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Getting to the root of the problem: litter decomposition and peat formation in lowland Neotropical peatlands

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Abstract Litter decomposition is an important control on carbon accumulation in tropical peatlands. We investigated the contribution of different litter tissues from two peatland tree species (*Raphia taedigera* and *Campnosperma panamensis*) to peat formation in four lowland tropical peatlands in the Republic of Panama. Leaves, stems, and roots decomposed at different rates; with roots being the slowest to decompose among tissues. The position of litter in the peat profile strongly influenced the decomposition rate of all tissue types. Roots decomposed up to five times faster at the surface than at 50 cm depth. Molecular characterization of litter and peat profiles by tetramethylammonium-pyrolysis–gas chromatography–mass spectrometry (TMAH-Py-GC/MS) revealed that the peat is formed predominantly of decomposed roots and stems, as indicated by the high lignin, low methylated fatty acids and carbohydrate concentrations in these litter types. Taken together, these data demonstrate that roots play a fundamental role in the formation of lowland Neotropical peatlands.

Keywords Carbon · Litter decomposition · Root · Tropical peat · Pyrolysis · Mass spectrometry

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Introduction

Peatlands act as carbon (C) sinks due to an imbalance between the above-belowground production of plant material (net primary productivity, NPP) and its decay (Clymo 1984; Frolking and Talbot 2011; Laiho 2006; Turunen et al. 2002). Globally, peatlands hold ca. 610 Gt of C belowground (Page et al. 2011); equivalent to ca. 84 % of the total C in the atmosphere (Falkowski 2000). Lowland tropical peatlands currently store about 40–90 Gt C (Kurnianto et al. 2015) and have the highest peat accumulation rates in the world—up to 10 times faster than temperate, subarctic and boreal peatlands (Chimner and Ewel 2005; Dommain et al. 2011; Gorham et al. 2003). However, lowland tropical peatlands are located in regions where mean annual temperatures, precipitation, and plant litter decay rates are high (Yule and Gomez 2008). As the C balance of lowland tropical peatlands is closely related to NPP and rates of organic matter decomposition (Sjögersten et al. 2014), understanding the factors controlling litter decomposition rates and the proportional contribution of different components of NPP to peat formation is of considerable importance to determine how vegetation influences peat accumulation.

Litter decomposition pathways are determined, among other factors, by the position of the water table and hence the redox status of the peat, with aerobic conditions resulting in greater CO_2 emissions than anaerobic conditions (Brady 1997; Couwenberg et al. 2011; Jauhiainen et al. 2005). A lower water table has also been found to increase in situ (Brady 1997) and ex situ leaf litter decomposition rates (Wright et al. 2013). Drainage due to land use change triggers aeration and subsidence of the subsurface peat (Couwenberg et al. 2009), and a water table draw down in response to projected future droughts in Central America (Field et al. 2014) might also contribute to peat subsidence in the region. In addition, the common use of slash and burn agricultural practices in Neotropical peatlands increases nutrient availability in soil (Andriesse and Schelhaas 1987), exposes the peat and fresh root material to aerobic decomposition (Hoyos-Santillan 2014).

To date organic matter decomposition studies in the tropics have focused on surface decomposition of leaf litter (Chambers et al. 2000). However, to fully understand the link between litter decay and peat formation we need to know how the conditions within the peat profile control decomposition rates of different types of litter inputs. Different litter tissue types (Chimner and Ewel 2005; Gholz et al. 2000; Middleton and McKee 2001; Zhang and Wang 2015), plant species (Cornelissen et al. 2007; Yule and Gomez 2008) and plant functional types (Wright et al. 2013) show considerable differences in litter decomposition rates and mass loss. Indeed, slow degradation of leaf litter from peat swamp tree species and roots due to poor litter quality provides a potential mechanism for peat accumulation (Cornwell et al. 2008; Zhang et al. 2008).

Studies of peat composition, from direct observation of macro and microfossils (Phillips et al. 1997) and biomarkers analysis (Kuder and Kruge 2001), offer an opportunity to examine organic matter decomposition over longer time frames than conventional decomposition studies using litterbags. Tetramethylammonium-pyrolysis–gas chromatography–mass spectrometry (TMAH–Py–GC/MS) represents an alternative method to characterize peat composition and to explore plant material accumulation/decomposition through time (Carr et al. 2010; McClymont et al. 2011; Parsi et al. 2007; Steward et al. 2009), providing a mechanistic understanding of decomposition processes in relations to the organic chemistry of the litter inputs that form peat (Schellekens et al. 2015). For example, Py–GC/MS has been used to identify vegetation shifts that occurred through thousands of years in peat deposits (Schellekens et al. 2009).

We hypothesized that root tissue constitutes the main component of the peat deposits in Neotropical peatlands. To test this hypothesis, we conducted a 2 year in situ litter decomposition study using litter (leaf, root, and stem tissue) from: *Raphia taedigera* (Mart.), a canopy forming palm in the Arecaceae family, and *Campnosperma panamensis* (Standl), an evergreen broadleaved hardwood tree in the Anacardiaceae family. These species belong to contrasting plant functional groups, which commonly form distinct forest communities in Neotropical peatlands (Phillips et al. 1997). The objective of the litter decomposition study was to determine the most slowly decomposing tissue type in two different forest communities dominated by different functional groups. In addition, we used TMAH–Py–GC/MS to compare the organic chemistry of different tissues

(leaves, roots and stems) from *R. taedigera* and *C. panamensis* to that of stratigraphic peat profiles from the same sites as where the litter decomposition study was conducted. The objective of this comparison was to determine if peat chemistry is similar to that of slowly decomposing litter tissue (roots according to our hypothesis).

Materials and methods

Site description

This study was conducted in the north-western Caribbean coast of Panama, where several large peatlands are located within the Bocas del Toro province, *e.g.* the San San Pond Sak wetland ($\approx$164 km^2). Seven forest communities have been identified in these peatlands (Phillips et al. 1997), and two were used in this study: palm swamps dominated by *R. taedigera* and mixed forests dominated by *C. panamensis*. The region receives a high annual precipitation rate of 3092 $\pm$ 181 mm and the mean annual air temperature is 25.9 $\pm$ 0.3 °C (2003–2011; Smithsonian Tropical Research Institute Physical Monitoring Program). There is no pronounced seasonality with respect to either rainfall (dry–wet season) or temperature (Wright et al. 2011), although there are two periods receiving somewhat lower rainfall from February to April and August to September (Hoyos-Santillan 2014).

