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Stoichiometry of decomposing *Spathodea campanulata* leaves in novel puertorrican forests

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ABSTRACT

One of the challenges in the restoration of degraded lands is the re-establishment of soil structure and fertility. Novel forests that regenerate on recently abandoned and degraded agricultural lands are among the first biotic systems that begin the process of soil rehabilitation. The rate of litter decomposition and associated element mobility is one of many processes that contribute to the understanding of how ecosystem-level processes restore eroded soils. We studied the stoichiometry of *Spathodea campanulata* leaves decomposing in novel subtropical moist forests. We found that the speed of leaf decomposition was high (annual decomposition constant of 5.0 to 2.6 or half-life of 51 to 98 days). *Spathodea* leaf mass loss was particularly fast during the first 16 days of decomposition (half-life of 33 days). Leaf litter was characterized by high chemical quality with low C/N, C/P, and N/P. During the leaf decomposition process, macroelements (N, P, K, Ca, and Mg) were more mobile than microelements (Al, Mn, Fe, and Na). As leaf litter decomposed, nitrogen increased in concentration, the quantity of all macroelements decreased, and microelements tended to increase in both concentration and quantity. Because of the rapid rate of decomposition and high chemical quality of *Spathodea* leaf litter, it appears that the potential for yielding residual soil organic matter from its leaves is reduced, but this is a tradeoff with the rapid release of elements, which contributes to the high juvenile tree density and primary productivity observed in novel *Spathodea* forests.

1. Introduction

Puerto Rico's forest cover was at its lowest historical level of about 5 to 10 percent of the total land area during the decades of the 1950s and 1960s (Brandeis and Turner, 2013). At that time, Picó (1969) examined the condition of insular soils for agricultural purposes and found that about 28 percent had minimal or no erosion problems and between 30 and 40 percent offered no conservation challenge. However, about half of the soils were considered inferior agricultural soils with conservation problems. Specifically, 47.73 percent of the insular soils were reported by the USDA Soil Conservation Service (now the Natural Resources Conservation Service) as exhibiting severe erosion with a loss of over 75 percent of the topsoil. After this historic moment when forest cover reached its minimum, agricultural lands were abandoned due to population migration to cities (Rudel et al., 2000), and forest cover began to rise to the present 60 percent (Brandeis and Turner, 2013). However, the species composition of these naturally emerging forests was different from that of historic forests (Lugo and Helmer, 2004) and they have been identified as novel forests (Martinuzzi et al., 2013) in part because the dominant species are naturalized introduced tree species. Understanding the functioning of novel forests is important because they are increasingly common in the world (Hobbs et al., 2013) and can play a significant role in rehabilitating degraded soils (Lugo, 2004).

Originally from tropical Africa and recognized for its beautiful flowers, *Spathodea campanulata* Beauv. (African tulip tree) colonized abandoned agricultural lands in Puerto Rico and became the most common tree in the Island, dominating most novel forests (Brandeis and Turner, 2013; Martinuzzi et al., 2013). *Spathodea* forms novel forests in the subtropical moist forest life zone (Abelleira Martínez, 2009). Our studies show that the physiognomy and structural attributes of novel *Spathodea* forests are similar to those of native forests of similar age and location (Abelleira Martínez et al., 2010) but aboveground productivity, biomass, and element accumulation is higher in *Spathodea* forests (Lugo et al., 2011, 2012). We also know that after canopy closure, native tree species regenerate in the forest understory and that these species assemblages vary mainly due to geological substrate and soil properties (Abelleira Martínez, 2010). Thus, novel forests play a vital function in ecological restoration following land degradation and

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abandonment after agricultural use but the underlying ecological mechanisms by which they do so are poorly understood.

The growth and dominance of introduced species after land abandonment is not accomplished through competition with native tree species because native tree species do not colonize abandoned degraded lands. An exception is *Tabebuia heterophylla*, which is capable of colonizing abandoned and degraded lands but usually at higher elevations than *Spathodea* (Little and Wadsworth, 1964; Weaver, 2000). *Cecropia schreberiana*, the predominant native successional tree species, is unable to colonize degraded sites (Silander, 1979), but we have observed this species growing under the canopy of *Spathodea*. After the introduced species form a forest canopy, native species are able to establish and grow under their canopy, not before. The factors that regulate this assembly of novel species combinations are complex. They include, for example, the harsh physical and biotic conditions for seed dispersal and germination (Silander, 1979; Molina Colón et al., 2011). We address the possible role of stoichiometric changes due to decomposing leaf litter in contributing to the colonization of native tree species on degraded agricultural lands. For example, we address the increasing nitrogen availability through leaf decomposition in nitrogen-depleted soils.

