Nutrient-specific solubility patterns of leaf litter across 41 lowland tropical woody species

Laura A. Schreeg,[1,2,3,4] Michelle C. Mack,[1] and Benjamin L. Turner[3]

[1]*University of Florida, Department of Biology, Gainesville, Florida 32611 USA*
[2]*University of Florida, School of Natural Resources and the Environment, Gainesville, Florida 32611 USA*
[3]*Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Republic of Panama*

Abstract. Leaching is a mechanism for the release of nutrients from litter or senesced leaves that can drive interactions among plants, microbes, and soil. Although leaching is well established in conceptual models of litter decomposition, potential nutrient solubility of mineral elements from recently senesced litter has seldom been quantified. Using a standardized extraction (1:50 litter-to-water ratio and four-hour extraction) and recently senesced leaf litter of 41 tropical tree and liana species, we investigated how solubility varies among elements, and whether the solubility of elements could be predicted by litter traits (e.g., lignin, total element concentrations). In addition, we investigated nutrient forms (i.e., inorganic and organic) and ratios in leachate. Water-soluble elements per unit litter mass were strongly predicted by total initial litter element concentrations for potassium (K; $r^2 = 0.79$), sodium (Na; $r^2 = 0.51$) and phosphorus (P; $r^2 = 0.66$), while a significant but weaker positive relationship was found for nitrogen (N; $r^2 = 0.36$). There was no significant relationship for carbon (C) or calcium (Ca). Element-specific solubility varied markedly. On average 100% of total K, 35% of total P, 28% of total Na, 5% of total N, 4% of total Ca, and 3% of total C were soluble. For soluble P, 90% was inorganic orthophosphate. The high solubility of K, Na, and P as inorganic orthophosphate suggests that these nutrients can become rapidly available to litter microbes with no metabolic cost. Few common predictors of decomposition rates were correlated with element solubility, although soluble C (milligrams per gram of litter) was negatively related to lignin content ($r^2 = 0.19$; $P < 0.004$). Solubility of elements was linked within a species: when a species ranked high in the soluble fraction of one element, it also ranked high in the solubility of other elements. Overall nutrient-specific patterns of solubility from recently senesced litter emphasize that litter elements cannot be treated equally in our conceptual and empirical models of decomposition. The relatively high potential solubility of P as orthophosphate from fresh litter advances our understanding of ecological stoichiometric ratios and nutrient bioavailability in tropical forests.

Key words: Barro Colorado Island, Panama; decomposition; leaching; litter traits; nutrient cycling; terrestrial ecosystems.

Introduction

Decomposition of leaf litter is a key ecosystem flux of carbon (C) and mineral nutrients that is critical for maintaining primary productivity in many systems (Heilman and Gessel 1963, Attiwill and Adams 1993, McGrath et al. 2000, Sayer 2006). Litter leaching, or the water extraction of soluble elements from litter, is an important component of decomposition. In addition to acting as a vector of nutrient release from litter, leachate can drive soil–microbe interactions (Cleveland et al. 2002, Bowman et al. 2004, Wieder et al. 2008, Wurzburger and Hendrick 2009) and influence physicochem-

ical interactions in the soil (Muir et al. 1964, Strobel et al. 2001, Schreeg et al., *in press*). Leaching has long been highlighted in conceptual models of decomposition (Melin 1930, Attiwill 1968, Gosz et al. 1973), and initial rapid nutrient loss from recently senesced litter has been ascribed to leaching (Swift et al. 1981, Prescott et al. 1993). Solubility of litter C has been studied extensively (Currie and Aber 1997, Bernhard-Reversat 1999, Cleveland et al. 2006, Wieder et al. 2009), but solubility of mineral elements from recently senesced litter has received less attention.

Studies of C solubility often use indices of potential solubility that involve water extraction of litter under controlled laboratory conditions (Nykvist 1963, Allison and Vitousek 2004, Don and Kalbitz 2005, Wieder et al. 2009). In contrast, studies that discuss litter solubility of non-C elements tend to rely on trends from one of several approaches: (1) litterbag studies (Gosz et al. 1973, Schlesinger and Hasey 1985, Pastor et al. 1987); (2) comparison of covered and uncovered standing dead

[4] Present address: Ecology and Evolutionary Biology, Brown University, 80 Waterman Street, Box G-W, Providence, Rhode Island 02912 USA.
E-mail: Laura_Schreeg@brown.edu

biomass (Morton 1977, Ganzert and Pfadenhauer 1986); (3) data extrapolated from solubility of living leaves and/or throughfall collections (Ostman and Weaver 1982, Chapin and Kedrowski 1983, Boerner 1984); and (4) correlations between litter element concentration and precipitation (Chuyong et al. 2000). These approaches, however, do not directly test solubility of recently senesced litter, and their interpretations of solubility may be confounded by a number of factors. For example, decomposition curves generated from litterbag studies hint at solubility patterns, but patterns may be masked by immobilization of elements. If an element is released through water extraction but immediately immobilized by litter microbes, solubility would not be detected in a litterbag study. Assuming the solubility of live leaves is similar to that of senesced leaves is also not sufficient because the biochemistry of senescence changes element forms and location (Chapin and Kedrowski 1983, Lim et al. 2007), translating into different expectations for solubility ranks and magnitudes for elements in live, mature, and senesced material (Tukey 1970). Relying on correlations between litter element concentrations and precipitation to understand litter solubility is complicated by concurrent changes in plant nutrient uptake or retranslocation, with solubility being only one possible underlying driver of a correlation (Wood et al. 2005). To understand the role of element solubility from recently senesced litter in terrestrial nutrient cycling, complementary data on potential solubility of fresh litter is needed.