Study sites

Two palm swamp sites and two mixed forests sites were selected for this study (Fig. 1; Table 1). The maximum distance between the sites was $\sim$50 km. All sites were freshwater (conductivity less than 200 µS cm^{-1}), with the water table at or just below (−10 cm) the peat surface for most of the time. Maximum recorded water fluctuations were +0.15 to −0.4 m relative to the peat surface, with surface water well above the peat surface at times of high rainfall. Dissolved O_2 concentrations in the pore water were up to 3.31 ppm at the surface, but as low as 0.2 ppm at 0.5 m in the peat profile. Palm sites were monodominant (>80 % of basal area), with large standing biomass (basal area of 103 m^2 ha^{-1}) with large amounts of palm leaf litter at the surface (*R, taedigera* is highly productive and its pinnate leaves are up to 10 m at the sites) and a dense (200 g m^{-2} of root in the top 10 cm of the peat profile) but shallow fibrous root system extending to approximately 1.1 m depth (Sjögersten et al. 2011; Wright et al. 2011) (ESM_1). The tree basal area at mixed forest sites was 13 m^2 ha^{-1} with *C. panamensis, Sympohonia globulifera, Cassipourea eliptica,* and *Euterpe precatoria* comprising most of the biomass, i.e., 38.7, 21.7, 25.0, and 10.0 % of basal area respectively (Sjögersten et al. 2011). The mixed sites had large amounts of *C. panamensis* leaf litter (but relatively less surface litter compared to the very high litter inputs at the palm sites) at the surface, but also had leaf litter from other species. The *C. panamensis* root system was characterized by woody lignified structural roots reaching at least 1 m depth, abundant surface knee roots, and thinner lateral roots in the surface peat and litter layer (Wright et al. 2011) (ESM_1). The density of the thinner lateral roots was ca. 50 g m^{-2} in the surface 10 cm of the peat profile (Wright et al. 2011). Microtopography within all sites consisted of shallow ponds and raised areas (close to trees associated with root structures). At each site, permanent vegetation census plots of 0.1 ha (20 × 50 m) were established in 2009. Within each plot, the collection of peat cores, litter samples, and the installation of litterbags was carried out.

Experimental design and methodology

Long-term decomposition study

A long-term in situ litter decomposition study was used to investigate the importance of (i) litter position within the peat profile, comparing decomposition rates between the peat surface and at 0.5 m depth and (ii) litter tissue types for long-term decay rates. For this study, litterbags containing leaf, root, or stem tissue from the two target species (*R. taedigera* and *C. panamensis*) were incubated at the study sites (Table 1). *R. taedigera* litter was incubated at the two palm swamp sites and *C. panamensis* litter was incubated at the two mixed forest sites. This approach integrates litter quality and decomposition environment associated with the two contrasting forest communities. Litter quality and the environment are intrinsically linked due to adaptation of the decomposer community to both the dominant litter inputs and site properties. Therefore, when we use the term to

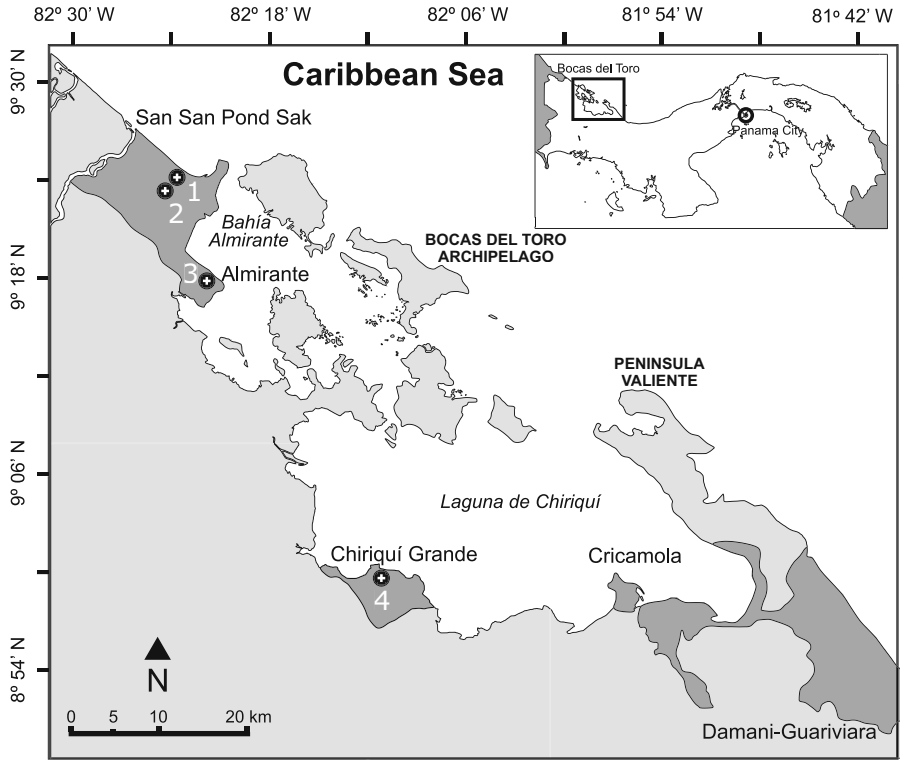

Fig. 1 Map of the north western region of the Caribbean coast of the Republic of Panama. Locations of the four study sites are shown and numbered according to Table 1; darker zones correspond to wetlands areas identified from aerial and satellite imagery

Table 1 Location and characteristics of study sites

Site		Coordinates	Distance to the coast (m)	Dominant vegetation (Basal area m^2 ha^{-1})	Peat depth (m)[c]
1	San San Pond Sak 1[a]	9°25′29.20″N, 82°24′05.60″W	500	*R. taedigera* (98.9)	1.87 ± 0.05
2	San San Pond Sak 2[b]	9°25′15.00″N, 82°24′14.64″W	1000	*C. panamensis* (38.7)	3.62 ± 0.19
3	Almirante Bay	9°18′17.46″N, 82°21′07.14″W	200	*C. panamensis* (45.8)	1.65 ± 0.15
4	Chiriquí Grande	8°58′28.22″N, 82°07′52.85″W	140	*R. taedigera* (80.5)	0.96 ± 0.07