During our studies of novel *Spathodea* forests, we have observed the abruptness of the interface between the forest's litter layer and the soil surface: the organic layers of the O and A1 horizons are usually absent or poorly developed. In some instances it appears as if these novel forests are growing with a litter layer that shows no transition to the surface soil layer below. This does not occur in native forests. The lack of a developed transition between litter and soil, in spite of high native juvenile tree species abundance and density (Abelleira Martínez et al., 2010), has led us to hypothesize that one reason why native species fail to colonize degraded agricultural soils is because of an elemental imbalance (*sensu* Sterner and Elser, 2002, p 42) between the elemental supply of the soil and the elemental requirements of native successional tree species. In other words, the stoichiometry of a degraded soil does not meet the requirements of the community of native tree species that grew there before soil degradation changed elemental quantities and ratios. Empirical support for this assertion are the organic matter and nitrogen concentration values in the top 10 cm of agricultural soils during the 1930's when cultivation was the prevailing land use in Puerto Rico. Roberts (1942) reported median soil organic matter (SOM) and nitrogen concentrations of 3.6 and 0.18 percent, values that are 3.6 and 2.4 times lower than for soils with forest cover.

The ecological processes that could reverse the elemental imbalance of eroded soils, i.e., those that regulate soil fertility *sensu* Swift et al. (1979), include litterfall, root growth, and the decomposition of litter atop the soil and roots belowground. Novel forests can restore these processes on degraded and abandoned agricultural lands. We know that novel forests dominated by the angiosperm *Spathodea* have high litterfall rates (Abelleira Martínez, 2011) but we lack information on litter decomposition rates. The objective of this paper is to quantify rates of *Spathodea* leaf decomposition, including elemental fluxes such as macro (N, P, K, Ca, and Mg) and microelements (Al, Fe, Mn, and Na) in novel *Spathodea* forests known to grow on degraded lands. Macro and microelements are essential nutrients for plant growth whose supply in the soil is either large (macroelements) or very small (microelements). We recognize that Na and Al are not essential plant nutrients, but are included with the microelements due to their plant physiological importance and their importance to higher trophic levels of the food chain. Our quantification of decomposition rates and stoichiometric variation will provide information about the potential rate of humus formation and elemental fluxes in these forests, and shed light on their role, if any, in the rehabilitation of the interface between litter and soil on previously deforested and degraded sites. This is a step to help us establish whether novel forest litter decomposition helps reduce elemental imbalance between soil and native pioneer tree species, and whether this may be an additional mechanism that facilitates the establishment of native tree species in novel *Spathodea* forests.

Table 1
Characterization of study forests by age and environmental conditions at research sites. Data not available is N/A.

Parameter	Perchas	Cibuco II	Pugnado
Age (yr)	39	38	24
Elevation Above Mean Seal Level (m)	200	10	10
Range of Annual Rainfall (mm)	1906 to 2032	1524 to 1906	1524 to 1906
Understory Mean Monthly Air Temperature (°C)	N/A	22 to 26	21 to 25
Understory Mean Monthly Air Humidity (%)	N/A	84 to 100	86 to 100

2. Materials and methods

2.1. Study sites

We conducted our study on three sites located in the subtropical moist forest life zone (*sensu* Holdridge, 1967; Ewel and Whitmore, 1973), on each of three geologic substrates defined by landform and terrain (*sensu* Monroe, 1976; Bawiec et al., 2001) and representative of where novel *Spathodea* forests are found in the region (Abelleira, 2009). The sites, characterized in Table 1, were: Cibuco II a *Spathodea* forest on a riparian alluvial floodplain; Pugnado, a forest on a closed karst depression; and Perchas, a forest on a volcanic mountain slope (see map in Fig. 1 of Abelleira et al., 2010). Site age was determined from interviews with local inhabitants, aerial photography from 1963, 1971, 1977–1978 (Ramos and Lugo, 1994), and 1985. Age was estimated as the mid-point between the most recent and oldest photos showing use and abandonment (Abelleira, 2010). The range of annual rainfall for 1981 to 2010 was obtained from NOAA (2018). *In-situ* mean monthly temperature and relative humidity was sampled in the forest understory (~2m above ground) during 2006 to 2007 (Abelleira, 2010). Corresponding *in-situ* microclimatic data are not available for Perchas, but temperature is likely slightly lower and relative humidity slightly higher at this site due to its higher elevation and mean annual rainfall.