Studies that do quantify potential solubility of litter elements, setting the stage for the current study, have evaluated only a few species and/or single mineral elements (Chapin and Moilanen 1991, Ibrahima et al. 1995, Aerts and de Caluwe 1997). Therefore, despite more than a half-century of research on decomposition, we know strikingly little about how solubility from recently senesced litter varies among elements and as a function of litter traits.

The leaching of nutrients from recently senesced litter could provide nutrients (such as orthophosphate and inorganic and organic N forms) that are readily available for plant and microbial uptake, without requiring mineralization and the metabolic costs of enzyme production (Sinsabaugh et al. 2002). (We note this is unlike the leaching of litter that is in later stages of decomposition when biological mineralization and abiotic leaching likely operate in tandem.) Differential element solubility of recently senesced litter could therefore influence the bioavailability of nutrients, with implications for understanding nutrient limitation of ecosystem processes. For example, both N and P may limit primary productivity in terrestrial ecosystems (Vitousek and Farrington 1997, Elser et al. 2007). Litter P has been documented as having higher solubility than N for single species using a rain exclusion experiment (Chapin and Moilanen 1991) and direct leaching experiments (Parsons et al. 1990, Polglase et al. 1992).

However, larger patterns of differential P and N solubility and the forms (inorganic vs. organic) of nutrients released have been little investigated and could underpin a fundamental difference in litter N and P interactions with precipitation.

If general element-specific patterns exist across species, knowledge of the solubility of nutrients in recently senesced litter may further refine the role of ecological stoichiometry in predicting ecosystem processes. Recently, C quality has been shown to be a stronger control on litter decomposition than stoichiometric ratios in a tropical system (Hättenschwiler and Jørgensen 2010). Differential litter element solubility could similarly improve our interpretation of traditional stoichiometric ratios. It follows that differences in litter nutrient solubility, and thus nutrient bioavailability, could help explain positive relationships between precipitation and decomposition rates of common litter types (Austin and Vitousek 2000, Powers et al. 2009), at least where soils are not saturated and anoxic (Schuur 2001).

Elements are known to differ in mobility within both live and senescing leaves (Fisher 2007), and it seems plausible that this should translate into general element-specific patterns in the initial solubility of litter with soluble fractions that are similar among species (Attiwill 1968). For K and Ca, it seems well established that ranks in solubility differ, with K ranking higher in solubility than Ca (e.g., Gosz et al. 1973). As previously mentioned, there is evidence that P can have higher solubility than N (Chapin and Moilanen 1991). Furthermore, initial solubility has been shown to make only a small direct contribution to overall mass loss (Nykvist 1963, Wieder et al. 2009), highlighting that C ranks low in solubility.

Litter element solubility in tropical rain forests, which are characterized by high precipitation and high litterfall (Vitousek 1984), is likely to have a strong influence on nutrient cycling. We therefore focused on a tropical rain forest in Panama (specifically a lowland tropical moist forest) to investigate general patterns in element solubility and leachate chemistry for recently senesced leaves of 41 woody species. We use two metrics of litter element solubility: (1) water-soluble element, which we define as the quantity of water-extracted element expressed on a litter mass basis (dry mass equivalent), and (2) the soluble fraction, or the percentage of total litter element that is water extracted. We hypothesized that due to differential element mobility and location in leaves, litter elements would differ in potential soluble fractions following a ranking of K > Na > P > N > Mg, Ca, C, with the soluble fraction being relatively consistent among species. We expected that variation among species would be underpinned by some species showing higher relative solubility of all elements and would be partially explained by common metrics of litter quality (i.e., litter lignin content, C:N, lignin:N). Relationships in leachate stoichiometry and inorganic/

organic nutrient forms were also investigated to better understand bioavailability.

METHODS

Sample collection and preparation

Leaf litter was collected weekly from January 2006–2007 from Poacher's Peninsula, the southern point of Barro Colorado Island (BCI) in Panama. BCI supports a lowland tropical moist forest and mean annual precipitation is 2600 mm. Approximately 95% of the rainfall occurs during the eight-month wet season, and the rate of litterfall is highest during the distinct dry season between January and April (Wieder and Wright 1995). Litter was collected in 59 0.25-m^2 traps elevated above the forest floor (Wright and Cornejo 1990). The traps locations covered 9 ha and there is no known gradient in soil nutrient status (Yavitt et al. 1993). Litter was removed from the traps, dried at 60°C, sorted to the species level, and stored in plastic zip bags. At the end of the collection period, litter was bulked by species and well mixed. Petioles were removed and litter was cut into ~25-cm^2 pieces before analysis. Subsamples were taken to determine conversion factors of stored litter to fresh oven-dried (60°C) masses. Litter represented 41 species, spanning 25 families, and included canopy, midstory, and understory trees and lianas. The average collection per species was 244 g of litter (range 39–700 g). Species names and collection data are listed in Appendix A.

Water extractions and chemical analysis

A 1:50 litter-to-solution ratio and a four-hour extraction time were used for all water extracts. A four-hour extract duration has been shown to encompass the highest rate of loss, but does not represent exhaustion of extractable elements (L. A. Schreeg, unpublished data). Litter-to-solution ratio has little influence on element water solubility on a per gram litter basis during short-duration laboratory extracts indices (L. A. Schreeg, unpublished data) and therefore has little impact on the metrics of solubility used in this laboratory index. In terms of field fluxes, 1:50 litter-to-solution ratio reasonably reflects expected litter contact with precipitation during the wet season or pulsed precipitation events. For example, considering an eight-month wet season, 2600 mm annual precipitation, and inputs of 420 g litter/m^2 during the dry season (calculated from Sayer and Tanner 2010), estimated litter contact with precipitation on a daily basis would be roughly 1:25 (grams of litter per milliliter of precipitation) and ratios of contact of fresh litter with precipitation would decrease throughout the wet season (based on an assumption of decreased inputs and standing pools of fresh litter).

