates MD, Matrix L. 2007. The lme4 package. R Package Version 2:74.
- Bates M, Venables B, Team MRC. 2011. Package ‘splines’. R Version 2: 1–15.
- Battle JM, Golladay SW. 2001. Hydroperiod influence on breakdown of leaf litter in cypress-gum wetlands. *The American Midland Naturalist* 146:128–145.
- Boerjan W, Ralph J, Baucher M. 2003. Lignin biosynthesis. *Annual Review of Plant Biology* 54:519–546.
- Bottino F, Cunha-Santino MB, Bianchini I. 2016. Decomposition of particulate organic carbon from aquatic macrophytes under different nutrient conditions. *Aquatic Geochemistry* 22:17–33.
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.
- Bruder A, Schindler MH, Moretti MS, Gessner MO. 2014. Litter decomposition in a temperate and a tropical stream: the effects of species mixing, litter quality and shredders. *Freshwater Biology* 59:438–449.
- Buono G, Oesterheld M, Nakamatsu V, Paruelo JM. 2010. Spatial and temporal variation of primary production of Patagonian wet meadows. *Journal of Arid Environments* 74:1257–1261.
- Chimner RA, Bonvissuto GL, Cremona MV, Gaitan JJ, López CR. 2011. Condiciones ecohidrológicas de humedales a lo largo de un gradiente de precipitación en la Patagonia, Argentina. *Ecología Austral* 21:329–337.
- Cornwell WK, Cornelissen JH, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O, Hobbie SE, Hoorens B, Kurokawa H, Pérez-Harguindeguy N, Quested HM, Santiago LS, Wardle DA, Wright IJ, Aerts R, Allison SD, van Bodegom P, Brovkin V, Chatain A, Callaghan TV, Díaz S, Garnier E, Gurvich DE, Kazakou E, Klein JA, Read J, Reich PB, Soudzilovskaia NA, Vaieretti MV, Westoby M. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* 11:1065–1071.
- Coûteaux M-M, Bottner P, Berg B. 1995. Litter decomposition, climate and litter quality. *Trends in Ecology & Evolution* 10:63–66.
- Crego RD, Nielsen CK, Didier KA. 2014. Climate change and conservation implications for wet meadows in dry Patagonia. *Environmental Conservation* 41:122–131.
- Cuassolo F, Díaz-Villanueva V. 2019. Exóticas en humedales: Análisis de las comunidades vegetales de mallines naturales y urbanos en la ciudad de Bariloche. *Ecología Austral* 29:405–415.
- Dang CK, Schindler M, Chauvet E, Gessner MO. 2009. Temperature oscillation coupled with fungal community shifts can modulate warming effects on litter decomposition. *Ecology* 90:122–131.
- Datry T, Corti R, Claret C, Philippe M. 2011. Flow intermittence controls leaf litter breakdown in a French temporary alluvial river: the “drying memory.” *Aquatic Sciences* 73:471–483.
- Datry T, Foulquier A, Corti R, Von Schiller D, Tockner K, Mendoza-Lera C, Clement JC, Gessner MO, Moleon M, Stubbington R, Gücker B. 2018. A global analysis of terrestrial plant litter dynamics in non-perennial waterways. *Nature Geoscience* 11:497–503.
- Davidson EA, Janssens IA. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440:165–173.
- de Neiff AP, Neiff JJ, Casco SL. 2006. Leaf litter decomposition in three wetland types of the Paraná River floodplain. *Wetlands* 26:558–566.
- Didion M, Repo A, Liski J, Forsius M, Bierbaumer M, Djukic I. 2016. Towards harmonizing leaf litter decomposition studies using standard tea bags—a field study and model application. *Forests* 7:167.
- Djukic I, Kepfer-Rojas S, Schmidt IK, Larsen KS, Beier C, Berg B, Verheyen K. 2018. Early stage litter decomposition across biomes. *Science of the Total Environment* 628:1369–1394.
- Dossou-Yovo W, Parent S-É, Ziadi N, Parent É, Parent L-É. 2021. Tea Bag Index to Assess Carbon Decomposition Rate in Cranberry Agroecosystems. *Soil Systems* 5:44.
- Ferreira V, Chauvet E. 2011. Future increase in temperature more than decrease in litter quality can affect microbial litter decomposition in streams. *Oecologia* 167:279–291.
- Follstad Shah JJ, Kominoski JS, Ardón M, Dodds WK, Gessner MO, Griffiths NA, Hawkins CP, Johnson SL, Lecerf A, LeRoy CJ, Manning DWP, Rosemond AD, Sinsabaugh RL, Swan CM, Webster JR, Zeglin LH. 2017. Global synthesis of the temperature sensitivity of leaf litter breakdown in streams and rivers. *Glob Chang Biol* 23:3064–3075.
