



Impact of Simulated Changes in Water Table Depth on Ex Situ Decomposition of Leaf Litter from a Neotropical Peatland

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Received: 12 July 2012 / Accepted: 18 December 2012 / Published online: 18 January 2013
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Abstract Although water table depth is commonly regarded as the primary determinant of litter decomposition rate in tropical peatlands, this has rarely been tested experimentally. This study explored the influence of flooding on decomposition of litter from three dominant plant species in a neotropical peatland. The non-flooded treatment reduced the mass remaining after 14 months from 84 to 81 % for *Raphia taedigera*, 65 to 58 % for *Camposperma panamensis*, and 69 to 58 % for *Cyperus* sp. The proportions of carbon, nitrogen and phosphorus in the labile, semi-labile and recalcitrant carbon pools, did not reliably predict differences among species in the mass loss rate of litter. Phosphorus was rapidly lost from litter, while carbon losses, including soluble carbon, were slower, but significant for all fractions. The non-flooded treatment substantially reduced the quantity of C remaining in the residue fraction of leaf litter after 12 weeks, with 31, 19 and 6 % less remaining in the non-flooded treatment for *R. taedigera*, *C. panamensis* and *Cyperus* sp. This suggests that lower water table depth on litter decay increase degradation of mainly aliphatic and aromatic carbon in the residual fraction. Thus, although lowering the water table increased decomposition, the chemical composition of litter clearly influences peat accumulation.

Keywords Litter decomposition · Nutrient cycling · Tropical peatland · Vegetation communities

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Introduction

Tropical peatlands are an important global carbon (C) store, with stocks amounting to *c.* 90 Gt-C (Page et al. 2011). The thickness of peat deposits shows substantial spatial variation among tropical peatlands (Phillips et al. 1997; Page et al. 1999). Peat accumulation in the tropics is promoted by the high, aseasonal, plant productivity and slow decomposition of litter caused by waterlogging (Wright and Reddy 2001; Bernal and Mitsch 2008; Zhang et al. 2008; Kayranli et al. 2010). Carbon inputs derive from a diverse range of vegetation communities via inputs of above-ground biomass as litter to the peat surface, and also within the peat profile as a result of root exudation/senescence and microbial turnover (Kao et al. 2003; Chimner and Ewel 2005; Jauhiainen et al. 2005; Hirano et al. 2009). The relative contributions of carbon to peatlands from fine litter, including leaves, coarse woody debris and roots are broadly similar, with fine litter input being marginally greater (Mahli et al. 2011). Decomposition of leaf litter is important for the rapid return of nutrients to the ecosystem (Schreeg et al. 2012) and may also make an important contribution to peat formation (Brady 1984; Yule and Gomez 2009).

Several environmental factors affect the decomposition rate of senesced biomass in wetlands, including substrate temperature, moisture content, site nutrient status and litter quality. Site conditions and litter quality, defined here as a combination of organic matter chemistry and nutrient concentration, are well established determinants of litter decomposition (Miyajima et al. 1997; Rejmánková and Houdkova 2006; Guo et al. 2008; Yule and Gomez 2009; Cheesman et al. 2010). Thus, litter containing easily degradable material decomposes more rapidly than that from species containing more recalcitrant material (Kao et al. 2003; de Neiff et al. 2006; Crawford et al. 2007). Low nutrient concentrations in leaves may also limit decomposition rate (DeBusk and

Reddy 2005; Rejmánková and Sirova 2007; Fennessy et al. 2008; Wang et al. 2010). However, little is currently known regarding the influence of species composition and variation in site conditions on litter decomposition rates in forested tropical peatlands (but see Brady 1984; Yule and Gomez 2009). Furthermore, the trajectory from the chemistry of the initial litter to that of the organic material present in peat and the rate at which a more stable humified residue is formed remain poorly understood (Baumann et al. 2009). Given that peat chemistry is a strong predictor of greenhouse gas emissions (Wright et al. 2011), a sound understanding of the processes involved in peat formation is important to predict future impacts on tropical C stocks under changing climatic conditions. Indeed, the water balance of tropical wetlands may be disrupted by the predicted 4–5 °C increase in temperature and 20–30 % decrease in precipitation in parts of the tropical Americas (Meehl et al. 2007).

With respect to abiotic controls of decomposition, wetlands in tropical regions experience more consistent temperatures during the annual cycle (Grisi 1997; Waddington et al. 1998; Joiner et al. 1999; Jauhiainen et al. 2005) than higher latitude systems (Kadlec and Reddy 2001; Guo et al. 2008). However, the water table can vary markedly in tropical regions with pronounced seasonality in rainfall (Jauhiainen et al. 2005). This is important because drawdown of the water table increases aeration of the litter and surface peat layers, thereby increasing aerobic decomposition (Schwendenmann et al. 2003; Jauhiainen et al. 2005). By contrast, the formation of anoxic conditions when the water table reaches the peat surface following rainfall limits decomposition and promote peat accretion (Miyajima et al. 1997; Wright and Reddy 2001; Battle and Golladay 2007). Changes in water table depth are of particular concern with respect to the future functioning of tropical peatlands as C sinks (Meehl et al. 2007) because even modest drawdown may impact strongly on litter degradation rates at the peat surface (Belyea and Baird 2006), with implications for C accumulation and greenhouse gas emissions.

The present study focussed on the decomposition of leaf litter, which was expected to be more rapid than that of roots and woody tissue (Chimner and Ewel 2005). Furthermore, small changes in the water level in peatlands are likely to impact directly on leaf litter on the peat surface. Specifically, the study explored the impact of the degree of flooding on decomposition rates of litter from three distinct vegetation communities in the San San Pond Sak tropical peatland in Panama (Troxler 2007; Sjögersten et al. 2011), thereby representing a substantial range of leaf litter chemistry. Laboratory incubations of leaf litter from the three dominant plant species (*Raphia taedigera*, *Camposperma panamensis* and *Cyperus* sp.) were used to test the hypothesis that flooding decreases the decomposition rate for litter types with differing litter chemistry.