Water extracts had three replicates per species, with the exception of ammonium and nitrate measurements, which only had two replicates per species. Water extract replicates were conducted on different days and were drawn from the same bulked species litter. Two grams of litter (oven-dried mass equivalent (ODM)) were placed carefully in 125-mL wide-mouth polyethylene bottles, and 100 mL of deionized water was added. Bottles were placed on a shaker table on the low setting (180 oscillations per minute) for four hours. The solution was poured off into beakers and then into tubes for centrifugation (78.5 km/s^2 for 10 minutes). After centrifuging, supernatant was immediately poured off and divided for chemical analyses. Phosphate-P and pH were either analyzed immediately or samples were stored at 4°C overnight and analyzed within 24 hours. Dissolved organic C (DOC) samples were acidified to pH ~3 and stored at 4°C until analysis the next day. After centrifuging, subsamples for future digests of total N, analysis of ammonium and nitrate, and analysis for cations and total P were frozen at −35°C and stored for a maximum of 11 weeks.

Molybdate reactive P (MRP) was read at 880 nm with a Hach DR 5000 UV-vis spectrophotometer (Hach Limited, Loveland, Colorado, USA). Molybdate reactive P is commonly considered to be inorganic orthophosphate, but may include some organic and condensed P compounds that are hydrolyzed during the assay (Worsfold et al. 2005). Dissolved organic C concentrations, operationally defined in this study as organic C remaining in supernatant after centrifuging, were determined by a Shimadzu TOC-V_{CSH} Total Organic Carbon analyzer (Shimadzu Scientific Instruments, Columbia, Maryland, USA). Solution pH was determined using a Hach Sension 3 pH meter. A sodium hydroxide/potassium persulfate oxidation was used to determine total solution N concentrations (modified from Valderrama 1981). All N concentrations (total N, ammonium, and nitrate) were determined colorimetrically on a Latchat Quikchem 8500 autoanalyzer (Hach Limited, Loveland, Colorado, USA). Cation and total P concentrations were determined by inductively coupled plasma optical emission spectrometry (ICP–OES) using an Optima 2100 (PerkinElmer, Waltham, Massachusetts, USA).

Elemental composition of initial litter was determined by grinding and homogenizing 10 g of litter (petioles removed) per species. From this bulked sample, percent C and N of nonextracted litter were determined on ground samples using a total element combustion analyzer (Thermoelectron Flash EA 1112 series; ThermoFisher Scientific, Waltham, Massachusetts, USA). A nitric acid digest of ground litter followed by ICP–OES analysis was used to determine total P and cations. Percent lignin was estimated using an Ankom fiber digester (Ankom Technology, Macedon, New York, USA). The method operationally defines lignin as the fraction of mass remaining after sequential extraction of a neutral detergent, acid detergent, and acid extract, minus the ash mass. Analytical triplicates were analyzed from the 10 g of ground litter from the bulked sample of each species.

TABLE 1. Initial litter chemistry and water solubility of litter elements during a four-hour 1:50 litter-to-solution ratio extract.

Element	Initial litter chemistry (mg of element/g dry mass)			Soluble fraction (% of total element)			Water-soluble element (mg of element/g dry mass)		
	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
C	459.79	46.46	0.10	3.3	1.8	0.6	14.69	7.49	0.51
Ca	16.66	6.20	0.37	4.2	4.5	1.1	0.69	0.80	1.17
K	4.62	2.35	0.51	101.2	25.4	0.3	4.50	1.98	0.44
Mg	4.22	2.20	0.52	20.5	12.6	0.6	0.82	0.68	0.83
N	13.56	3.62	0.27	4.6	2.1	0.5	0.63	0.37	0.27
Na	0.93	0.41	0.44	28.0	10.3	0.4	0.25	0.11	0.45
P	0.61	0.18	0.30	34.6	10.4	0.3	0.21	0.10	0.49

Notes: Data represent 41 species with the exceptions of soluble P and K, which had only 40 species included in the analysis. Initial litter chemistry had one value per species. For the solubility data, means were found by averaging across three extracts per species.

Statistical analysis

The water-soluble element on a litter mass basis was calculated as the element extracted per gram of dry mass of litter during the four-hour extraction period. The soluble fraction, or the percentage of total nutrient released during the water extraction, was calculated as the water extractable element on a mass basis divided by the total litter concentration of the respective nutrient on a dry-mass basis. Soluble fractions across species were summarized as means with standard deviations and coefficients of variation (CV) using the species averages. A Principal Components Analysis (PCA) was used with centered and scaled data in order to evaluate if solubility rankings among elements were similar within species.

Linear regressions were used to investigate if the water-soluble element on a litter mass basis could be predicted by the initial litter element concentration, percent lignin, lignin : N, or C:N. For the water-soluble element on a litter mass basis, the dependent variables were investigated with simple linear regressions and then select combinations were investigated using multiple regressions. For each element, models of lignin and total litter element, lignin : N and total litter element, and C:N and total litter element were compared to models that included only the total litter element. Model selection was based on Akaike's information criterion (AIC) values. A difference of two AIC units was the criterion for considering models to be different.

For N and P, relationships between total extracted inorganic nutrient and total nutrient (inorganic + organic forms) were investigated using simple linear regressions. Correlations among solution nutrients (C:N, C:P, N:P, on a molar basis) were analyzed using Spearman's rho. All analyses were conducted in R (R Development Core Team 2010).