Peat depth corresponds to the distance between the surface peat and the underlying mineral soil

[a,b] San San Pond Sak sites 1 and 2 correspond to Sites 1 and 2 respectively from Sjögersten et al. (2011)

[c] Peat definition: 30 % of dry weight organic matter (Joosten and Clarke 2002). Depths correspond to the mean values recorded, considering the distance from the surface peat to the underlying sand or clay depending on the location of the sites where the peat cores were collected (mean ± SE, $n = 4$)

"species" in the context of decomposition of e.g., *R. taedigera* litter incubated in the palm forest site, this refer to the combined effect of litter inputs (species) and site (forest community).At each site litterbags were placed in three randomly selected locations within the vegetation census plots. Litterbags were installed in March 2010 and subsequently 72 litterbags (9 from the surface and 9 from 0.5 m depth from each site) were collected sequentially in December 2010, May 2011 and April 2012. For this purpose, three litter bags of each tissue type were placed in random locations at each of the incubations sites at the start of the experiment, giving a total of 216 litterbags (2 depths × 3 tissue types × 4 sites (two of each forest community for true replication) × 3 collection dates × 3 site level replicates).

R. taedigera and *C. panamensis* litter for the litterbags was collected specifically at each of the study sites. Litter consisted of recently senesced leaves, freshly cut leaf stalks (petioles) or stems (ca. 5 cm in diameter), and lateral roots from 0 to 0.2 m depth, diameter 2–4 mm. After collection the litter was cleaned with deionized water and air-dried for 5 days. To allow comparable masses to be weighed out, the litter material was cut into smaller pieces: leaves were cut into ca. 2 × 2 cm pieces, roots were cut into ca. 1 cm lengths, and stems were cut into ca. 1 cm thick discs to ensure that a cross section of the stem tissue was used. Litter was weighed (leaves: ca. 2 g; stems and roots: ca. 1 g), placed separately into pre-weighed polyester mesh litterbags (0.1 × 0.1 m; 560 µm mesh), and tied with polyamide thread ($\varnothing = 0.8$ mm). Litter bags were placed directly on the peat surface avoiding hollows; for the below-ground incubation (0.5 m), a narrow slit was cut into the peat and the litterbags were manually inserted to a 0.5 m depth into the peat. To aid recovery, litter bags were tied to a string which was securely attached to the ground surface. After collection, the litterbags were carefully rinsed with deionized water. Although it is possible that fine litter (<560 µ) was lost during the cleaning process, resulting in a slight over estimation of the decomposition rates, all litterbags were subjected to the same treatment allowing for cross comparison. After rinsing, bags were opened and the litter visually inspected to remove new root growth. Litter was then dried at 70 °C for a minimum of 48 h until constant weight was reached.

Litter and peat chemistry

To compare litter organic chemistry of the current dominant litter forming species with the organic chemistry of the underlying peat, we undertook molecular biomarkers analysis of litter tissue and peat from each of the four study sites (SSPS1, SSPS2, Almirante and Chiriquí) using TMAH–Py–GC/MS. Peat cores were collected between April and June 2010 using a Russian peat corer. Peat cores were taken in sequential segments of 0.5 m with 48 mm in diameter, and sampling continued through the entire peat horizon until the underlying mineral soil was reached. Due to the presence of coarse root material in the top layers, it was difficult to collect intact samples of the surface peat. Thus, surface peat samples (0.1 × 0.1 × 0.1 m) were collected manually adjacent to the coring location. Both the 0.5 m core segments and the surface peat samples were wrapped in aluminum foil and placed in plastic boxes for transportation (<3 h) to the laboratory at the Smithsonian Tropical Research Institute's, Bocas del Toro Research Station, where they were stored at 4 °C until processing.

Peat and litter characterization

Peat cores were split into 10 cm sections and sampled at 0.5 m intervals. Different depths were selected for chemical characterization (from the surface to the bottom of the peat profile), as well as subsamples of the litter material collected from the four study sites for the litter decomposition experiment. Dry weight was determined by gravimetric analysis after oven drying 10 g fresh weight (fw) of peat and litter samples at 70 °C for 70 h (Wright et al. 2011). Total carbon (TC) and total nitrogen (TN) were determined on homogenized peat and litter samples using a total element analyzer (Flash EA 1112, CE Instruments, Wigan, UK).

For TMAH–Py–GC/MS analysis, samples (0.5 mg) were individually placed in quartz tubes and secured in place using quartz wool plugs (Carr et al. 2010). Prior to pyrolysis, 10 µL of a 0.25 µg μL^{-1} solution of 5-α-cholestane in hexane was added to each sample to enable quantification. In addition, each sample was soaked with 10 µL tetramethylammonium hydroxide (TMAH) to prevent thermal degradation of monomeric structures during the pyrolysis process (Carr et al. 2010). Py-GC/MS analyses were carried out using a CDS 1000 pyroprobe coupled with a gas chromatographer and mass spectrometer (Perkin Elmer Clarus 500 GC/MS) equipped with a CP Sil 5CB-MS column [30 m × 0.25 mm (0.25 µm film thickness)]. Samples were introduced into a preheated interface (310 °C) and pyrolyzed at 610 °C for 15 s. The GC injector temperature was set to 280 °C and the GC oven temperature was held at 40 °C for 2 min and was heated at a rate of 4 °C min^{-1} and was held at 320 °C for 20 min. A total of 40 major TMAH–Py–GC/MS products were identified based on retention time and MS spectra. The amount of products selected from the pyrograms in this study are lower in comparison with previous studies using TMAH–Py–GC/MS (Carr et al. 2010), but the fatty acids ranged

from short to long (e.g. C_{12} to C_{31}), and the products related to lignin included the principal lignin precursor monomers (i.e., *p*-coumaryl, coniferyl, and sinapyl alcohols).