- Fox J, Weisberg S, Adler D, Bates D, Baud-Bovy G, Ellison S, Firth D, Friendly M, Gorjanc G, Graves S, Heiberger R. 2012. Package ‘car’. Vienna: R Foundation for Statistical Computing 1–151.
- García-Palacios P, McKie BG, Handa IT, Frainer A, Hättenschwiler S. 2016. The importance of litter traits and decomposers for litter decomposition: a comparison of aquatic and terrestrial ecosystems within and across biomes. *Functional Ecology* 30:819–829.
- Geraldes P, Pascoal C, Cássio F. 2012. Effects of increased temperature and aquatic fungal diversity on litter decomposition. *Fungal Ecology* 5:734–740.
- Glazebrook HS, Robertson AI. 1999. The effect of flooding and flood timing on leaf litter breakdown rates and nutrient

- dynamics in a river red gum (*Eucalyptus camaldulensis*) forest. *Australian Journal of Ecology* 24:625–635.
- Gonçalves AL, Graça MA, Canhoto C. 2013. The effect of temperature on leaf decomposition and diversity of associated aquatic hyphomycetes depends on the substrate. *Fungal Ecology* 6:546–553.
- Graça M, Poquet J. 2014. Do climate and soil influence phenotypic variability in leaf litter, microbial decomposition and shredder consumption? *Oecologia* 174:1021–1032.
- Gusewell S, Freeman C. 2005. Nutrient limitation and enzyme activities during litter decomposition of nine wetland species in relation to litter N:P ratios. *Functional Ecology* 19:582–593.
- Hättenschwiler S, Jørgensen HB. 2010. Carbon quality rather than stoichiometry controls litter decomposition in a tropical rain forest. *Journal of Ecology* 98:754–763.
- Helsen K, Smith SW, Brunet J, Cousins SA, De Frenne P, Kimberley A, Kolb A, Lenoir J, Ma S, Michaelis J, Plue J. 2018. Impact of an invasive alien plant on litter decomposition along a latitudinal gradient. *Ecosphere* 9:1–15.
- Iñiguez-Armijos C, Rausche S, Cueva A, Sánchez-Rodríguez A, Espinosa C, Breuer L. 2016. Shifts in leaf litter breakdown along a forest–pasture–urban gradient in Andean streams. *Ecology and Evolution* 6:4849–4865.
- IPCC. 2007. Climate change 2007–impacts, adaptation and vulnerability: Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (M. Parry, M. L. Parry, O. Canziani, J. Palutikof, P. Van der Linden, C. Hanson Eds. Vol. 4). Cambridge, UK: Cambridge University Press.
- Irisarri G, Oesterheld M, Paruelo J, Baldassini P, Arocena D, Oyarzabal M. 2012. Impacto de la erupción de volcán Puyehue y el déficit de precipitaciones sobre la producción de materia seca del suroeste de Río Negro. Informe técnico. Facultad de Agronomía UBA1–13.
- Jaeger B. 2017. R2glmm: computes R squared for mixed (multilevel) models. R package version 0.1 2: 1–12.
- Jobbágy EG, Paruelo JM, León RJ. 1995. Estimación del régimen de precipitación a partir de la distancia a la cordillera en el noroeste de la Patagonia. *Ecología Austral* 5:047–053.
- Kandus P, Minotti P, Malvárez AI. 2008. Distribution of wetlands in Argentina estimated from soil charts. *Acta Scientiarum. Biological Sciences* 30:403–409.
- Keuskamp JA, Dingemans BJ, Lehtinen T, Sarneel JM, Hefting MM. 2013. Tea Bag Index: a novel approach to collect uniform decomposition data across ecosystems. *Methods in Ecology and Evolution* 4:1070–1075.
- Kirschbaum MUF. 2006. The temperature dependence of organic-matter decomposition—still a topic of debate. *Soil Biology and Biochemistry* 38:2510–2518.
- Kuznetsova A, Brockhoff PB, Christensen RH. 2017. lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software* 82:1–26.
- Langhans SD, Tiegs SD, Gessner MO, Tockner K. 2008. Leaf-decomposition heterogeneity across a riverine floodplain mosaic. *Aquatic Sciences* 70:337–346.
- Langhans SD, Tockner K. 2006. The role of timing, duration, and frequency of inundation in controlling leaf litter decomposition in a river-floodplain ecosystem (Tagliamento, northeastern Italy). *Oecologia* 147:501–509.