Materials and Methods

Site Description

The study site was the Changuinola peat deposit, an ombrotrophic domed peatland which forms part of the San San Pond Sak wetland in Bocas del Toro Province on the Caribbean coast of western Panama (cf. Sjögersten et al. 2011; Wright et al. 2011 for detailed site description). Nutrient concentrations in the surface peat and leaf tissues of the dominant species vary greatly among vegetation types and are generally low in the interior and increase towards the edge of the peatland (Troxler 2007; Sjögersten et al. 2011). The current study focussed on the dominant litter types at three locations spanning the nutrient gradient. These included a relatively nutrient-rich site dominated by *Raphia taedigera* (a canopy-forming palm), an intermediate site dominated by *Camposperma panamensis* (an evergreen canopy-forming hardwood tree species) and a nutrient-poor site dominated by *Cyperus* sp. (c. 1 m tall sedge). The texture of the peat varies between the interior (coarse) and edge (fine) of the peatland (Phillips et al. 1997; Wright et al. 2011), indicating differing rates of decomposition and/or differences in the source of litter. The peat is shallower at the edge of the peatland than in the interior i.e. c. 2 m under *R. taedigera*, c. 4 m under *C. panamensis* and c. 8 m under *Cyperus* sp. (Phillips et al. 1997). Peat chemistry differs among sites, with carbohydrate content being greatest in the coarser peat found in the interior and least in the fine peat under *R. taedigera*. Strong differences in pore water chemistry among vegetation communities were also evident as dissolved carbon and nitrogen concentrations were higher in the *R. taedigera* palm swamp than at the two sites closer to the centre of the peatland (Wright et al. 2011). The redox potential suggests mildly reducing conditions as mean values were respectively 235±32, 222±29, 194±23 mV at the *R. taedigera*, *C. panamensis* and *Cyperus* sp. sites (Wright et al. 2011).

Mean annual temperature is 27 °C, with low intra-annual variability and a mean annual precipitation of 3,209 mm between 1992 and 2001 (Estadística Panameña 2001). Annual rainfall at Bocas del Toro (CS700 rain gauge, Campbell Scientific Inc, Utah, USA) varied greatly between years, being 2,823, 2,405 and 2,963 mm in 2006, 2007 and 2008, respectively. The water table ranges annually from just above to just below the peat surface (maximum range c. ±20 cm), with no distinct period of drawdown. Mean temperature 10 cm below the peat surface is c. 25 °C and shows little intra and inter-annual variation (Wright 2011).

Long Term Litter Decomposition

Long-term decomposition rates for leaf litter from three dominant vegetation communities were measured to

determine the role of leaf litter input to peat formation. Litter from *R. taedigera* and *Cyperus* sp. was collected as standing dead leaves, while *C. panamensis* litter comprised newly fallen dry leaves collected from the peat surface. The litter was air-dried to constant mass and cut into *c.* 1.5×1.5 cm pieces. Weighed litter samples for *R. taedigera* and *C. panamensis* (*c.* 1.5 g each) and *Cyperus* sp. (*c.* 1.0 g) were placed in 10×10 cm nylon bags. To assess experimentally the influence of the water level on decomposition rate, litter bags from each site were randomly allocated to non-flooded (NF) and flooded treatments (F). These were placed in trays containing a 3 cm layer of washed silica sand to act as an inert base; fine nylon mesh was placed over the sand to separate it from the litter bags. The trays were inoculated with 100 mL of peat suspension (*c.* 10 mL of peat mixed with 90 mL of distilled water) from the site from which the litter was obtained (e.g. peat suspension from the *R. taedigera* site was added to the trays containing *R. taedigera* litter). The peat used for the suspensions was collected from the peatland surface (0–10 cm depth) and stored at 6 °C prior to addition to the trays. Distilled water was used to provide two treatments: sand in the NF treatment was fully wetted but with no surface pooling, while the water level was 5 cm above the sand surface in the F treatment. The NF treatment resulted in slightly drier litter conditions compared to the average field situation. The water level was maintained by topping up the trays on a weekly basis. These treatments simulated saturated and flooded field conditions.

The trays containing litter bags for each species were randomly placed in a dark incubator at 30 °C to reflect the upper range of substrate temperature at the field site. The trays were repositioned at monthly intervals to take account of any systematic variation in temperature. Five randomly selected bags for each site and treatment were sampled after 1, 2, 3, 9, 13 and 15 months (i.e. a total of 60 bags for each species), air-dried and weighed before being ashed at 550 °C for 3 h. The remaining organic matter was calculated as a percentage of the original value based on their initial weights.

Litter Chemistry and Short Term Decomposition

To determine initial litter chemical composition and the rate of release of nitrogen (N), phosphorus (P) and carbon (C), a short-term incubation experiment was carried out using litter from all three sites. Samples (3.5 g) were placed in 10×10 cm mesh bags for *R. taedigera* and *C. panamensis*, while 1.0 g samples were used for *Cyperus* sp.; these were subjected to the NF and F treatments described above at 30 °C. To determine whether decomposition rate and nutrient release from chemically more recalcitrant fractions were more sensitive to variation in the water level than easily extractable fractions, litter bags from each site were randomly

allocated to non-flooded and flooded treatments. These were then placed in trays between layers of washed synthetic sponge, which acted as an inert base and avoided mineral contamination of the litter bags. These were inoculated with 100 mL of peat suspension as described above. The water level was maintained 3 cm above the litter bags in the flooded treatment and just below the bags in the non-flooded treatment. To assess the impact of treatment on decomposition, five randomly selected samples were air-dried and weighed for each litter type and treatment after 1 and 12 weeks (25 bags in total, including five bags selected initially, per species).