Compound concentrations were estimated by integrating the areas obtained in the pyrogram and calculating its corresponding concentration using the 5-α-cholestane as an internal standard; concentrations were expressed in relation to the total C content in the peat sample as $\mu g_{compound}$ mgC^{-1}. The information gained from TMAH–Py–GC/MS analyses is only semi-quantitative; for example, although the sample is almost entirely burned during the pyrolysis process, significant amounts of carbon are transformed into small molecules such as HCN, CO_2, and CH_4 which are difficult to quantify (Bruchet et al. 1990). Additionally, it is important to consider that TMAH–Py–GC/MS produces the methyl esters of carboxylic acids and methyl ether of alcohols (Challinor 1989). Thus, this method allows to identify the fatty acids and lignin monomers as their corresponding fatty acid methyl esters (FAME) and methylated lignin unit derivatives respectively (Mulder et al. 1992). Considering this, each TMAH–Py–GC/MS product was assigned a chemical class based on their molecular similarity to their probable molecular origin (ESM_2) (Schellekens 2013). A total of 7 main classes were defined: *FA* fatty acids, *AL* aliphatic, *Lg* lignin, subdivided in the three monolignols (derived from: *p*-coumaryl alcohol, coniferyl alcohol, and sinapyl alcohol); *Ar* aromatic, *Ph* phenol, *PA* poly-aromatic hydrocarbons, and *PS* poly-saccharides. Prist-1-ene, which has been reported as a product of chlorophyll pyrolysis (Ishiwatari et al. 1991), was given its own category. The short and long methylated fatty acids (Short $< C_{20}$ and Long $> C_{20}$) were further grouped in separate categories to aid data interpretation.

Statistical analyses

The remaining mass of litter and the decomposition rates were calculated as proportions of the initial mass remaining at the end of the experiment (Wieder and Lang 1982). Linear mixed models were used to compare the remaining mass of litter and decomposition rates, and were fitted by using Residual Maximum Likelihood (REML). Level of significance of the differences between the fixed effects was estimated by Wald tests using an F distribution. Significance was attributed at $P < 0.05$. For comparison of TC, TN and C:N in the initial litter species (*R. taedigera* and *C. panamensis*) and tissue (leaves, stems, and roots) were used as fixed factors and site as the random factor. For the analysis of the percentage of initial mass remaining and the decomposition rates constants of litterbags placed in situ for 2 years, the incubation depth (surface and belowground), the different tissues (leaf, stem and root), and the two different species (*R. taedigera*-palms swamp and *C. panamensis*-mixed forest) were used as fixed factors and the site as random factor. To facilitate the comparison of the litter decay rates with other data sets (Wieder and Lang 1982), the litter decay dynamics were investigated using single ($X_n = X_0 \times e^{-kt}$) (Olson 1963) and double exponential decay models (Adair et al. 2010). In our study the goodness of fit was generally better when the data was fitted to a single negative exponential decay function, so these are the models presented here. The single exponential models were fitted using the default routine from Genstat; the decomposition rate constant (k) was calculated form the linear regression of the percentage of initial mass remaining versus time ($\mathrm{Ln}\ (X_n/X_0) = -kt$), where k corresponded to the slope of the regressions (Chen et al. 2002). Similarities in the molecular composition of the litter and peat samples from different depths were explored by Principal Component Analysis (PCA) (Vancampenhout et al. 2008), based on correlation matrices. The multivariate analysis included the 40 products identified by the TMAH–Py–GC/MS analyses, which were used as molecular fingerprints. The PCAs were used to describe the full TMAH–Py–GC/MS products dataset in terms of two new uncorrelated variables (component factors), which were interpreted in terms of synthetic factors such as peat botanical origin and degree of decomposition (Buttler et al. 1994). Results throughout the text and figures are presented as mean ± SE. Statistical analyses were performed in GenStat (VSN International 2011), whereas figures were produced using SigmaPlot 12.

Results

Chemical and molecular characterization of litter

The litter chemistry varied between the different tissue types and species (Table 2). For *R. taedigera*

Table 2 *R. taedigera* and *C. panamensis* senescent litter: Total carbon (TC), nitrogen (TN) (g g_{dw}^{-1} × 100), and TMAH–Py–GC/MS characterization (μg mgC^{-1}). Data is presented as mean ± SE

	Tree species	Leaf	Tissue Stem	Root
Nutrient				
Total carbon	*R. taedigera*	48.5 ± 0.53	48.6 ± 0.44	49.1 ± 0.73
	C. panamensis	53.8 ± 1.35	49.5 ± 0.47	50.3 ± 0.83
REML outputs for TC	Species: $F_{1,12} = 14.7$, $P < 0.01$; Tissue: $F_{2,12} = 3.9$, $P > 0.05$; Species × Tissue: $F_{2,12} = 4.94$, $P < 0.05$			
Total Nitrogen	*R. taedigera*	1.34 ± 0.05	0.27 ± 0.02	1.11 ± 0.15
	C. panamensis	0.49 ± 0.03	0.44 ± 0.07	0.54 ± 0.06
REML outputs for TN	Species: $F_{1,12} = 37.85$, $P < 0.001$; Tissue: $F_{2,12} = 25.25$, $P < 0.001$; Species × Tissue: $F_{2,12} = 25.25$, $P < 0.001$			
C:N	*R. taedigera*	36.4 ± 1.94	166 ± 13.8	45.8 ± 6.40
	C. panamensis	110.1 ± 15.5	115.49 ± 16	95.7 ± 12
REML outputs for C:N	Species: $F_{1,12} = 6.04$, $P < 0.05$; Tissue: $F_{2,12} = 21.47$; Species × Tissue: $F_{2,12} = 14.79$, $P < 0.001$			
Molecular precursor				
Lignin	*R. taedigera*	38.92	72.04	146.78
	C. panamensis	12.20	15.69	117.48
Short FAME[a]	*R. taedigera*	26.47	4.30	3.20
	C. panamensis	15.39	5.84	1.28
Long FAME	*R. taedigera*	8.70	2.28	3.36
	C. panamensis	3.88	2.10	3.76
Carbohydrates	*R. taedigera*	7.67	1.17	1.34
	C. panamensis	1.99	2.20	1.49
Chlorophyll	*R. taedigera*	1.63	0.24	0.09
	C. panamensis	0.78	0.03	0.94