- Leberfinger K, Bohman I, Herrmann J. 2010. Drought impact on stream detritivores: experimental effects on leaf litter breakdown and life cycles. *Hydrobiologia* 652:247–254.
- Lenth R, Lenth MR. 2018. Package ‘lsmeans.’ *The American Statistician* 34:216–221.
- Li X, Cui B, Yang Q, Lan Y, Wang T, Han Z. 2013. Effects of plant species on macrophyte decomposition under three nutrient conditions in a eutrophic shallow lake, North China. *Ecological Modelling* 252:121–128.
- Lorenz K, Lal R, Preston CM, Nierop KG. 2007. Strengthening the soil organic carbon pool by increasing contributions from recalcitrant aliphatic bio (macro) molecules. *Geoderma* 142:1–10.
- MacDonald E, Brummell ME, Bieniada A, Elliot J, Engering A, Gauthier TL, Saraswati S, Touchette S, Tourmel-Courchesne L, Strack M. 2018. Using the Tea Bag Index to characterize decomposition rates in restored peatlands. *Boreal Environment Research* 23:221–235.
- Magrin GO, Marengo JA, Boulanger JP, Buckeridge MS, Castellanos E, Poveda G, Scarano FR, Vicuña S. 2014. 2014: Central and South America. *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, V. R. Barros, C. B. Field, D. J. Dokken, M. D. Mastrandrea, K. J. Mach, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, L. L. White Eds. Cambridge, United Kingdom and New York: Cambridge University Press. pp. 1499–66
- Marcé R, Obrador B, Gómez-Gener L, Catalán N, Koschorreck M, Arce MI, Singer G, von Schiller D. 2019. Emissions from dry inland waters are a blind spot in the global carbon cycle. *Earth-Science Reviews* 188:240–248.
- Mariluan GD, Díaz Villanueva V, Albariño RJ. 2015. Leaf litter breakdown and benthic invertebrate colonization affected by seasonal drought in headwater lotic systems of Andean Patagonia. *Hydrobiologia* 760:171–187.
- Martínez A, Larrañaga A, Pérez J, Descals E, Pozo J. 2014. Temperature affects leaf litter decomposition in low-order forest streams: field and microcosm approaches. *FEMS Microbiology Ecology* 87:257–267.
- Medeiros AO, Pascoal C, Graca MAS. 2009. Diversity and activity of aquatic fungi under low oxygen conditions. *Freshwater Biology* 54:142–149.
- Minden V, Kleyer M. 2015. Ecosystem multifunctionality of coastal marshes is determined by key plant traits. *Journal of Vegetation Science* 26:651–662.
- Molles MC, Crawford CS, Ellis LM. 1995. Effects of an experimental flood on litter dynamics in the middle Rio Grande riparian ecosystem. *Regulated Rivers: Research & Management* 11:275–281.
- Mora-Gómez J, Eloşegi A, Duarte S, Cássio F, Pascoal C, Romaní AM. 2016. Differences in the sensitivity of fungi and bacteria to season and invertebrates affect leaf litter decomposition in a Mediterranean stream. *FEMS Microbiology Ecology* 92:1–12.
- Mori T, Aoyagi R, Taga H, Sakai Y. 2021. Effects of water content and mesh size on tea bag decomposition. *Ecologies* 2:175–186.
- Núñez MN, Solman SA, Cabré MF. 2009. Regional climate change experiments over southern South America. II: Climate change scenarios in the late twenty-first century. *Climate Dynamics* 32:1081–1095.
- Ochoa-Hueso R, Delgado-Baquerizo M, King PTA, Benham M, Arca V, Power SA. 2019. Ecosystem type and resource quality are more important than global change drivers in regulating early stages of litter decomposition. *Soil Biology and Biochemistry* 129:144–152.

- Paccagnella YC, Bianchini I, da Cunha-Santino MB. 2020. Decomposition dynamics of two aquatic macrophytes: response of litter interaction with temperature and dissolved oxygen availability. *Brazilian Journal of Botany* 43:1047–1059.
- Palmia B, Bartoli M, Laini A, Bolpagni R, Ferrari C, Viaroli P. 2019. Effects of Drying and Re-Wetting on Litter Decomposition and Nutrient Recycling: A Manipulative Experiment. *Water* 11:1–21.
- Pessag N, Flaherty S, Solman S, Pascual M. 2020. Climate change in northern Patagonia: critical decrease in water resources. *Theoretical and Applied Climatology* 140:807–822.
- Petraglia A, Cacciatori C, Chelli S, Fenu G, Calderisi G, Gargano D, Abeli T, Orsenigo S, Carbognani M. 2019. Litter decomposition: effects of temperature driven by soil moisture and vegetation type. *Plant and Soil* 435:187–200.