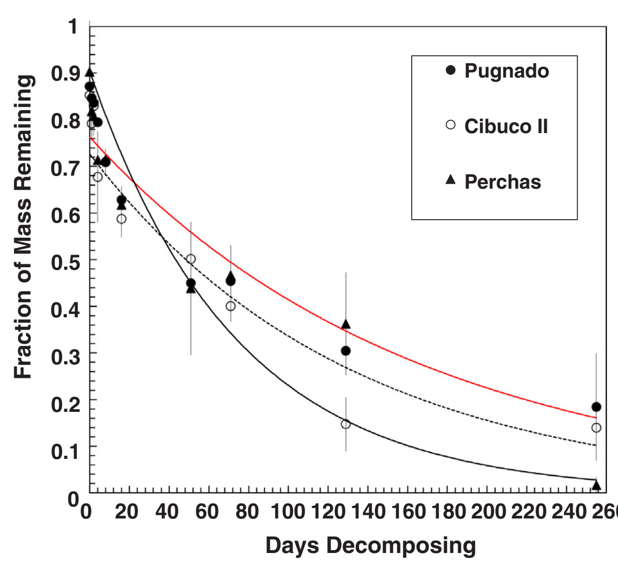

Fig. 1. Decomposition rate of *Spathodea campanulata* leaves in three locations with different geologic substrates: Perchas (volcanic), Pugnado (karst), and Cibuco II (alluvial). All sites are located in the subtropical moist forest life zone. Lines represent an exponential fit, Section 3.1 contains the statistical parameters. Standard error of the mean is shown for each triplicate collection. Red line is for Pugnado, dotted line is for Cibuco II, and black line is for Perchas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The soil on Cibuco II is derived from non-volcaniclastic sedimentary deposits from the Quaternary, on Pugnado from similar deposits embedded in calcium carbonate rock from the Oligocene, and in Perchas from weathering of extrusive volcaniclastic material from the Cretaceous (Monroe, 1976; Acevido, 1982; Bawiec et al., 2001). The valley where Cibuco II is located is covered by seasonally flooded mollisols that typically harbor high fertility and agricultural productivity (Acevido, 1982; Beinroth et al., 2003). Continuous use for sugar cane plantations since the sixteenth and up to the twentieth century depleted these soils in P and K relative to others in Puerto Rico (Álvarez Nazario, 1982; Picó, 1969; Vélez Ramos and Muñoz, 1991; Sotomayor Ramírez and Martínez, 2006; Abelleira and Lugo, 2008). Like Cibuco II, the karst depression where Pugnado is located contains floodable mollisols on flat to low slopes (7 to 15 percent) and might have been used the first half of the twentieth century (Picó, 1969; Ewel and Whitmore, 1973). The crops planted before abandonment in Pugnado consisted of fruits such as citrus, avocado and plantains, tuber such as cassava and yams, and were concentrated in lower ground where deep soils rich in organic matter were found (Doerr and Hoy, 1957; Monroe, 1976; Acevido, 1982). Volcanic mountain slopes in subtropical moist Puerto Rico were chiefly used for shade and sun coffee, tobacco and fruits (Picó, 1969; Domínguez Cristóbal, 2000). In Perchas (50 to 70 percent slope), the main crops were sun coffee and tobacco. Coffee remains a common crop in Puerto Rico's mountains but mostly at higher elevations (Miller and Lugo, 2009). Grazing was common in fallow years between crops or after abandonment on all sites, which is common throughout Puerto Rico. Information on forest structure, species composition, aboveground litter, biomass, and element stocks, land use history and spatial distribution of the sites is available in Lugo et al. (2006), Abelleira (2009 2010), Abelleira et al. (2010), Lugo et al. (2011, 2012) and Pérez et al. (2012).

2.2. Experimental design and sampling

At each site we collected freshly fallen leaves using large bed sheets left overnight at the sites. Typically, senesced leaflets fall off *Spathodea's* compound leaf, leaving the rachis on the canopy to fall subsequently, and therefore we collected leaflets for the experiment. Whole *Spathodea* leaflets of all available sizes, henceforth simply referred to as leaves, were selected and about 6 g dry-mass were placed in decomposition plastic bags made of polyethylene screen mesh (mesh size of 1 mm). A total of 99 bags were filled with leaves for 33 bags per site. Bags were immediately placed in the field in July 24, 2006 using a random array and were randomly collected in triplicates at the following schedule in days after being placed on the field: 0, 1, 2, 4, 8, 16, 51, 71, 129, 255, and 585. Bags placed on each site were filled with leaves that were collected on each corresponding site. The remaining material from the collection after 585 days, if any, was difficult to relate to the original material. However, we chemically analyzed the contents of those bags as well. All collected bags were immediately returned to the laboratory.