The quality of the initial litter and litter recovered after 1 and 12 weeks of incubation was assessed by sequential fractionation, an operationally defined estimation of the lability of C, N and P (*n*=5; McLauchlan and Hobbie 2004). Dried litter samples were ground to fine powder using a ball mill before placing 1 g sub-samples of *R. taedigera* and *C. panamensis* and 0.5 g samples of *Cyperus* sp. in 25 mL screw-top plastic tubes. Initial extraction in water (milliQ) was used to determine the most labile fraction (inorganic nutrients, sugars, amino acids). To achieve this, the litter bags were shaken in 20 mL of water, placed in a shaking water bath at 30 °C for 12 h and filtered. The remaining litter material was extracted in acid (6 M hydrochloric acid (HCl) at 116 °C for 16 h) to determine substances of intermediate lability (e.g. hemicellulose and cellulose). Both filtrates were analysed for dissolved organic carbon (DOC) and total nitrogen (TN) using a TOC-V/TN analyser (Shimadzu Corp, Kyoto, Japan). Total phosphorus (TP) was measured using standard molybdate colorimetry with an absorbance wavelength of 880 nm following reduction using ascorbic acid.

The non-acid-extractable residual fraction containing the recalcitrant portion of the litter (e.g. lignin and long chain aliphatic molecules) was analysed for total C (TC) and total N (TN) by automated combustion (Flash EA 1112 Series, CE Instruments Ltd, UK). Total P (TP) was determined by ashing at 550 °C for 3 h and dissolution in 1 M H₂SO₄ with P detection by standard molybdate colorimetry as described above.

Statistical Analysis

The results were analysed by analysis of variance (ANOVA) using Genstat Version 10.1 (Lawes Agricultural Trust, Rothamsted Experimental Station). Factors included were 'litter type', 'water level', 'sample removal time' and their interactions; mass loss from the litter samples, C, N and P concentrations and % of the initial values remaining following the three extraction procedures were the response variables. Exponential decay curves were fitted to results from the long term mass loss experiment. Simple linear

regression analysis was used to test for relationships between decomposition rate and initial litter chemistry. Differences between treatments are reported when $p < 0.05$.

Results

Initial Litter Composition

Total C was 589 ± 14 , 603 ± 13 and 662 ± 27 mg C g⁻¹ in *R. taedigera*, *C. panamensis* and *Cyperus* sp. litter, respectively (litter types, $p = 0.08$). Total N also did not differ significantly among litter types (20.5 ± 0.69 , 18.5 ± 0.97 and 20.2 ± 1.08 mg N g⁻¹ for *R. taedigera*, *C. panamensis* and *Cyperus* sp., respectively; $p > 0.4$). In contrast, total P varied significantly between litter types, being greatest for *R. taedigera* (136 ± 1 μg P g⁻¹), intermediate for *C. panamensis* (90 ± 3 μg P g⁻¹) and lowest for *Cyperus* sp. (42 ± 11 μg P g⁻¹; $F_{2,14} = 44.25$, $p < 0.001$). The initial C:N, C:P and N:P ratios were lowest for *R. taedigera* litter and greatest for *Cyperus* sp. C:N ratios were 29, 32 and 34 and the C:P ratios were 4330, 6720 and 15530 respectively for *R. taedigera*, *C. panamensis* and *Cyperus* sp. litter. The corresponding N:P ratios were 151, 205 and 460.

Carbon, N and P were held in different proportions in the water-extractable, acid-extractable and residual fractions of leaf litter (element × fraction: $F_{4,133} = 1608$, $p < 0.001$; Fig. 1). The proportions of C and N were greatest in the residual fraction, while a larger proportion of N than C was held in the acid-extractable fraction. Phosphorus was overwhelmingly confined to the water- and acid-extractable fractions.

The proportion of C in the residual fraction was initially greatest for *C. panamensis*, while the proportions of N and P

in this fraction were greatest for *Cyperus* sp. (Fig. 1; Table 1a). Litter from *Cyperus* sp. contained the greatest proportion of acid-extractable C of all three litter types, but the lowest proportion of N and P. Water-extractable C was greatest for *R. taedigera*, while the corresponding value for N was greatest for *Cyperus* sp.; the proportion of water-extractable P was comparable for *R. taedigera* and *C. panamensis*.

Long Term Litter Decomposition

Camposperma panamensis litter exhibited the greatest mean mass loss of organic matter (40 % after 15 months), followed by *Cyperus* sp. (30 % loss) and *R. taedigera* (19 %; Fig. 2; Tables 1b, 2). Decomposition rate was most rapid at the start of the incubation period for all three litter types and greatest for *C. panamensis* (Table 1b). The loss of litter mass over time was best predicted (based on the model fit and the significance of the relationship) using single exponential decay curves (Fig. 2; Table 2). Flooding consistently reduced decomposition rates for *C. panamensis* and *Cyperus* sp. litter compared to the non-flooded treatment. However, the effect was modest, with c. 10 % less mass loss occurring after 15 months under flooded conditions (Table 1b). Organic matter loss for *R. taedigera* litter was initially greater in the flooded than in the non-flooded treatment (Fig. 2a), but the reverse applied after 10 months of incubation (Table 1b).