- Pettit NE, Davies T, Fellman JB, Grierson PF, Warfe DM, Davies PM. 2012. Leaf litter chemistry, decomposition and assimilation by macroinvertebrates in two tropical streams. *Hydrobiologia* 680:63–77.
- Pinheiro J, Bates D, DebRoy S, Sarkar D, Heisterkamp S, Van Willigen B, Maintainer R. 2017. Package 'nlme'. Linear and nonlinear mixed effects models, version 3.
- Pinna M, Basset A. 2004. Summer drought disturbance on plant detritus decomposition processes in three River Tirso (Sardinia, Italy) sub-basins. *Hydrobiologia* 522:311–319.
- Pinsonneault AJ, Moore TR, Roulet NT. 2016. Temperature the dominant control on the enzyme-latch across a range of temperate peatland types. *Soil Biology and Biochemistry* 97:121–130.
- R Core Team. 2013. R: A language and environment for statistical computing.
- Reynolds S. 1970. The gravimetric method of soil moisture determination Part IA study of equipment, and methodological problems. *Journal of Hydrology* 11:258–273.
- Riutta T, Slade EM, Bebbler DP, Taylor ME, Malhi Y, Riordan P, Macdonald DW, Morecroft MD. 2012. Experimental evidence for the interacting effects of forest edge, moisture and soil macrofauna on leaf litter decomposition. *Soil Biology and Biochemistry* 49:124–131.
- Sarneel JM, Sundqvist MK, Molau U, Björkman MP, Alatalo JM. 2020. Decomposition rate and stabilization across six tundra vegetation types exposed to > 20 years of warming. *Science of the Total Environment* 724:1–9.
- Seelen LM, Flaim G, Keuskamp J, Teurlincx S, Font RA, Tolunay D, Fránková M, Šumberová K, Temponeras M, Lenhardt M, Jennings E. 2019. An affordable and reliable assessment of aquatic decomposition: tailoring the Tea Bag Index to surface waters. *Water Research* 151:31–43.
- Singh R, Shushni MA, Belkheir A. 2015. Antibacterial and antioxidant activities of *Mentha piperita* L. *Arabian Journal of Chemistry* 8:322–328.
- Suseela V, Tharayil N, Xing B, Dukes JS. 2013. Labile compounds in plant litter reduce the sensitivity of decomposition to warming and altered precipitation. *New Phytologist* 200:122–133.
- Tiegs SD, Costello DM, Isken MW, Woodward G, McIntyre PB, Gessner MO, Chauvet E, Griffiths NA, Flecker AS, Acuña V, Albariño R. 2019. Global patterns and drivers of ecosystem functioning in rivers and riparian zones. *Science Advances* 5:1–8.
- Trevisan SCC, Menezes APP, Barbalho SM, Guiguer ÉL. 2017. Properties of mentha piperita: a brief review. *World J Pharm Med Res* 3:309–313.
- Von Schiller D, Datty T, Corti R, Foulquier A, Tockner K, Marcé R, García-Baquero G, Odriozola I, Obrador B, Elosegi A, Mendoza-Lera C. 2019. Sediment respiration pulses in intermittent rivers and ephemeral streams. *Global Biogeochemical Cycles* 33:1251–1263.
- Webster J, Benfield E. 1986. Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics* 17:567–594.
- Wider RK, Lang GE. 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. *Ecology* 63:1636–1642.
- Xie Y, Xie Y, Xiao H, Chen X, Li F. 2019. The effects of simulated inundation duration and frequency on litter decomposition: A one-year experiment. *Limnologia* 74:8–13.
- Yajun X, Yonghong X, Xinsheng C, Feng L, Zhiyong H, Xu L. 2016. Non-additive effects of water availability and litter quality on decomposition of litter mixtures. *Journal of Freshwater Ecology* 31:153–168.
- Yue K, García-Palacios P, Parsons SA, Yang W, Peng Y, Tan B, Huang C, Wu F. 2018. Assessing the temporal dynamics of aquatic and terrestrial litter decomposition in an alpine forest. *Functional Ecology* 32:2464–2475.
- Zhang D, Hui D, Luo Y, Zhou G. 2008. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *Journal of Plant Ecology* 1:85–93.
- Zhang M, Cheng X, Geng Q, Shi Z, Luo Y, Xu X. 2019. Leaf litter traits predominantly control litter decomposition in streams worldwide. *Global Ecology and Biogeography* 28:1469–1486.
- Zukswert JM, Prescott CE. 2017. Relationships among leaf functional traits, litter traits, and mass loss during early phases of leaf litter decomposition in 12 woody plant species. *Oecologia* 185:305–316.