Data is presented as mean ± SE

Plant material used for litterbag decomposition experiments

[a] FAME, Methylated fatty acids

concentrations of TC (49.04 ± 0.73 %) were greatest in the roots, the highest TN (1.34 ± 0.05 %) was found for leaf tissue, and stems had the highest C:N (166 ± 13); whilst in *C. panamensis* leaves had the highest concentrations of TC (53.89 ± 1.35 %), roots had the greatest TN (0.54 ± 0.06 %), and stems had the highest C:N (115.49 ± 16) again. The TMAH-Py-GC/MS data shows substantial differences in the chemical composition among litter tissues from the two species. The $lignin_{Py}$ was higher in the root tissues, whereas the short chain FAME compounds were higher in the leaves (Table 2). By using the lignin related compounds obtained from the TMAH-Py-GC/MS analyses, it was possible to calculate a $lignin_{Py}$:N ratio. The highest $lignin_{Py}$:N ratio was estimated for the *R. taedigera* stems (24.8), followed by the root tissues of both species (*R. taedigera* = 13.22; *C. panamensis* = 21.75); in contrast, the lowest $lignin_{Py}$:N ratio was consistently observed in leaves of both species (*R. taedigera* = 2.9; *C. panamensis* = 2.5). Furthermore, substantial differences were observed in the abundance of the TMAH–Py–GC/MS products related to each of the three monolignols; with *R. taedigera* palm presenting high concentrations of p-coumaryl alcohol products, whereas *C. panamensis* litter was richer in coniferyl alcohol moieties (ESM_3).

In situ litter decomposition

Litter decomposition was significantly different between the incubation depths, species, and tissues (Fig. 2, Table 3). Litter mass loss at the surface was consistently faster than belowground. Mass loss of *R.*

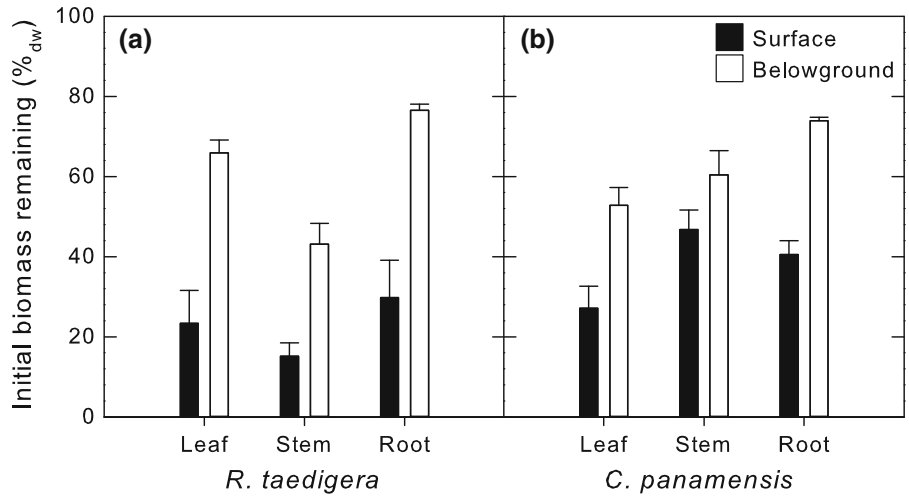

Fig. 2 Initial biomass remaining ($\%_{dw}$; mean ± SE) of **a** *R. taedigera* and **b** *C. panamensis* litter (leaves, stems, roots) after 24 months in situ incubation in palm or mixed forest communities, respectively. Summary of REML output is presented in Table 3

Table 3 Summary of REML outputs for percentage of initial biomass remaining and the decomposition rate constant (k) after 2 years of incubation in situ

	F	df	*P*
% initial biomass remaining			
Species	6.04	1,51	<0.05
Depth	108.5	1,51	<0.001
Tissue	9.52	2,51	<0.001
Species × depth	4.80	1,51	<0.05
Species × tissue	7.38	2,51	<0.01
Depth × tissue	3.40	2,51	<0.05
Species × depth × tissue	0.03	2,51	>0.05
Decomposition constant rate (k)			
Species	1.49	1,2	>0.05
Depth	36.0	1,10	<0.001
Tissue	4.22	2,10	<0.05
Species × depth	1.87	1,10	>0.05
Species × tissue	3.33	2,10	>0.05
Depth × tissue	0.02	2,10	>0.05
Species × depth × tissue	0.13	2,10	>0.05

The data used for these analyses include two sites per species (*R. taedigera* Chiriquí and PS1; *C. panamensis*: Almirante and PS2)

Species R. taedigera and *C. panamensis, Tissue* leaf, stem, root; depth (m) 0, 0.5

taedigera litter at the palm sites was higher than *C. panamensis* litter at the mixed forest sites, whereas belowground, *R. taedigera* litter decomposed less than that of *C. panamensis*. Stems were the most labile tissue of *R. taedigera*, while leaves were the most labile tissue of *C. panamensis*. Roots decomposed slowest among all tissues both at the surface (*R. taedigera*: 0.59 ± 0.04 years^{-1}; *C. panamensis*: 0.45 ± 0.01 years^{-1}) and belowground (*R. taedigera*: 0.13 ± 0.01 years^{-1}; *C. panamensis*: 0.17 ± 0.005 years^{-1}) (Fig. 3, Table 3; individual decomposition rates are provided in ESM_4 in the online resources). Our data shows that the roots of *R. taedigera* and *C. panamensis* decompose five and three times faster at the surface than belowground, respectively (Fig. 3c, f). The incubation depth affected the relative recalcitrance of the tissue from the different species. When decomposed at the surface, roots remained the most recalcitrant tissue of *R. taedigera*. However, *C. panamensis* stems degraded more slowly than its roots at the peat surface. With respect to the nutrient dynamics of the litter decomposing at the surface, the TC did not vary through time ($F_{1,34} = 3.72$, $P > 0.05$). In contrast, TN showed a steep decrease during the first 9 months ($F_{1,34} = 19.29$, $P < 0.001$).