Two data points were removed from the analyses. For P, *Faramea occidentalis* was removed because it had a notably low soluble P fraction, and it also had the highest concentration of extracted aluminum (Al) out of the 41 species investigated (1.3 mg/g dry mass). This was 160 times greater than any other species. We reason that

the high Al concentration could result in significant aluminum phosphate precipitation, decreasing the reading for solution P concentration (calculations not shown). For K analyses, *Uncaria tomentosa* was identified as an analytical outlier because extractable K was 172% of the total K. While other species also showed K solubility >100% (see *Results: Element solubility* for explanation), the value for *Uncaria tomentosa* was 26 percentage points greater than any of the other 40 species.

RESULTS

Element solubility

Litter elements showed differential solubility. Potassium had the highest average soluble fraction (101%) while C had the lowest soluble fraction (3%; Table 1). Measurements of the water-soluble element on a litter mass basis and total element concentration of litter were measured on separate subsamples drawn from the bulked sample, which may explain the >100% soluble fraction in the case of K (Table 1). In comparison to K, Na had a much lower soluble fraction, despite being another monovalent cation. On average, 28% of total Na was extracted. The soluble fraction of P was 35%, much greater than that of C, and also higher than that of N (5%; Table 1). There was high variation in the soluble fraction of Mg among species (Table 1).

On a litter mass basis, more C was extracted than any of the other elements investigated (14.7 mg/g litter; Table 1) during the four-hour extraction. Potassium ranked second (4.5 mg/g litter). All other elements had <1 mg of extracted element per gram of leaf litter (Table 1). Water-soluble element data are listed by species in the Supplement. We do note that litter for this study was oven dried (60°C), which can lead to slightly increased solubility for some species and element combinations compared to air drying (L. A. Schreeg, *unpublished data*). For example, the effect of drying temperature on N solubility was significant for one of eight species investigated (L. A. Schreeg, *unpublished data*). The direction of the effect for the one significant species

was consistent with that of P, with the litter dried at 60°C showing higher solubility than the litter dried at 22°C. The effect of drying temperature on P solubility was significant for two of the eight species (L. A. Schreeg, *unpublished data*).

Predictors of element solubility

Total element concentration was a significant predictor of soluble element on a litter mass basis for K, Mg, N, Na, and P (Fig. 1), but not for Ca ($P = 0.13$) or C ($P = 0.12$), as evaluated by linear regression. Exploring total element concentration as a predictor of soluble element on a mass basis was possible because of the large range of initial concentrations for a given element (Table 1, Fig. 1; species-specific data are in the Supplement). For example, litter P and N each varied by a factor of two, and K varied by a factor of six (Fig. 1). The linear relationships were strongest for elements that showed the highest average soluble fraction. For K, total litter K was found to explain 79% of the variance in soluble K on a litter mass basis. Total litter P explained 66% of the variation in soluble P on a litter mass basis, and litter Na accounted for 51% of the variance in soluble Na on a litter mass basis. For Mg, N, and P, the intercepts were not significantly different from zero ($P = 0.07$, 0.40, 0.09, respectively), demonstrating that the soluble fraction of these elements was not significantly influenced by litter element concentration. The intercept terms were significantly >0 in the case of K (intercept = 0.95, $P = 0.006$) and Na (intercept = 0.07, $P = 0.04$), indicating that the soluble fraction of these elements decreases with increased litter concentration of the respective element.

Overall, percent lignin had little to no ability to explain variation in water-soluble elements among species. In simple linear regressions, percent lignin was only a significant predictor for soluble C on a litter mass basis, and this relationship was weak ($r^2 = 0.19$; $P = 0.004$). In multiple regression analyses, including lignin as a predictor variable in models of soluble element on a litter mass basis vs. total litter concentration only slightly improved model fit for C ($\Delta AIC = 4.5$) and Na ($\Delta AIC = 3.4$).

Water-soluble K, N, and P on a litter mass basis showed negative relationships with C:N ($r^2 = 0.28$ and $P < 0.001$ for K; $r^2 = 0.37$ and $P < 0.001$ for N; $r^2 = 0.18$ and $P = 0.007$ for P). Soluble C, K, and N on a litter mass basis were also negatively related to lignin:N ($r^2 = 0.18$; $P = 0.006$ for C; $r^2 = 0.19$; $P = 0.005$ for K; $r^2 = 0.25$; $P < 0.001$ for N). These significant regressions may be driven by relationships between water-soluble K, N, P, and total litter N concentrations ($r^2 = 0.18$ and $P = 0.007$ for water-soluble K and total litter N; $r^2 = 0.22$ and $P = 0.002$ for water-soluble P and total litter N; Fig. 1). When included as an additional variable in multiple regressions of water-soluble element as a function of total litter element, neither the addition of C:N nor the addition of lignin:N improved the model fit.

Soluble fractions were investigated as a function of % lignin, lignin:N, and C:N. The soluble fraction of C was negatively related to % lignin ($r^2 = 0.30$ and $P < 0.001$) and lignin:N ($r^2 = 0.10$ and $P = 0.002$). The soluble fraction of N was negatively related to lignin:N ($r^2 = 0.10$ and $P = 0.04$) and C:N (also $r^2 = 0.10$ and $P = 0.04$). Other elements did not have significant relationships between their soluble fractions and % lignin, lignin:N or C:N.

Solubility of elements was a general property of the species evaluated. A PCA with the soluble fraction showed that 57% of the variation was explained by the first axis and loadings for C, Ca, K, Mg, Na, P, and N were in the same direction (Table 2). This suggests that when a species ranked high in the soluble fraction of one element, it also had high solubility of other elements, relative to the other species. *Prionostemma aspera*, *Quararibea asterolepis*, and *Alchornea costaricensis* had the highest solubility ranks, while *Beilschmiedia pendula*, *Virola surinamensis*, and *Apeiba membranacea* ranked lowest (Appendix A). Results were similar for element solubility on a litter mass basis, although the variance explained by the first axis was slightly less (49%, data not shown).