Temporal and Water Table Effects on Extractable and Residual C, N and P

On a mass basis, C, N and P concentrations in the different fractions showed contrasting trends (Table 3) because water-extractable C and P concentrations declined strongly with

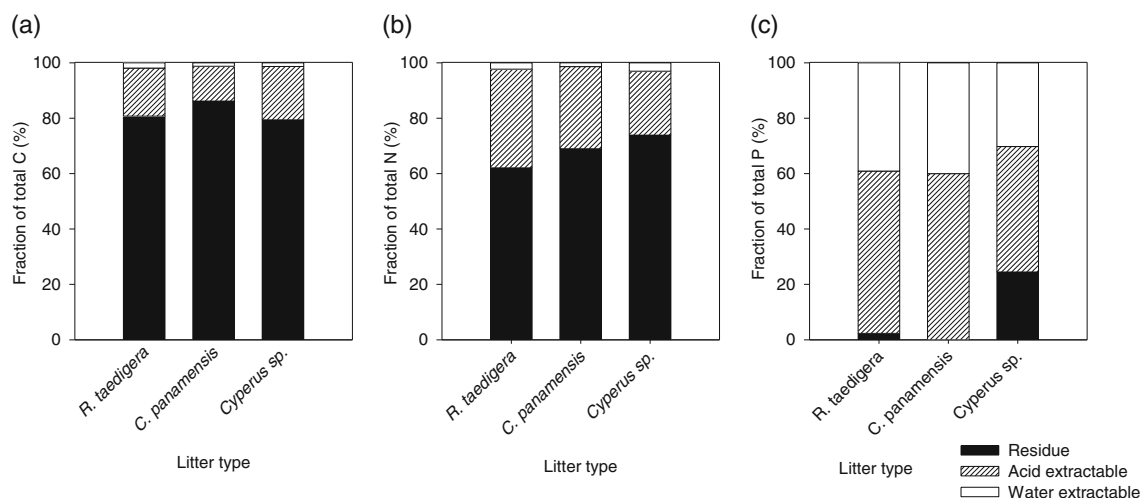


Fig. 1 Initial litter composition with respect to the mean proportions of **a** carbon (C), **b** nitrogen (N) and **c** phosphorus (P) in the water-extractable and acid-extractable fractions and residue of litter from *Raphia taedigera*, *Camposperma panamensis* and *Cyperus* sp. expressed as % of the total. $n = 5$

Table 1 ANOVA summaries for (a) % of total of C, N and P present in the water-extractable (W_{ext}), acid-extractable (A_{ext}) and residue fractions shown in Fig. 1, and (b) the long-term litter bag experiment shown in Fig. 2

a)	Fraction	Factor	Statistics
	W_{ext} C	Litter type	$F_{2,13}=19.95, p<0.001$
	W_{ext} N	Litter type	$F_{2,14}=13.70, p<0.001$
	W_{ext} P	Litter type	$F_{2,14}=4.38, p<0.05$
	A_{ext} C	Litter type	$F_{2,13}=26.87, p<0.001$
	A_{ext} N	Litter type	$F_{2,14}=13.84, p<0.001$
	A_{ext} P	Litter type	$F_{2,14}=4.38, p<0.05$
	Residue C	Litter type	$F_{2,13}=29.86, p<0.001$
	Residue N	Litter type	$F_{2,14}=12.44, p<0.001$
	Residue P	Litter type	$F_{2,14}=4.38, p<0.05$
b)	Litter type	Factors	Statistics
	<i>R. taedigera</i>	Treatment	$F_{1,55}=1.12, p=0.3$
		Time	$F_{5,55}=101.3, p<0.001$
		Time \times Treatment	$F_{5,55}=9.02, p<0.05$
	<i>C. panamensis</i>	Treatment	$F_{1,57}=8.61, p<0.05$
		Time	$F_{5,57}=3.71, p<0.05$
		Time \times Treatment	$F_{5,57}=0.58, p=0.6$
	<i>Cyperus</i> sp.	Treatment	$F_{1,57}=15.37, p<0.005$
		Time	$F_{5,57}=52.11, p<0.001$
		Time \times Treatment	$F_{5,57}=1.45, p=0.3$

time ($F_{2,87}=712.54, p<0.001$; $F_{2,87}=77.45, p<0.001$), while water-extractable N increased ($F_{2,87}=77.08; p<0.001$). There was an overall increase in the concentration of acid-extractable C ($F_{2,85}=10.85, p<0.001$) in the litter, while N and P concentrations in this fraction decreased ($F_{2,85}=18.5, p<0.001$; $F_{2,87}=849.66, p<0.001$; Table 3). There was no strong temporal change in the residue fraction on a mass basis for C, N or P.

Water-extractable C expressed as a percentage of the initial C content was lower in the flooded than in the non-flooded treatment at the end of the experiment for all litter

types (Fig. 3a; Table 4). Values declined to *c.* 30 % remaining after 12 weeks of incubation and were lowest for *R. taedigera*. Water-extractable P also declined strongly with time to *c.* 40 % remaining for *R. taedigera* and *C. panamensis* litter, whilst *Cyperus* sp. litter showed an even greater decline to *c.* 15 % (Fig. 3g; Table 4). The influence of water table treatment varied among litter types, with % P remaining being marginally greater in the water-extractable fraction in the flooded treatment of *R. taedigera* and *C. panamensis* litter, whereas the opposite was true for *Cyperus* sp. The influence of water table treatment on water-extractable N also varied between litter types and was greatest for *C. panamensis* (Fig. 3d; Table 4).

In general, acid-extractable C, N and P declined more slowly with time (Fig. 3b, e, h; Table 4) and was not strongly influenced by the treatment. The quantity of C remaining in the residue fraction at the end of the experiment was 30, 18 and 6 % lower in the non-flooded than the flooded treatment for *R. taedigera*, *C. panamensis* and *Cyperus* sp. litter, respectively (Fig. 3c; Table 4). In contrast, the water table treatment had no significant effect on the quantity of N or P remaining in the residual fraction (Fig. 3 f, i; Table 4).