Molecular characterization of peat cores

The abundance of fatty acids (>C_{20}) was higher in the upper peat layers and declined with depth (ESM_5). The short fatty acids were dominated by C_{16} and C_{18} chain lengths; their concentrations varied widely throughout the peat profile and high concentrations were not restricted to the upper layers but were also

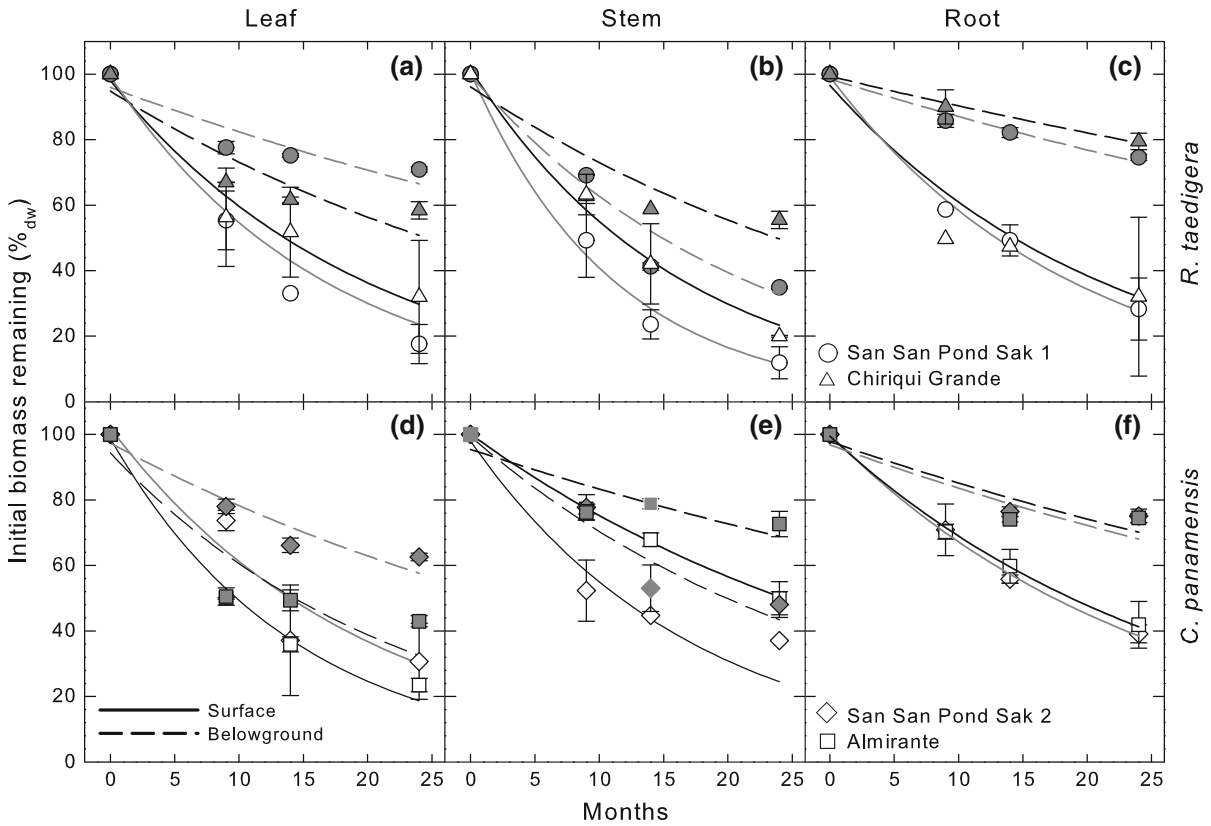

Fig. 3 Initial biomass remaining ($\%_{dw}$; mean ± SE, n = 3) during in situ litter decomposition. Figures **a** and **d**; **b** and **e**; and **c** and **f** include the leaf, stem, and root tissue, respectively. Symbols *open circled* and *open triangle* correspond to *R. taedigera* palm swamp sites (i.e. San San Pond Sak 1 and Chiriquí Grande); whereas *open diamond* and *open square* correspond to *C. panamensis* mixed forest sites (i.e. San San Pond Sak 2 and Almirante). *Open* and *closed* symbols indicate if the litter was incubated at the surface or 0.5 m belowground, respectively. *Solid lines* and *dashed lines* correspond to the single exponential decay models fitted to the actual litter mass remaining data (i.e. not the means shown in the figure) reflecting decomposition rates at the surface and 0.5 m belowground respectively. REML analysis was performed on the decomposition rate constant (*k*); a summary of the statistical analyses results is presented in Table 3

observed in deeper peat layers (ESM_5). The pyrolysis products related to lignin moieties were highest in the upper layers of the peat cores (ESM_5). However, each lignin monomer presented a distinct distribution through the stratigraphic profile of the peat cores. The products related to *p*-coumaryl alcohol were highest in the top 0.5 m of the peat cores and declined rapidly with depth. The products related to coniferyl alcohol were the most abundant of the three monolignols and also declined with depth. Sinapyl alcohol products were the least abundant monolignols in the peat cores and did not follow a consistent trend with depth. In parallel with the lignin monomers, TMAH–Py–GC/MS products related to polysaccharides were highest in upper layers and declined with depth. Finally, the distribution of prist-1-ene in the peat profile was similar to that of the long fatty acids, with concentrations being greatest in the upper peat layers and declining with depth (ESM_5).

Principal component analysis of TMAH–Py–GC/MS products

We applied principal component analysis (PCA) to all the TMAH–Py–GC/MS products (i.e. 40) in the peat and litter samples from each site. The scores and loadings of principal components 1 (horizontal axis) and 2 (vertical axis) explained most of the observed