Leachate chemistry

Leachate stoichiometry among species was similar for N:P (rho = 0.63, $P < 0.0001$; 6.6 ± 2.6 (average on molar basis ± SD); Appendix B). The relationships between leachate C and N (rho = 0.53, $P < 0.0004$, 31.03 ± 16.5) and C and P (rho = 0.42, $P = 0.007$, 192.1 ± 129.7) were also significant, but these ratios were not as similar among species as N:P. Orthophosphate was strongly related to total P in the extracts ($r^2 = 0.99$; Fig. 2) with $>94\%$ of all extracted P in the inorganic orthophosphate form, when averaged across species. Inorganic N, which on average was 95% ammonium, was also positively related to total N in extracts across species (Fig. 2). However, in contrast to P, a smaller percentage of extractable N was in inorganic form (25% when averaged across species [range of 6–52%]). Solution pH ranged from 4.3 to 6.4.

Leachate stoichiometry was compared to stoichiometry of fresh litter and leached litter (Fig. 3; stoichiometry of leached litter was calculated and not directly measured). Due to the higher solubility of P compared to N or C, leaching had a greater influence on N:P and C:P ratios compared to C:N (Fig. 3).

DISCUSSION

Our results illustrate that litter elements have differential solubility. Our data set demonstrates exceptionally high potential solubility of K (100% of K was released during a four-hour extract) and supports the trend that has been previously suggested from litterbag studies (Gosz et al. 1973). Although high solubility of leaf litter P has often been noted (Chapin et al. 1978, Lousier and Parkinson 1978, Parsons et al. 1990,
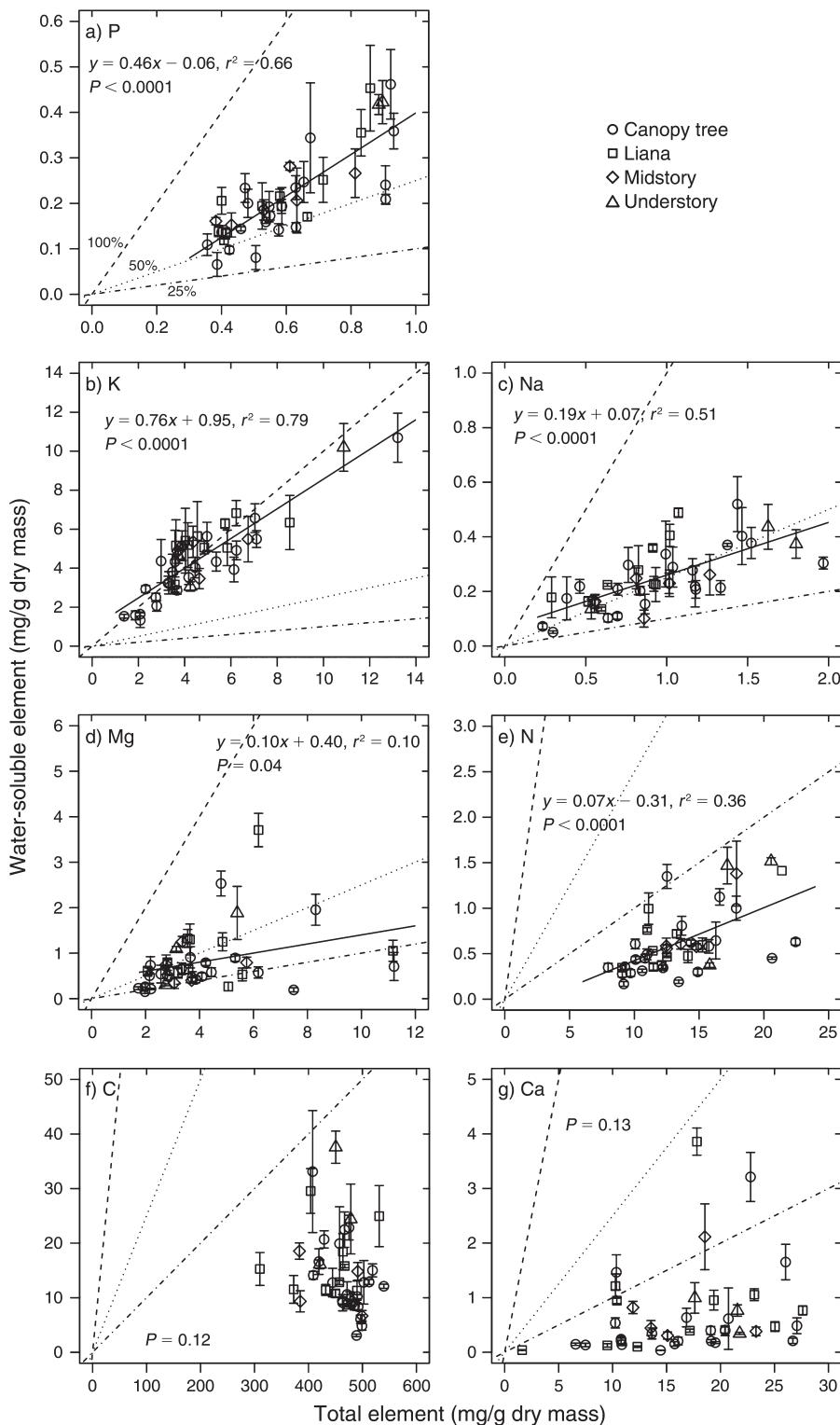
FIG. 1. Linear relationships between a soluble element on a litter mass basis and total initial litter element concentration. Extracted elements are the average of three extracts (±SE) using a four-hour extraction time that involved shaking. Total litter element concentration is based on one analysis drawn from 10 g of litter. Dashed lines indicate slopes of 1:1, 1:2, and 1:4 with zero intercepts, which represent soluble fractions of 100%, 50%, and 25%, respectively (refer to soluble fraction labels in the P plot).