2.3. Chemical analyses

In the laboratory, we first discarded any green material or soil that may have contaminated the bags. The remaining content of each bag was dried to constant mass at 65 °C, carefully extracted, and weighted to the nearest mg. After weighing, the leaf material inside each bag was ground and processed for chemical analysis. The moisture factor and ash content of the sample were determined using a LECO model TGA701 Thermo gravimetric Analyzer (LECO-Corp, 2009). In the TGA 701, the mass loss of each sample was monitored until constant mass was achieved at the designated temperature (105 °C and 490 °C for moisture and ash, respectively; ground material was analyzed for phosphorus, potassium, calcium, magnesium, aluminum, manganese, iron, and sodium with a Plasma Emission Spectrometer (Spectro Ciros ICP). We used the digestion method recommended by Luh Huang and Schulte (1985). Samples were digested with concentrated HNO_3, 30% H_2O_2, and concentrated HCl. Total nitrogen and total carbon were analyzed by means of a LECO TruSpec CN Analyzer using a modified dry combustion method modified according to LECO-Corp (2005). In this method, samples are combusted at elevated temperatures (950 °C) in a stream of pure oxygen (99.99%). The combustion process converts any form of carbon and nitrogen into CO_2, NO_x, and N_2. Analyzing duplicates every ten samples determined precision. To ensure the completeness of elemental recovery, reference materials of known chemical composition were determined in every batch of forty samples (for total carbon and total nitrogen every 20 determinations). These reference materials included peach leaves (NIST-1547) and pine needles (NIST-1575a) obtained from the National Institute of Standards and Technology, USA. The reference materials used in the total carbon and nitrogen determinations included tobacco leaves, orchard leaves, and alfalfa, obtained from LECO Corporation (St. Joseph, MI).

We chemically analyzed 186 samples that resulted in 281 analyses that included carbon, nitrogen and ash; and 2154 analyses that included the macro and microelements. At Perchas, we only had sufficient material to analyze macro and microelements up to the 129-day collection date. At the other sites we analyzed for all elements up to the 255-day collection date. We analyzed the carbon and nitrogen of the 255-day and 585-day collection dates for two sites: Perchas and Cibuco II. For Pugnado, the analysis for ash included up to the 129-day collection date. The quantity of element at each collection date was determined by multiplying its concentration by the remaining dry weight in the corresponding decomposition bag. All elemental ratios are molar ratios.

2.4. Data analysis

The data set (including chemical results) was analyzed with an exponential model using Infostat Statistical Software (Di Rienzo et al., 2003). We report three decomposition constants reflecting the process between 0 and 16 days (K_{16}), 51 and 256 days (K_L), and for the whole measurement period from 0 to up to 512 days (K_{ALL}). To test for differences among decay rates (K-values), the fraction of mass remaining for each time period was ln-transformed, and the data fit to the linear decay equation: Ln (mass remaining/original mass) = $-K \times t$, where $-K$ = the decay rate and t = time in days. Slope equality ($p = .05$) among the three sites was tested using dummy variable (site) regression analysis (SAS version 9.4, SAS Institute, Cary, NC). If slopes differed, intercept equality was also tested to generate a common equation. The decomposition constant is the decay rate, or K values, obtained from the regression equations.

The daily decomposition constant was extrapolated to a year for comparison with decomposition constants in the literature. To estimate the half-life (time to decompose half of the material) and the time required for 95 percent of the material to be decomposed we used 0.693/K and 3/K, respectively. The time units of the half-life (days or years) depend on the unit of the K value used.

3. Results

3.1. Initial chemical conditions

Spathodea leaves at the volcanic site (Perchas) had the lowest potassium and highest magnesium concentrations among the three sites at

Table 2
Initial elemental concentration of decomposing *Spathodea campanulata* leaves. All data are in mg/g except N, C, and ash, which are in percent. Values are the mean of three or four replicate samples and the standard error of the mean is in parenthesis. Element ratios are molar ratios and all values are rounded. The last row depicts the concentration (same units as the data above) in litter of 22 *Spathodea campanulata* forests in Puerto Rico (our sites not included). These data are from Erickson et al. (2014). Empty cells mean data are not available.

Site	N	P	K	Ca	Mg	Al	Fe	Mn	Na	Ash	C	C/N	C/P	N/P
Perchas	1.1 (0.1)	1.4 (0.)	4.1 (0.6)	40 (0.8)	7.1 (0.6)	1.1 (0.3)	5.1 (1.0)	0.1 (0.03)	0.3 (0.2)	14 (0.1)	44 (0.2)	47 (0.3)	819 (5)	18 (0.8)
Cibuco II	1.3 (0.2)	2.6 (0.2)	12.4 (0.8)	39 (1.1)	3.9 (0.2)	0.6 (0.1)	0.4 (0.2)	0.03 (0.04)	0.4 (0.1)	14 (0.3)	44 (0.2)	40 (1)	443 (3)	11 (0.6)
Pugnado	1.1 (0.5)	0.9 (0.1)	7.5 (0.8)	50 (1.1)	2.4 (0.1)	1.3 (0.4)	9.5 (1.7)	0.1 (0.1)	0.2 (0.1)	15 (0.7)	44 (0.5)	45 (0.5)	1337 (4)	29 (0.6)
Litter	2.0	1.0	2.8	31	3.4	1.4	1.5	0.1	0.2		48	26	522	21

time zero of the experiment (Table 2). *Spathodea* leaves at Cibuco II (alluvial site) had the highest phosphorus and potassium concentrations and the lowest concentration of aluminum, iron, and manganese, and lowest C/N and C/P among the three sites. *Spathodea* leaves at the karst site (Pugnado) had the lowest phosphorus concentration, intermediate potassium concentration, highest calcium and iron concentrations, and the highest C/P and N/P among leaves of the three sites.