The flooding treatment affected the elemental ratios in some of the fractions examined. The C:N ratio for the water-extractable fraction was initially 25, 29 and 15 for *R. taedigera*, *C. panamensis* and *Cyperus* sp. litter, respectively. After 12 weeks, the corresponding values in the non-flooded treatment had decreased greatly to 5.7, 4.9 and 3.3. C:N ratio was *c.* 3 for all litter types in the flooded treatment (Treatment effect: $F=11.31, p<0.05$). By contrast, there was no significant effect of the flooding treatment on C:P and N:P ratios.

C:N ratios in the acid-extractable fraction were not affected by the flooding treatment and were much greater for *Cyperus* sp. (29) than for *R. taedigera* and *C. panamensis* ($p<0.05$), for which the values were similar (15 and 14 respectively). The C:N ratio in the residue fraction was *c.* 40 and did not vary significantly among treatments or litter types. P-values were

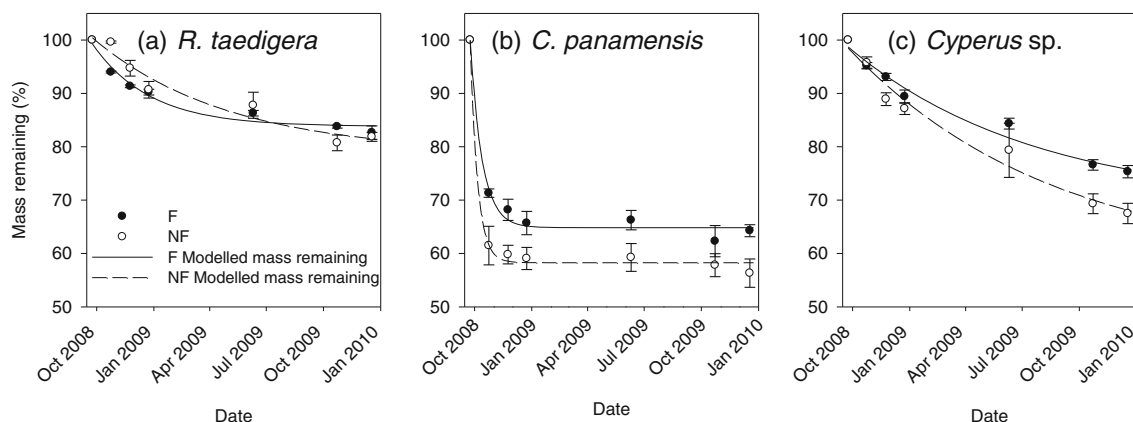


Fig. 2 Timecourses for the mass of litter remaining as a percentage of the initial value for **a** *Raphia taedigera*, **b** *Camptosperma panamensis* and **c** *Cyperus* sp. in the non-flooded (NF) and flooded (F) treatments. Curves are the best fit exponential regressions (cf. Table 2). Means \pm SEM are shown; $n=5$

Table 2 Parameters and statistics for the single exponential decomposition models (mass remaining = $A + B \times R^{\text{time}}$) shown in Fig. 3. NF and F denote non-flooded and flooded treatments

Parameter	<i>R. taedigera</i>		<i>C. panamensis</i>		<i>Cyperus</i> sp.	
	NF	F	NF	F	NF	F
R	1.00	0.99	0.92	0.95	1.00	1.00
B	21.7	15.5	41.7	35.1	40.9	29.5
A	78.7	83.8	58.3	64.8	57.6	69.2
σ^2	82.5	89.9	83.6	94.1	90.1	93.7
F	78.5	143.5	85.0	258.2	156.3	248.2
<i>p</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

R is the decay constant for the first order model

B is the initial proportion of labile material in both water table treatments (expressed as %)

A is the asymptote of the exponential model (expressed as % mass remaining)

Table 3 Concentration of C, N and P in the water extractable, acid extractable and residue fractions in *R. taedigera*, *C. panamensis* and *Cyperus* sp. litter after 0, 1 and 12 weeks (W) of incubation under non-flooded (NF) and flooded (F) conditions. Means \pm SEM are shown; $n=5$