TABLE 2. First three components of principal components analysis using the soluble fraction.

Variable or statistic (soluble fraction)	Component		
	1	2	3
C	−0.401	<|0.1|	<|0.1|
Ca	−0.379	−0.230	0.531
K	−0.363	−0.287	−0.597
Mg	−0.480	<|0.1|	0.179
N	−0.387	0.446	0.253
Na	−0.351	−0.459	−0.272
P	−0.245	0.668	−0.431
Proportion of variance	0.57	0.17	0.10
Cumulative proportion	0.57	0.73	0.83
Standard deviation	1.99	1.08	0.83

Note: Loadings are given for C, Ca, K, Mg, N, Na, and P; values are given for proportion of variance, cumulative proportion, and standard deviation.

Polglase et al. 1992, Attiwill and Adams 1993), it has seldom been quantified across species or in contrast to other nutrients. In our study, P was much more soluble than C or N; on average 35% of the total P was extracted in four hours (range 16–53%); in contrast, 3% of total C was soluble and <5% of total N (Table 1). Greater loss of litter P compared to N has been demonstrated during litter decomposition in tropical forests (Hättenschwiler and Jørgensen 2010), but litterbag studies more often report that P remained constant or became immobilized from the surrounding environment during initial phases of decomposition (Attiwill 1968, Staaf and Berg 1982, Hobbie and Vitousek 2000, McGroddy et al. 2004). Relatively high potential solubility of P from recently senesced litter may initially seem at odds with these results. However, an element can be solubilized from litter without leaving the litter environment, perhaps due to microbial immobilization by litter microbes. Alternatively, water-extracted P may be removed from litter while P from the surrounding soil environment is immobilized. In addition, depending on precipitation and time that litter sits in litter traps, soluble nutrients may have been removed prior to initiating the litterbag study.

The proportion of nutrients in organic vs. inorganic form was another striking difference between P and N. Almost all water-extracted P was inorganic, while N was largely organic (Fig. 2). Because P solubility was high, and because a large percentage of P was leached as orthophosphate, it is likely to be readily available to litter microbes, roots, or involved in physicochemical interactions with soil minerals (Mattingly 1975). The dominance of orthophosphate, rather than organic P, in leachate may be related to chemistry in live leaves and chemical changes during senescence. In live leaves, phosphate is a critical part of ATP cycling and is also stored in vacuoles as a reserve to maintain cytoplasm orthophosphate at a constant concentration (Lauer et al. 1989, Sinclair and Vadez 2002). Inorganic P has been shown to range from 10% to 50% of the total foliar P (Bieleski 1973, Ostertag 2010), while up to 75% of leaf N

can be present in leaf chloroplasts, largely as proteins (Hörtensteiner and Feller 2002). During senescence, catabolism converts compounds from the growth phase of the leaf to compounds that are exportable before leaf abcission (Lim et al. 2007). The breakdown of lipid membranes and nucleic acids, which are rich in P, increases concentrations of orthophosphate (Chapin and Kedrowski 1983), which can then be remobilized (Pérez-Amador et al. 2000). In contrast, N can be retranslocated in organic forms, such as amino acids (Hörtensteiner and Feller 2002). Due to both live leaf concentrations and requirements for remobilization, the inorganic form of P is likely a larger percentage of total element in a senesced leaf compared to N, which may underlie differences in N and P solubility and
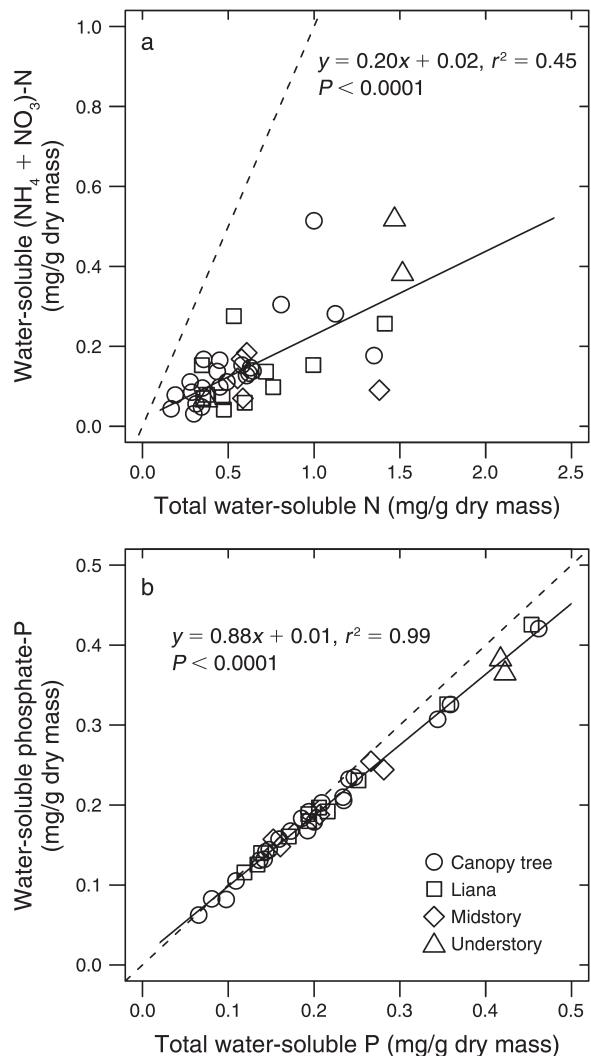

FIG. 2. Regressions of (a) inorganic N on total N and (b) inorganic P on total P in water extracts. Total N was determined through a persulfate digest; total P was read using inductively coupled plasma optical emission spectrometry, while phosphate-P and inorganic N were obtained colorimetrically. Dashed lines indicate slopes of 1:1.

nutrient form in leachate. As a competing explanation for the dominance of orthophosphate, residual enzymes on litter may convert soluble organic P to orthophosphate. The relative contributions of these mechanisms (i.e., mineralization by residual enzymes vs. orthophosphate presence and preferential solubility) remain to be tested.