3.2. Change in mass, carbon, and elemental ratios

For the entire time period of 255 days for which samples were successfully retrieved from all study sites, Perchas had the quickest leaf decomposition rate: K_{ALL}/day = −0.0137 vs. −0.00704 for the other two sites (Fig. 1). Decay rates and intercepts did not differ between the two sites with the lower rates of decay, Pugnado and Cibuco II. The K_{ALL}-value for Perchas was significantly greater than the other two sites ($p < .0001$). The equation for Pugnado and Cibuco II was: Ln (fraction of mass remaining) = $-0.00704 \times t - 0.29843$ ($R^2 = 0.872$), showing common slope and intercept for the two sites. The equation for Perchas was: Ln (fraction of mass remaining) = $-0.0137 \times t - 0.10114$ ($R^2 = 0.908$), showing unique slope and intercept. By day 512, there was very little residual leaf material left in the bags that we placed in the field at the beginning of the study.

Table 3
Regression equations, their statistical significance, and half-life and 95 percent decomposition times for total mass of leaves of *Spathodea campanulata* left decomposing for different time periods in three locations on volcanic (Perchas), karst (Pugnado), and alluvial (Cibuco II) geological substrates within the subtropical moist forest life zone of Puerto Rico. The decomposition constant (K) is the exponent of e. Equations for leaf mass decomposition for the whole experiment are reported in Section 3.2.

Time Decomposing	Regression Equation	R^2	p value	Half-Life (days)	95% Decomposition (days)
Perchas					
16 days	$y = 0.8424\ e^{-0.021x}$	0.86	< .01	33	143
51 to 255 days	$y = 1.5538\ e^{-0.017x}$	0.91	< .05	41	176
Pugnado					
16 days	$y = 0.8646\ e^{-0.021x}$	0.98	< .001	33	143
51 to 255 days	NS*				
Cibuco II					
16 days	$y = 0.8221\ e^{-0.022x}$	0.83	< .02	32	136
51 to 255 days	$y = 0.5499\ e^{-0.006x}$	0.72	< .05	116	500

* Not significant at $p < .20$.

We observed what appear to be two decomposition stages defined by different slopes of the decomposition rate (Fig. 1). The differences in slopes were significant. All sites exhibited the same leaf decomposition rate (K_{16}) during the first 16 days with a half-life of about 33 days and about 140 days for achieving 95 percent leaf decomposition (Table 3). Sites differed on the rates of decomposition after 16 days, when the decomposition process slowed down. The half-life and time to 95 percent decomposition for the 255-day duration of the experiment were 51 and 219 for Perchas, and 98 and 426 for Pugnado and Cibuco II, respectively.

Changes in carbon concentration and ash concentration and quantity over time were mostly not significant (Table A1). The reduction in C/N through the decomposition of *Spathodea* leaves was similar at all sites, with faster reductions during the first 16 days of decomposition (values in Table A2). The N/P increased over the whole experiment, with overall lower rates at Perchas (values in Table A2). At Cibuco II, the increase of N/P during the first sixteen days was higher than at the other sites. The relationship between C/P and time of decomposition tended not to be significant but N/P increased at Cibuco II and decreased at Perchas (values in Table A2).

3.3. Change in macroelements

Nitrogen concentration (Table A2 has all chemical data) increased through the decomposition process (K_{ALL}) at Perchas and Pugnado and at all sites through the first 16 days of decomposition (K_{16}, Table A3). Except for nitrogen concentration at Perchas and magnesium concentration at Cibuco II, we found no significant concentration change pattern during the second stage of the decomposition process (K_L). Phosphorus concentration declined at Cibuco II, increased at Perchas (K_{16} and K_{ALL}), and did not change at Pugnado. The K_{16} for magnesium concentration declined at all sites. The K_{16} and K_{ALL} for potassium concentration decreased across all sites. The K_{ALL} for calcium concentration was positive at Perchas, and was negative at Pugnado and Cibuco II. The K_{ALL} for magnesium concentration was positive at Cibuco II but was not significant at the other two sites.