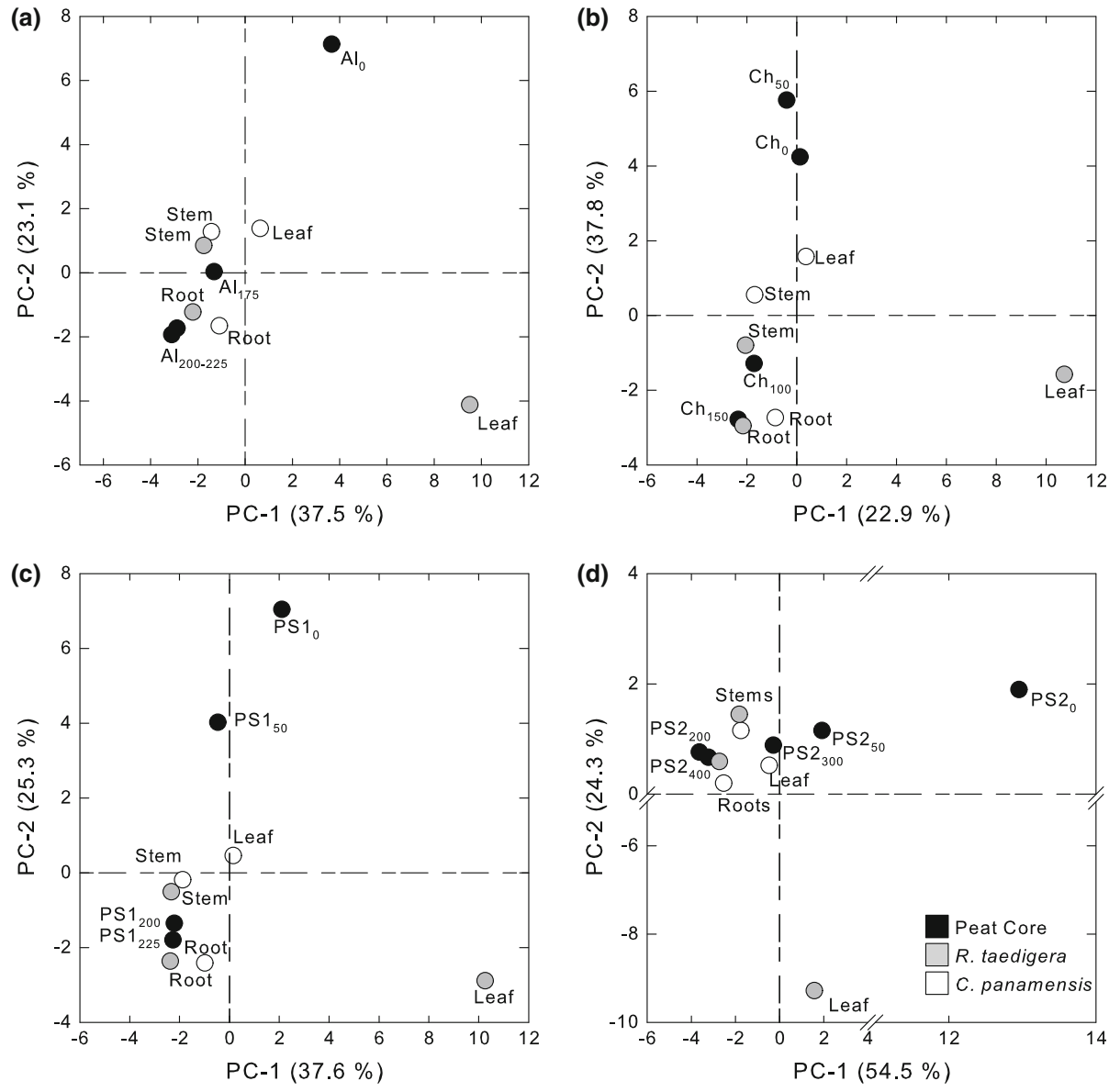

Fig. 4 Principal component scores from PCA analyses on the TMAH-Py-GC/MS chemical characterization of peat cores and *R. taedigera* and *C. panamensis* litter: **a** Almirante (Al-Mixed forest); **b** Chiriquí Grande (Chi-Palm swamp); **c** San San Pond Sak 1 (PS1-Palm swamp); and **d** San San Pond Sak 2 (PS2-Mixed forest). Symbols correspond to peat (*black*) and litter samples (*grey-R. taedigera* and *white-C. panamensis*). Subscripts indicate the relative depth from the surface of peat core samples (cm). The percentage of variance accounted by the loadings of the first two factors (i.e., PC-1 and PC-2) are presented in the x and y axis, respectively

variation, with the first factor contributing up to 54 % (Fig. 4; individual PCA factor's loadings are provided in Online Resource ESM_6). The first principal component (PC-1) separated the stratigraphic profile of the peat cores according to depth; presenting, in most of the cases, a strong separation between the top layer of the peat cores (0 m) and the underlying strata. The segregation of the upper layer of the peat core along PC-1 was primarily driven by the presence of fatty acids (C_{17}, C_{20}, C_{25}, and C_{26}), lignin moieties related to coniferyl alcohol, and prist-1-ene. By contrast, the separation along the second principal

component (PC-2) was mainly due to the influence of long fatty acids (C_{26}, C_{27}, C_{28}, and C_{31}), lignin moieties related to *p*-coniferyl and sinapyl alcohols, and polysaccharides. The score plots also suggest that stem and root tissues have similar chemical fingerprints, whilst leaf tissue is considerably different from both root and stem tissues (Fig. 4). The surface peat layers were more similar to leaf tissue; in contrast, as depth increased peat samples clustered with roots and stems.

Discussion

Abiotic and biotic controls of litter decomposition rates

The primary control of litter decomposition was the depth of the litter in the peat (Figs. 2, 3). Although factors such as pH or the concentration of phenolic compounds may limit decomposition at depth, the down-profile decline in O_2 concentration at these sites is likely to be the main driver of declining decomposition rates (Couwenberg et al. 2011; Freeman et al. 2001; Jauhiainen et al. 2005; Valiela and Wilson 1984; Wright et al. 2013). In addition, the depth related decline in the activity of many of the extracellular microbial enzymes involved in decomposition (Jackson et al. 2009) might also contribute to the decline in decomposition with depth.