The differences in N and P solubility result in a much lower N:P ratio in leachate than that in litter. Leachate N:P was 6.6 (range 2.3–14.8), while initial litter N:P was 51.4 (range 30.1–85.1) and the calculated N:P of leached litter was 76.9 (range 47.7–126.4; Fig. 3; molar ratios). The large difference in these ratios sets up contrasting expectations for N vs. P limitation to biological processes (Redfield 1958). Although thresholds for N and P limitation of microbial activity are not clear, we can use a microbial ratio of 7:1, determined by a review of global studies (Cleveland and Liptzin 2007), as a guide. The contrast between leachate and litter stoichiometry suggests leachate production may make P relatively less limiting to decomposition than litter stoichiometry predicts. If so, litter nutrient solubility could play into proposed models of vertical N limitation in tropical forests (Hedin et al. 2009). It is argued that because the litter layer is rich in C but relatively low in N, the litter may be a vertical layer in the forest profile where active N fixation could persist despite tropical systems being generally characterized by overall N richness (Jenny 1941, Vitousek 1984). While the mineral soil and litter can exchange N, limits on the exchange between these pools can decouple N-rich soil and relatively N-poor litter. Therefore, heterotrophic organisms associated with litter may continue to fix N, even though the underlying soil is N rich. This decoupling is framed as a hypothesis to explain the paradox that tropical forests can sustain high N availability over time (Hedin et al. 2009). We propose that the relatively low solubility of N and higher solubility of P support the hypothesis that N may be limiting to litter decomposition in some tropical forests.

Differential solubility of N and P also suggests an intriguing hypothesis for understanding decomposition of mixed litter combinations. Transfer of nutrients among species has been proposed as a mechanism underlying nonadditive effects of mixed species litter on decomposition rates (Gartner and Cardon 2004, Ball et al. 2009). Nutrient transfer is often considered to be due to biotic activity (Briones and Ineson 1996), but species variation in the magnitude of nutrients lost on a litter mass basis may be an additional mechanism. We note that the range of initial litter N in this study (0.80–2.25%) is similar to values from a lowland forest in French Guinea (0.68–2.01%), while the range of litter P in our study (0.036–0.093%) is higher (0.009–0.062%; Hättenschwiler et al. 2008). In addition, the molar N:P in this study was 51.4, while an average of 50 tropical forests was 62.7 (McGroddy et al. 2004). Because water-soluble P and N on a mass basis were functions of total
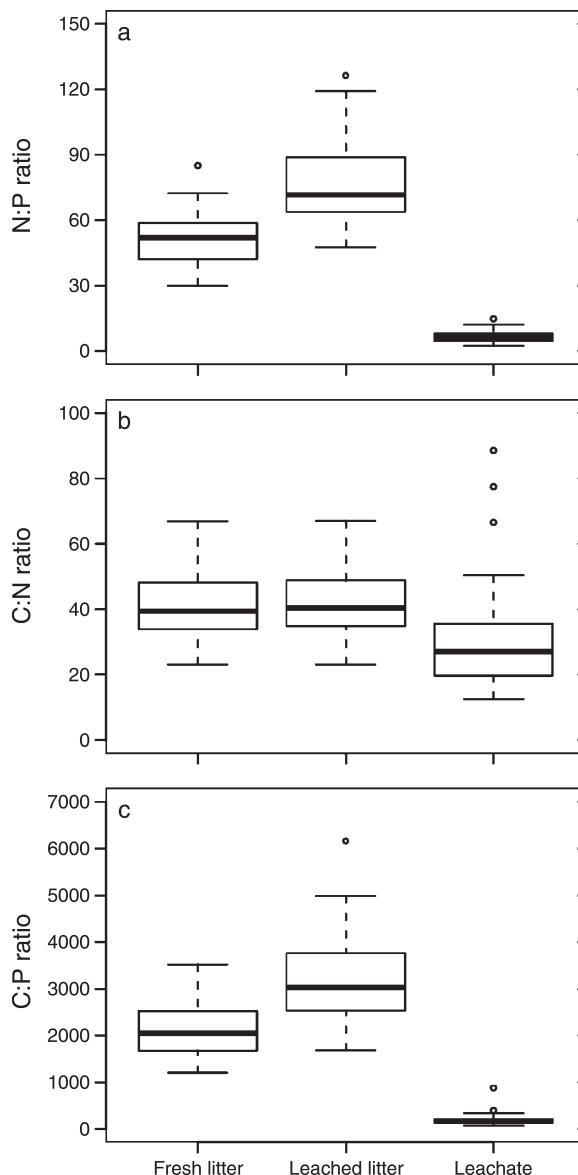

FIG. 3. Stoichiometry of initial (fresh) litter, leached litter, and litter leachate (from the four-hour extract; $n = 40$ or 41 species). Stoichiometry of leached litter was not measured directly. It was calculated by subtracting soluble element on a litter mass basis from the initial element litter concentration for each species. All values are on a molar basis. In the box plots, the horizontal line shows the median. The top and bottom limits of the box show the first and third quartiles, encompassing the interquartile range (IQR). Whiskers extend to 1.58 × IQR/square root (n). Data points beyond the whiskers are indicated by dots.

litter concentrations, and the intercepts of these relationships were zero, potential soluble fractions of P and N may be similar at other sites. It follows that the magnitude of P on a litter mass basis that is potentially released through water extraction may be lower in other systems. However, realized litter solubility depends on numerous factors including the amount and timing of

precipitation, topography, and water flow pathways. Transfer of soluble nutrients within mixed litter remains to be investigated, but our approach suggests litter solubility could provide insight to nonadditive decomposition rates of mixed litters.