All five macroelements declined in quantity through the decomposition process (K_{ALL}), with the fastest rates for potassium and the slowest for nitrogen and phosphorus at Cibuco II (Table A4). Loss of macroelements was faster for magnesium during the first 16 days (K_{16} compared to K_{ALL}). Nitrogen loss (K_{16}) through the first 16 days was not significant. Potassium quantity loss had the highest K_{16} among the five macroelements. Nitrogen quantity loss during the second stage of the process (K_L) was slow at Perchas and faster at Cibuco II.

3.4. Change in microelements

The significant changes in concentration (Table A5) and quantity

Table 4
Annual decomposition constant (K) and time required for 95 percent decomposition (3/K) of leaf material from trees in several tropical and subtropical environments. The ranges of values measured in each study are reported.

Location and Species	Annual K	3/K (years)
Puerto Rico, dry forest (Lugo and Murphy, 1986)		
1 to 2 yr-old to mature native vegetation	0.58 to 0.67	5.17 to 4.48
El Verde, wet forest (Wiegert and Murphy, 1970; Wiegert, 1970)		
Prestoea montana[a]	0.412 to 0.648	7.27 to 4.63
Croton poecilanthus	0.814 to 1.445	3.69 to 2.08
Manilkara bidentata	0.309 to 0.600	9.72 to 5.00
Sloanea berteriana	0.452 to 0.659	6.63 to 4.55
Dacryodes excelsa	0.465 to 0.812	6.45 to 3.69
Cecropia schreberiana[b]	0.400 to 0.717	7.51 to 4.18
Mixed litter	0.522 to 0.759	5.75 to 3.95
Puerto Rico moist secondary forest (Ostertag et al., 2003)		
Cubuy	1.62 to 1.90	1.85 to 1.58
Puerto Rico moist novel forests (this study)		
Perchas, *Spathodea campanulata*[c]	5.0	0.6
Pugnado and Cibuco II, *Spathodea campanulata*[c]	2.6	1.2
China, subtropical secondary broadleaf forest (Zhang et al., 2016)		
Six native species, low litter quality	0.3 to 0.6	10.0 to 5.0
Six native species, medium litter quality	0.7 to 1.0	4.3 to 3.0
Six native species, high litter quality	1.0 to 3.0	3.0 to 1.0
Venezuela, wet mature forests, three species each (Cuevas and Medina, 1988)		
Tierra Firme	0.58 to 5.00	5.1 to 0.6
Tall Amazon Caatinga	0.80 to 1.33	3.8 to 2.44
Low Bana	0.22 to 0.44	13.6 to 6.82
Hawaii, wet to rain forests (Vitousek, 2004)		
Metrosideros polymorpha	0.18 to 0.97	16.67 to 3.09
Fraxinus uhdei[c]	0.86	3.49
Mexico, Las Tuxtlas rain forests (Álvarez Sánchez and Becerra Enríquez, 1996)		
Five individual native tree species	1.10 to 4.02	2.73 to 0.75
Five Neotropical Forest Sites (Cusack et al., 2009)		
Seven native tree species	0.27 to 1.37	11.11 to 2.19

[a] *Euterpe globosa.*
[b] *Cecropia peltata.*
[c] Introduced and naturalized species.

(Table A6) of microelements during decomposition of *Spathodea* leaves were positive in all cases with the exception of sodium concentration and quantity, and the quantity of manganese at Cibuco II. Significant changes in microelement concentration were more prevalent than changes in microelement quantity. In general, when the concentration and quantity increased through decomposition, the slope of the concentration increase was not significant or steeper than the slope of the microelement quantity. As observed above for organic mass and macroelement curves, the slopes for K_{16} were steeper than for K_{ALL}, and the K_L tended to be not significant. The K_{ALL} for aluminum and iron quantity (with an exception at Pugnado) was not significant (Table A6).

4. Discussion

4.1. Leaf decomposition rates

Spathodea leaf decomposition rates, especially during the first 16 days are among the highest that we found in the tropical forest literature (Table 4). The initial decomposition rates of *Spathodea* leaves are high when compared with rates reported in the literature for native secondary forests in moist life zones in Puerto Rico, similar in climate to our study sites, and in geology and soils to our Perchas site in particular (Ostertag et al., 2003). Ostertag et al.'s (2003) study was conducted immediately after the passing of a hurricane, which created a one-day pulse in literfall and increased litterfall decomposition rates. Table 4 shows that the decomposition rates found in our study are higher than those reported for native forests on wet and dry forest life zones in Puerto Rico, and higher than those along an elevation gradient in Hawaii (Bothwell et al., 2014). Our rate of leaf decomposition results are also higher than those measured along a temperature gradient in Peru (Salinas et al., 2010), a successional age gradient in Guatemala (Ewel, 1976), and a comparison of three mature forests in the amazon (Cuevas and Medina, 1988). Lower K values than ours were found in seven Neotropical species decomposed under a variety of environmental conditions (Cusack et al., 2009), among 18 native tree species in subtropical China (Zhang et al., 2016), and two understory shrubs in subtropical Puerto Rico (Prather et al., 2018). *Spathodea* leaf decomposition rates were also higher than measured under different levels of tropical forest degradation in Borneo by Yeong et al. (2016).