Litter	Week	C (mg g^{-1})		N (mg g^{-1})		P ($\mu\text{g g}^{-1}$)	
		NF	F	NF	F	NF	F
Water extractable fraction							
<i>R. taedigera</i>	0	11.4 \pm 0.4	11.4 \pm 0.4	0.47 \pm 0.03	0.47 \pm 0.03	53 \pm 0.4	53 \pm 0.4
	1	4.2 \pm 0.3	2.7 \pm 0.1	0.65 \pm 0.05	0.38 \pm 0.01	12 \pm 3.2	36 \pm 4.6
	12	4.6 \pm 0.8	1.6 \pm 0.1	0.80 \pm 0.09	0.46 \pm 0.02	35 \pm 1.6	33 \pm 2.4
<i>C. panamensis</i>	0	7.3 \pm 0.4	7.3 \pm 0.4	0.25 \pm 0.02	0.25 \pm 0.02	36 \pm 1.5	36 \pm 1.5
	1	2.9 \pm 0.3	1.6 \pm 0.1	0.60 \pm 0.05	0.36 \pm 0.02	8 \pm 3.3	21 \pm 3.5
	12	4.3 \pm 0.3	1.4 \pm 0.1	0.91 \pm 0.10	0.42 \pm 0.03	22 \pm 4.7	18 \pm 6.1
<i>Cyperus</i> sp.	0	8.5 \pm 0.3	8.5 \pm 0.3	0.57 \pm 0.03	0.57 \pm 0.03	15 \pm 4.6	15 \pm 4.6
	1	2.6 \pm 0.3	1.5 \pm 0.1	0.66 \pm 0.12	0.48 \pm 0.08	2 \pm 0.2	2 \pm 0.3
	12	4.0 \pm 0.4	3.1 \pm 0.1	1.21 \pm 0.08	1.07 \pm 0.06	2 \pm 0.1	3 \pm 0.4
Acid extractable fraction							
<i>R. taedigera</i>	0	104.7 \pm 8.7	104.7 \pm 8.7	7.36 \pm 0.58	7.36 \pm 0.58	80 \pm 0.6	80 \pm 0.6
	1	107.1 \pm 7.1	104.3 \pm 6.5	7.74 \pm 1.15	5.77 \pm 0.46	0 \pm 0.0	1 \pm 0.9
	12	103.4 \pm 3.1	115.6 \pm 5.4	5.50 \pm 0.59	6.34 \pm 0.31	0 \pm 0.1	0 \pm 0.0
<i>C. panamensis</i>	0	75.9 \pm 1.3	75.9 \pm 1.3	5.43 \pm 0.07	5.43 \pm 0.07	54 \pm 2.3	54 \pm 2.3
	1	77.9 \pm 2.6	77.8 \pm 1.3	4.69 \pm 0.13	4.42 \pm 0.08	0 \pm 0.0	0 \pm 0.0
	12	78.3 \pm 2.3	75.2 \pm 2.0	5.65 \pm 0.29	5.61 \pm 0.31	0 \pm 0.0	0 \pm 0.0
<i>Cyperus</i> sp.	0	127.3 \pm 3.8	127.3 \pm 3.8	4.42 \pm 0.29	4.42 \pm 0.29	22 \pm 7	22 \pm 7.0
	1	113.0 \pm 12.6	134.8 \pm 13.7	3.98 \pm 1.26	3.88 \pm 0.95	0 \pm 0.0	0 \pm 0.0
	12	149.7 \pm 5.0	168.9 \pm 9.4	3.90 \pm 0.18	4.50 \pm 0.42	0 \pm 0.0	0 \pm 0.0
Residue fraction							
<i>R. taedigera</i>	0	494.0 \pm 8.3	494.0 \pm 8.3	12.72 \pm 0.33	12.72 \pm 0.33	3 \pm 0.2	3 \pm 0.2
	1	625.2 \pm 17.7	610.8 \pm 11.7	19.27 \pm 1.91	18.43 \pm 2.87	1 \pm 0.1	2 \pm 0.3
	12	417.3 \pm 27.0	611.6 \pm 30.5	13.20 \pm 1.31	14.26 \pm 0.79	2 \pm 0.4	2 \pm 0.2
<i>C. panamensis</i>	0	520.2 \pm 12.7	520.2 \pm 12.7	12.80 \pm 0.94	12.80 \pm 0.94	0 \pm 0.0	0 \pm 0.0
	1	661.1 \pm 13.1	581.8 \pm 62.1	20.81 \pm 3.70	16.40 \pm 2.57	0 \pm 0.1	0 \pm 0.2
	12	575.8 \pm 70.3	694.1 \pm 9.8	13.69 \pm 1.07	14.24 \pm 0.64	0 \pm 0.1	0 \pm 0.1
<i>Cyperus</i> sp.	0	525.8 \pm 24.3	525.8 \pm 24.3	14.44 \pm 1.52	14.44 \pm 1.52	6 \pm 0.7	6 \pm 0.7
	1	610.6 \pm 42.9	634.0 \pm 14.1	12.56 \pm 0.34	20.18 \pm 3.38	5 \pm 1.5	4 \pm 0.9
	12	486.9 \pm 32.3	556.7 \pm 48.9	12.81 \pm 1.14	16.24 \pm 1.85	7 \pm 1.2	8 \pm 1.4