Litter K has often been reported as having high solubility, an interpretation that largely comes from quick initial loss in litterbag studies and an inverse correlation between litter concentration and precipitation (e.g., Attiwill 1968, Gosz et al. 1973, Brinson 1977, Lousier and Parkinson 1978, Chuyong et al. 2000). By quantifying initial solubility of 41 species, this study confirms that K is highly soluble in lowland tropical forest litter. Potassium receives much less attention than N and P in studies of terrestrial nutrient cycling, even though K has been found to limit forest primary productivity in temperate forests (Tripler et al. 2006) and may act as a control on fine-root investment in a lowland tropical forest (Wright et al. 2011, Santiago et al. 2012). The high solubility of litter K for 40 species suggests that ecosystem cycling of K may be sensitive to variation and pulses in precipitation.

In contrast to K and the other mineral elements in this study, Ca and Mg solubility were not well predicted by total litter element concentration (Fig. 1). For Mg it would be interesting to investigate whether species-specific differences in soluble fractions are linked to resorption efficiency. We speculate that this relationship could result if biochemical changes during senescence increase Mg mobility and in turn influence solubility. For Ca, it may be interesting to investigate a relationship between litter solubility and fungal endophyte loads on live leaves. An understanding of the natural history and ecological significance of endophytic fungi is beginning to emerge (Lodge et al. 1996, Arnold 2010). Given that endophytes actively penetrate leaf cuticles and exude compounds to meet their nutritional needs (Arnold 2010) and that endophyte–foliar interactions have been documented to use calcium signals requiring the mobilization of Ca between cellular compartments (Vadassery and Oelmüller 2009), it seems plausible that endophyte loads on live leaves could influence litter Ca solubility. Finally, because water content decreases as active leaves transition to senesced litter, and Ca has an affinity to bind to cell walls and membranes (McLaughlin and Wimmer 1999), we hypothesize that differences in litter water absorption rate and capacity (Ibrahima et al. 1995) could serve as potential predictors of Ca solubility.

Sodium was found to have a much lower soluble fraction than K, which may be due to location in leaf cells. Sodium is a nonessential element but can sometimes serve as a K replacement (Subbarao et al. 2003), as both are small monovalent cations. Potassium is an essential element used for a number of functions and is found in the cytoplasm and vacuole. In contrast, Na can be concentrated in the vacuole, but very little is found in cytoplasm (Leigh and Jones 1986). It has been reported that the cytoplasm disappears during leaf senescence, but vacuole membrane permeability does not change (Thomas and Stoddart 1980), which could potentially influence solubility of nutrients from senesced litter. Sodium is essential in animal physiology (Schmidt-Nielsen 1997), and the dichotomy between plant concentrations and animal demands has been hypothesized as a mechanism underlying Na limitation of litter decomposition in an inland Amazon forest (Kaspari et al. 2009). Our study demonstrates that Na is relatively soluble and total litter Na is a predictor of extracted Na in fresh litter. Although Na has a lower soluble fraction than K, in instances where Na is limiting to decomposition (Kaspari et al. 2009), any movement away from litter during decomposition has the potential to significantly impact decomposition rates.

Water-soluble C showed significant but weak negative relationships with lignin ($r^2 = 0.19$; $P = 0.004$) and lignin : N ($r^2 = 0.18$; $P = 0.006$), which are common predictors of litter decomposition rates (Mellilo et al. 1982, Aerts 1997, Zhang et al. 2008). Soluble C on a litter mass basis and lignin may be related simply because soluble components increase when nonsoluble components of a leaf decrease. While the fraction of total C that is soluble is relatively small (3.3% found in this study; Table 1), soluble C is of interest because it could fuel microbial activity (Fontaine et al. 2003), and may partially underlie commonly observed relationships between decomposition rates and lignin predictors. This is supported by a study in a lowland tropical forest with high rainfall, where C solubility correlated positively with initial decomposition (0–50 days), but did not predict overall decomposition rates (Wieder et al. 2009).

Overall, this work demonstrates that elements in freshly senesced litter have differential solubility and emphasizes that elements cannot be treated equally in conceptual and empirical models of decomposition. Our study supports the generality that K from recently senesced litter is highly soluble and reveals that P is more soluble compared to N for the 41 tropical forest species evaluated. Soluble P was largely orthophosphate, which is the form of phosphorus that is readily available for plant and microbial uptake. Our results suggest solubility of recently senesced litter, and the influence of solubility on bioavailability of nutrients may refine traditional interpretations of how litter nutrient concentrations and element ratios relate to litter decomposition rates (Aerts 1997, McGroddy et al. 2004, Zhang et al. 2008). Finally, precipitation pulses and timing have been shown to induce significant changes in soil microbial dynamics (Kieft et al. 1987, Lodge et al. 1994, Turner and Haygarth 2001, Fierer and Schimel 2002, Cleveland et al. 2004). This study suggests that differential nutrient solubility of fresh litter in tropical forests is another avenue by which precipitation patterns could drive nutrient cycles.

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SUPPLEMENTAL MATERIAL

Appendix A

A species list with life-form, total composited litter, number of traps in which litter was found, and the axis 1 score from the PCA of soluble fraction (*Ecological Archives* E094-010-A1).

Appendix B

A figure showing the stoichiometry of soluble C, phosphate-P, and total N, on a litter mass basis (*Ecological Archives* E094-010-A2).

Supplement

Initial litter quality and water-soluble element data by species (*Ecological Archives* E094-010-S1).