During the initial decomposition phase, half of the *Spathodea* leaf material is decomposed in about 33 days, compared to months or years in most reports in the above studies (Table 2). Even as the process slows down, decomposition rates remain high during the second stage, and higher than those measured in the studies cited above, reflecting the high chemical quality of *Spathodea* leaf litter (Table 2). By high chemical quality, or resource quality *sensu* Swift et al. (1979), we mean high nutrient concentrations, particularly N and P, and low C/N, C/P, and N/P. Swift et al. (1979) include other indicators of high resource quality such as low lignin content and high palatability to animals, but we lack measurements of these parameters. Site conditions also affect decomposition rates as suggested by the faster rates at Perchas (Fig. 1).

4.2. Leaf decomposition and chemical quality

The chemical quality of decomposing litter has been recognized as all-important for determining the rate of the decomposition process. For example, Zhang et al. (2016) found that the chemical quality of plant litter from 18 tree species regulated litter decomposition regardless of other contributing factors such as soil fauna. Swift et al. (1979) shows how different litter chemical compounds decompose at different rates depending on their chemical quality. Sterner and Elser (2002) suggested that C/N and C/P account for up to 90 percent of the variation in the decomposition constant globally. In our study, the C/N and N/P values in our study are low at all sites (Table A2) in comparison with those reported for leaf litter from several biomes (McGroddy et al., 2004; Cusack et al., 2009). Only the tropical understory tree *Drypetes glauca* in a list of seven species from Neotropical sites reported by Cusack et al. (2009) and two understory shrubs in Prather et al. (2018) had a lower C/N but slower leaf decomposition rate than *Spathodea* leaf litter.

Similarly, the C/P of *Spathodea* leaf litter in our study are low, with the exception of Pugnado, with its low initial phosphorus concentration (Table 2). High calcium concentrations at the Pugnado karst site can immobilize phosphorus and this is reflected in the initial chemical concentrations of these two elements in leaves of that site (Table 2). The initial chemical quality of *Spathodea* leaves at Perchas does not show any anomalies that would explain the high K_{ALL} at this site other than the high magnesium and low potassium concentrations. The main difference between this site and the other two (Cibuco II and Pugnado) is the volcanic soil at Perchas vs. mollisols that flood at the other two sites. It is possible, but we do not know, that different decomposer communities and other environmental conditions, such as the absence of flooding accelerate decomposition rates at Perchas. Site conditions can regulate the rate of leaf decomposition as was found in Borneo where rates differed according to land cover and degradation (Yeong et al., 2016). However, the chemical quality of *Spathodea* leaves i.e., low C/N, C/P, and N/P, is sufficiently high to represent a labile substrate to the soil decomposer community.

4.3. Comparison by species

The rapid decomposition rate of *Spathodea* leaf litter at all three study sites contrasts with species-specific rates measured elsewhere and listed in Table 4. Decomposition rates for native forest species in the studies listed are similar among those sites but slower than what we found in novel forests of *Spathodea*. Vitousek (2004) also found higher rates of leaf decomposition for introduced *Fraxinus* trees in Hawaii than for the native primary forest species *Metrosideros polymorpha* (Table 4). In both cases, and in most comparative studies of leaf decomposition, the cause for fast decomposition rates is the initial chemical quality of the decomposing substrate. In the novel forests of Puerto Rico, the dominant introduced species produce litter of higher chemical quality than that of native forests (Erickson et al., 2014). Not all introduced species in Puerto Rico exhibit leaf litter of higher chemical quality than that of native species but many do, and more so *Spathodea* (Fig. 2 in Lugo et al., 2011). Our study suggests that this higher chemical quality results in rapid decomposition of organic matter and fast mobility of essential nutrients at the litter-soil interface, which means that the decomposition of *Spathodea* leaves can contribute to mitigating the elemental imbalance between degraded soils and the native forest species that are unable to grow on degraded sites.