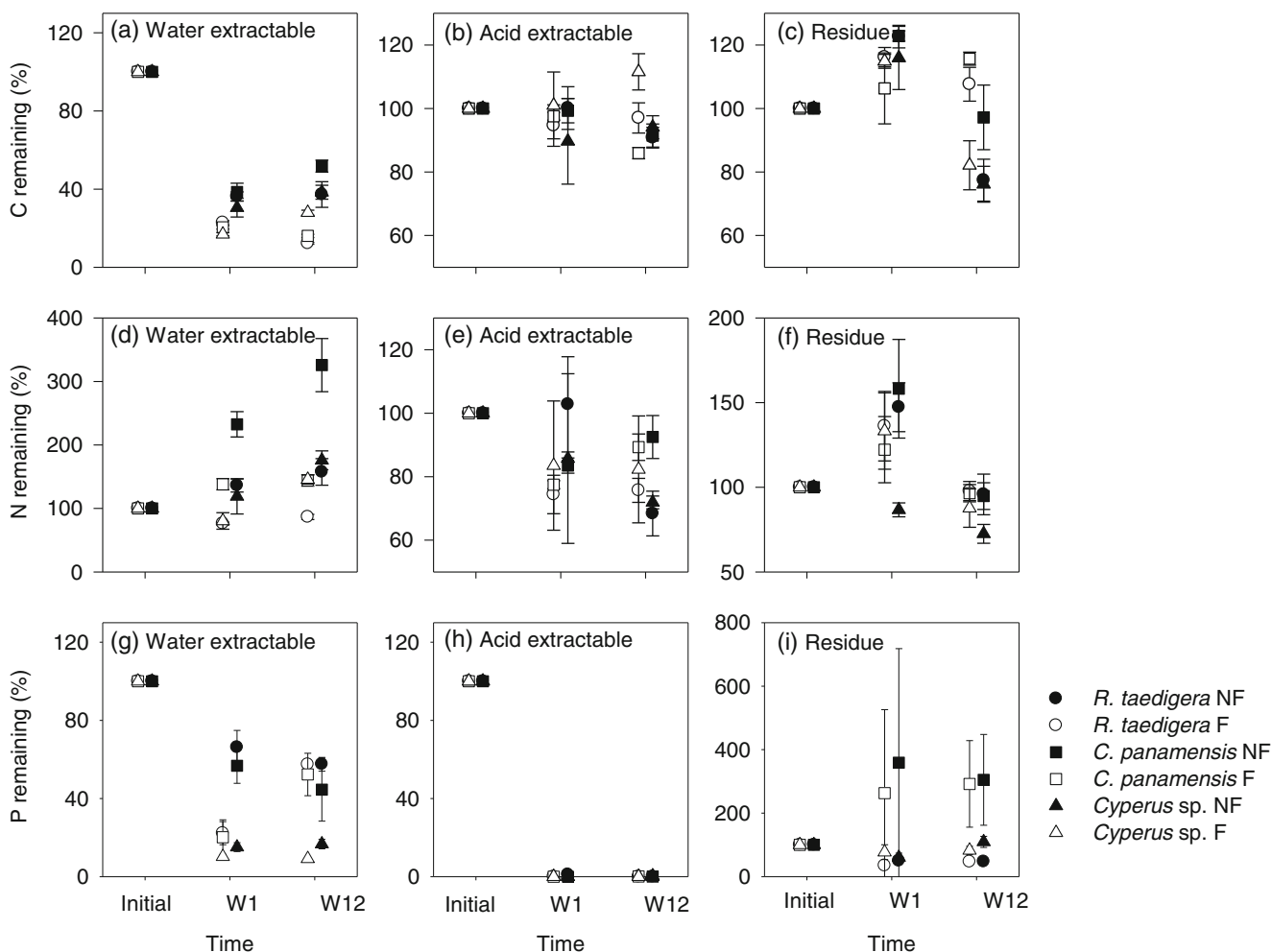


Fig. 3 Timecourses for the fraction remaining as a percentage of the initial for carbon (C) (a–c), nitrogen (N) (d–f) and phosphorus (P) (g–i) in the water-extractable (a, d, g), acid-extractable (b, e, h) and residue fractions (c, f, i) of litter from *Raphia taedigera*, *Camptosperma*

panamensis and *Cyperus* sp. in the non-flooded (NF) and flooded (F) treatments. W1 and W12 represent values obtained after one and 12 weeks of incubation

often below the detection limit for the acid-extractable and residual fractions (Table 3), thereby precluding reliable estimates of C:P and N:P; values for these ratios are therefore not presented.

Discussion

The observation that decomposition was more strongly affected by litter type than water table treatment (Fig. 2)

Table 4 Statistics describing effects of litter type, time and water table treatment (WT) on % of C, N and P remaining in the water-extractable, acid-extractable and residue fractions and C:N, C:P and N:P ratios for the water-extractable fraction data shown in Fig. 3

Response variable	Litter type	Time	Treatment
% C _{water}	F=9.47, $p<0.001$	F=166.34, $p<0.001$	F=93.31, $p<0.001$
% N _{water}	F=17.16, $p<0.001$	F=25.35, $p<0.001$	F=52.35, $p<0.001$
% P _{water}	F=71.84, $p<0.001$	F=29.88, $p<0.001$	F=8.77, $p<0.05$
% C _{acid}	F=111.21, $p<0.001$	F=7.70, $p<0.001$	F=4.51, $p<0.05$
% N _{acid}	F=24.59, $p<0.001$	F=1.46, $p=0.2$	F=0.22, $p=0.6$
% P _{acid}	F=50.44, $p<0.001$	F=934.65, $p<0.001$	F=0.88, $p<0.4$
% C _{residue}	F=2.7, $p=0.075$	F=8.00, $p<0.001$	F=5.66, $p<0.05$
% N _{residue}	F=0.24, $p=0.8$	F=7.42, $p<0.05$	F=1.18, $p=0.3$
% P _{residue}	F=120.3, $p<0.001$	F=6.15, $p<0.05$	F=0.2, $p=0.7$

supports the view that litter properties are the overriding influence on decomposition (Enriquez et al. 1993; Yule and Gomez 2009). However, as shown here, a lowering of the water table may increase mass loss in some litter types by c. 10 % over longer timescales (>15 months). Importantly, although a substantial quantity of mass was lost from both *C. panamensis* and *Cyperus* sp. litters, decay rates were much lower than those observed in situ in Micronesia (Chimner and Ewel 2005; Yule and Gomez 2009), suggesting that variation in the lability of litter may strongly influence C sequestration in peat. However, it is plausible that higher in situ degradation rates are linked to the field environment (e.g. presence of soil fauna) rather than litter quality per se.

The loss of organic matter was most rapid for litter from *C. panamensis* (Fig. 2), which was also the site where the CO₂ efflux from the peat surface was greatest (Wright 2011). This rapid mass loss suggests the presence of a high proportion of microbially easily-degradable material (Updegraff et al. 1995; Jonasson et al. 1999; Yule and Gomez 2009). However, comparison of the chemical characteristics of the litter reveals that, although litter from *R. taedigera* and *C. panamensis* contained similar quantities of labile and semi-labile C, N and P (Table 3), the former did not exhibit the same rapid initial loss of organic matter (Fig. 2). The rapid mass loss from *Cyperus* litter despite its lower labile and semi-labile N and P concentrations might be linked to its high cellulose:lignin ratio (DeBusk and Reddy 2005), combined with its high acid-extractable C, but low residual C content. The fact that single, rather than double exponential, decay curves provided the best model fit, suggest that the organic compounds in the leaf tissue follow the same decay trajectory. Chimner and Ewel 2005 found that single exponential curves were as powerful as double exponential ones in describing leaf litter decay. In contrast, they found that both root and wood decay appeared to be best described by double exponential decay curves, i.e. with one rate constant describing the rapid decay of labile C and one much lower rate constant describing the decomposition of more recalcitrant C.