Litter type interacted strongly with the position within the peat profile with regards to decomposition rates, suggesting that contrasting aspects of litter chemistry limit decomposition rates in different decomposition environments (Berg 2000; Hobbie 2005; Meier and Bowman 2008; Melillo et al. 1982). At the surface, litter of *R. taedigera* decomposed more rapidly (Leaves: +3.75 %; Stems: +31.62 %; Roots: +10.73 %) when compared to the litter of *C. panamensis* (Fig. 2). This could be related to the higher N concentration of *R. taedigera* litter (Melillo et al. 1984; Singh and Gupta 1977; Valiela and Wilson 1984) and/or inherent differences in decomposition environment between the two forest communities (Austin et al. 2014; Ayres et al. 2009; Hoyos-Santillan 2014). In regularly waterlogged conditions, the slow decomposition of lignin-rich litter, such as the roots and stems of *R. taedigera,* is plausibly linked to the inhibition of ligninolytic microorganisms, which require oxygen to efficiently depolymerize and solubilize lignin (Zeikus 1981). The recalcitrant nature of roots and their slow decomposition rate compared to leaves has been documented extensively (Aber et al. 1990; Bloomfield et al. 1993; Taylor et al. 1991). Our data on surface root decomposition rates (*R. taedigera*: 0.59 ± 0.06 yeras^{-1}; *C. panamensis*: 0.46 ± 0.03 years^{-1}) (Fig. 3; ESM_4) are comparable to other tropical ecosystems, which range from 0.33 to 1.49 years^{-1} (Chimner and Ewel 2005; Cusack et al. 2009; Scowcroft 2009; Silver and Miya 2001). Belowground, the much lower root decomposition rates (*R. taedigera*: 0.13 ± 0.02 years^{-1}; *C. panamensis*: 0.17 ± 0.01 years^{-1}) (Fig. 3; ESM_4) are comparable to those reported for wood and roots in temperate ecosystems (Tripathi et al. 2006; Trofymow et al. 2002). The leaf litter decay rates presented in this study are comparable to decay rates shown for a range of peat swamp tree species in Malaysia (Yule and Gomez 2008). Although limited, these data suggest that leaf litter decay rates may be broadly similar among tropical peat swamp forests.

Linking litter tissue type and chemistry to peat formation

There is a general consensus about woody material (branches, stems, rootlets, roots and rhizomes) being the main constituent of tropical peat (Joosten and Couwenberg 2008; Prager et al. 2006), but this consensus is based on direct physical analysis of peat (Anderson and Muller 1975; Esterle and Ferm 1994; Prager et al. 2006). By comparing the molecular composition of the peat profile to the different litter tissues, we demonstrate that roots and stems have similar chemical fingerprints to the peat in deeper horizons (Fig. 4). The distribution of the pyrolysis products through the stratigraphic profile of the peat cores reflected a selective preservation of the most recalcitrant biomacromolecules through time (Briggs 1999). The high abundance of TMAH–Py–GC/MS products related to plant derived polysaccharides, such as cellulose (e.g. methylated glucose), in the upper layers of the peat cores, may be attributed to the presence of organic matter derived from fresh vegetation litter in early stages of decomposition (Schellekens 2013); polysaccharides are highly susceptible to decomposition and are rapidly decomposed (Schellekens and Buurman 2011). Another of

the pyrolysis products that strongly distinguished the upper from the lower peat strata were the fatty acids. The presence of long-chain fatty acids can largely be attributed to plant material (Vancampenhout et al. 2008), specifically leaf alkanes (e.g. epicuticular waxes) (Nip et al. 1986). Furthermore, high abundance of C_{27}, C_{29} and C_{31} n-alkanes has been associated with the presence of foliar litter from higher plants, as they are major constituents of leaves alkanes (Eglinton and Hamilton 1967; Schellekens and Buurman 2011). It is plausible that the uneven distribution of the different monolignols (i.e., *p*-coumaryl, coniferyl, and syringyl) through the stratigraphic profile is the result of the different resistance to decomposition of each monolignol (Buurman et al. 2007). Harwood lignin (i.e. syringyl-guaiacyl lignin), rich in coniferyl alcohol, is the most stable type with respect to decomposition (Vancampenhout et al. 2008), and thus coniferyl alcohol is present throughout the peat profile in all the cores (ESM_5). By contrast, *p*-coumaryl alcohol is primarily found in the upper layers, as it is abundant in monocotyledonous plants. This is relevant in the tropics, as *p*-coumaryl is found in leaves and floral tissues of members of the palm family (Bu'Lock and Harbone 1980). Additionally, *p*-coumaryl is a major constituent of the cuticles of leaves of higher plants (Kolattukudy 1980), whereas coniferyl is associated with suberin from the epidermis and hypodermis of roots (Graça and Santos 2007). Thus, the TMAH–Py–GC/MS products associated with foliar litter are primarily allocated in the top layers of the peat cores but are absent in deeper strata. We suggest that foliar litter is rapidly decomposed, whereas the more recalcitrant molecules associated with stems and roots tissues remain as peat constituents.

This finding indicates that for tropical peatlands root and/or stem remnants constitute a major component of the peat material, as previously suggested by Chimner and Ewel (2005). With depth, root decomposition declined markedly when compared to other tissue types, possibly due to greater lignin content and the high lignin:N (Fig. 3; Table 2) (Talbot and Treseder 2012; Taylor et al. 1989). Taken together, the data obtained from the litter bag experiments showing the recalcitrant nature of root tissue and the molecular fingerprint of the peat, strongly suggests that roots may be the most important contributor to peat formation in these Neotropical peatlands. The TMAH–Py–GC/MS analysis does not quantify the total amount of root and/or stem tissue preserved in the peat. To place the litter decay data in the context of net C accumulation in tropical forested peatlands, data on belowground litter inputs are required. However, such data are currently limited, particularly for root and coarse wood tissue (Sjögersten et al. 2014), making it difficult to quantitatively establish the net contribution of each litter tissue type to peat formation in tropical forests. If this knowledge gap is overcome, improved understanding of the controls of peat accumulation would ultimately aid in the determination of potential ecosystems feedbacks on the climate system, such as C losses to the atmosphere, resulting from environmental changes within these ecosystems.

Conclusion

We conclude that the position in the peat profile is the dominant control of litter decomposition rates in Neotropical peatlands, creating a ca. 40 % change in mass loss between the surface and belowground. The second most important control of decomposition was litter tissue type with a ca. 20 % difference in mass loss between the most rapidly (leaves) and most slowly (roots) degrading tissues. We suggest that roots are an important contributor to tropical peat formation due to their slow degradation under anaerobic conditions. However, under aerobic conditions roots decompose at a similar rate to that of leaves. Thus, if the water table drops, either as a function of climate change (Field et al. 2014) or as consequences of land use change (Couwenberg et al. 2011; Couwenberg et al. 2009), the rapid decomposition of root material will likely make a major contribution to C emissions from Neotropical peatlands.

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