The decoupling of lability (as determined by the extraction method) and decomposition rate in our study is consistent with the more rapid litter decomposition rates found for lignin-rich litter (approximately comparable to the residue fraction, although the latter is likely also to contain recalcitrant aliphatic compounds; Raich et al. 2007). More rapid rates of humification and lower long-term mass losses have been reported for litter with a higher initial N content (Berg et al. 1982), potentially reflecting the slow decomposition of *R. taedigera* litter which had the greatest proportion of N in the more labile water- and acid-extractable fractions (Fig. 1). Furthermore, the differing microbial assembly and function associated with each vegetation community may govern

decomposition rates rather than the intrinsic thermodynamic stability of the organic compounds in litter per se (Allison et al. 2007; Sjögersten et al. 2011; Cheesman et al. 2012; Troxler et al. 2012).

An additional explanation for the observed lack of a relationship between litter chemistry and degradation rate is that the wet chemical methods used for extraction may not provide a suitable analogue for microbially-available C, N and P in litter. In recent reviews, Kleber (2010) and Schmidt et al. (2011) suggested that, although the chemistry of the organic matter contributes to its decomposition rate, this is ultimately determined by complex interactions between the substrate, microbial community, enzymatic activities and environmental conditions. In the context of our study, the more rapid degradation of C from the residue fraction (assumed to be mainly aliphatic and aromatic carbon (McLauchlan and Hobbie 2004)) in the non-flooded treatment (Fig. 3) clearly supports the notion that environmental factors control recalcitrance. This suggests that increased decomposition of the 'recalcitrant' C fraction under conditions of water table drawdown may reduce accumulation of peat as surface aeration is improved (Freeman et al. 2004; DeBusk and Reddy 2005).

Some clear trends are apparent for the changes in residual C, N and P within the litter. As expected, the water-extractable C and P fractions were rapidly depleted (Fig. 3), particularly in the flooded treatment, reflecting a high degree of leaching of this fraction (Qiu et al. 2002; Yule and Gomez 2009). By contrast, water-extractable N increased with time as N was released from the more recalcitrant litter fractions. The rapid leaching of P was probably due to release of inorganic P present in vacuoles and rapid metabolism of P held in molecules such as nucleic acids and ATP (Schreeg et al. 2012). There was also a loss of C from all fractions, albeit less rapid, reflecting a combination of microbial respiration and leaching of C (Wright and Reddy 2001). The differing timecourses for the release of P and N are likely to be linked to N held in slowly degrading complex organic molecules (Millard 1988; Berlin et al. 2005), with the result that N was lost more slowly than P from litter.

The greater ex situ mass loss rates induced by the non-flooded treatment for litter from the two sites located closest to the centre of the peatland (Fig. 2) was comparable in magnitude to the impact of reduced water tables on in situ litter decomposition in south east Asia (Brady 1984) and boreal and temperate wetlands (Szumigalski and Bayley 1996; Haraguchi et al. 2003; Williams and Yavitt 2003). The clear effect of the flooding treatment on ex situ mass loss rates suggests that litter decomposition at these sites may be highly sensitive to even small decreases in the height of the water table, which has important implications for the contribution of litter to long term C accumulation in tropical peatlands. However, further in situ work is needed

to assess the influence of soil fauna and substrate nutrient status on the control of decomposition rate by the height of the water table.

The different rates of N and P loss from the litter reflect the nutrient status of the peatland from which it was collected. Rapid leaching of P from decomposing litter (Fig. 3) loss in surface run-off offers a plausible explanation for the strong gradient in P concentration across San San Pond Sak peatland and the exceedingly low P value for peat from the interior (Sjögersten et al. 2011). In contrast, the immobilisation of N, which occurred during litter decomposition, followed by integration of the remaining organic material into the peat, might account for the lack of strong gradients in total N in the surface peat (Sjögersten et al. 2011). The combination of the observed rapid loss of P from litter and substantial microbial accumulation may have served to increase P concentration in the surface peat (Sjögersten et al. 2011) relative to the parent litter. The influence of nutrient limitation on the degradation of organic material in situ requires further study to establish the relative importance of nutrient supplies and water table depth in determining litter decomposition in tropical peatlands (Fennessy et al. 2008; Wang et al. 2010).

Current climate change predictions for the region suggest a 4–5 °C increase in mean temperature and 20–30 % decrease in annual precipitation (Meehl et al. 2007). Although it is difficult to estimate the impact of such changes on the level of the free water surface in peatlands, reduced precipitation over periods of 1–2 months currently cause the water table fall to *c.* 20 cm below the peat surface (S. Sjögersten, pers. obs.); this would result in increased litter decomposition according to the observations reported here. With respect to land use changes, agricultural exploitation of forested tropical peatlands has caused water tables to fall 1 m below the peat surface in south-east Asia, leading to substantial C losses (Jauhiainen et al. 2005). In contrast, the small scale subsistence agriculture that occurs in undrained peatland forests in the Bocas del Toro region of Panama has a much smaller impact on the degree of flooding of the peat surface and hence is likely to have a smaller impact on C losses. Although some areas in Bocas del Toro support commercial banana plantations on drained peatlands, the predicted extent of climate change may represent an equally severe threat as agricultural expansion to the functioning and C sink strength of wetlands in the region.

Acknowledgments Emma Wright acknowledges the award of a PhD scholarship from the UK Biotechnology and Biological Sciences Research Council. The project was also supported by a University of Nottingham New Investigator grant. Alexander Cheesman was funded by a grant from the USDA–CREES National Research Initiative (No. 2004-35107-14918). We thank Darren Hepworth for laboratory assistance and staff at the Smithsonian Tropical Research Institute station in Bocas del Toro for logistical support.

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