4.4. Element mobility

As has been reviewed by Berg and McClaugherty (2003), Sanderman and Amundson (2005), and Berg and Laskowski (2006), the movement, concentration, and quantity of macroelements during leaf decomposition exhibit contrasting patterns with that of organic mass (carbon and total mass; compare Tables 3 and A1 with Tables A3 and A4). During the first 16 days when mass was decomposing at the fastest rates (K_{16}), nitrogen concentration increased at all sites at a fairly rapid rate. Meanwhile, calcium increased in concentration at Pugnado, as did magnesium at Cibuco II (positive K_L) and phosphorus at Perchas (positive K_{16} and K_{ALL}). The quantity of all macroelements decreased through the decomposition process, but the K_{16} and K_{ALL} for phosphorus tended to be low while those for potassium were the highest at all sites, reflecting the high mobility of potassium (Cuevas and Medina, 1988; Marschner, 2012). On average, the decomposition constants were slower for microelements than for macroelements illustrating that the former have lower mobility probably because of the tendency for the immobilization of microelements during decomposition. Microelements tended to increase both in concentration and in quantity across sites (Tables A5 and A6), a phenomenon reviewed by Berg and Laskowski (2006), who suggested that importation of these elements was possible through the activity of colonization of microorganisms and/or by mobilization due to changes in pH.

4.5. Comparison with other systems

The patterns of change in element concentration that we observed were not always similar to those reported for *Pinus sylvestris* (Scots pine) by Berg and McClaugherty (2003) and Berg and Laskowski (2006), for which leaf decomposition has been described in greater detail than for any other species and ecosystem. Our results are consistent with those of Cuevas and Medina (1988) in the Venezuelan amazon. For example, the increase in phosphorus concentration with decomposition observed in Scots pine did not occur with *Spathodea* where phosphorus concentration declined at two sites but increased in Perchas. Also, manganese concentration tended to increase in our study but decreased in the Scots pine forests studied by Berg and colleagues. Leaf litter of Scots pine has very low phosphorus concentration and high manganese concentration, the opposite of *Spathodea*. Low phosphorus concentration can limit the decomposition rates for Scots pine leaves and manganese can drive the decomposition of lignin (Berg and Laskowski, 2006). In contrast, the high phosphorus concentration in *Spathodea* leaves does not appear to be a limiting factor and the increase in manganese concentration may be reflecting the growth of decomposers that catabolize the low lignin content in leaves of this species.

Adair et al. (2008) used a 3-pool model to analyze long-term decomposition rates in a diversity of climates. They identified three pools of chemical quality in litter: labile, intermediate, and recalcitrant, which they associated with various ratios of cellulose, lignin, and nitrogen. Similar analytical emphasis with a variety of decomposition models and description of various decomposing pools with different half-lives have been used by Cusack et al. (2009). Wider and Lang (1982) examined six different statistical models for analyzing decomposition data and found single and double exponential models as the best way of fitting mass loss data over time with an element of biological realism. We found that *Spathodea* leaf litter decomposes so fast that only two distinct decomposition rates were evident. We found no evidence of recalcitrant litter. Nevertheless, changes in litter quality such as micronutrient accumulation and increase in concentration through the leaf decomposition process observed in our study contributes to a temporary enrichment of the forest floor location where leaves are decomposing. *Spathodea* leaves and roots are known to have secondary compounds known to be antifungal (Ngouela et al., 1991; Pianaro et al., 2007). These compounds may affect decomposition rates and the mobility of macro and microelements through their effect on fungi. Evaluating whether this is so can further clarify the role of *Spathodea* forests in rehabilitating degraded and abandoned agricultural lands.

4.6. The rehabilitation role of leaf decomposition in Spathodea forests

Our ultimate objective was to deduce the role of the decomposition of *Spathodea* leaves in the rehabilitation of degraded soils. Our results show that the decomposition of *Spathodea* leaves is very rapid and that very little leaf material remains a year and a half after leaves fall to the forest floor. We believe that the chemical quality of *Spathodea* leaves makes these leaves very labile to decomposers. It also appears that *Spathodea* leaf decomposition is not a main source of carbon for the build-up of SOM. The soil rehabilitation role of *Spathodea* leaf decomposition appears to be the concentration and rapid recirculation of plant nutrients on degraded sites. This acceleration of nutrient fluxes and feedbacks to soil processes restores forest dynamics through higher nutrient availability and productivity. Facilitating the availability of nutrients contributes to the establishment of native tree species that otherwise could not cope with the low chemical quality of the substrate left after abandonment of agricultural activities.

Other data support these working hypotheses on the role of *Spathodea* leaf decomposition in puertorrican novel forests. For example, Erickson et al. (2014) found that the leaf litter of novel forests was increasing the availability of nitrogen and phosphorus island-wide relative to historical forests and thus accelerating nutrient cycling (last row of Table 2). The leaf litter on the forest floor of novel forests has higher nitrogen, aluminum, and carbon concentrations, and N/P than freshly fallen leaves. Concentrations of potassium, calcium, and iron in this litter are lower than in freshly fallen leaves, as are the C/N and C/P ratios. In fact, Erickson et al. (2014) reported low accumulation of leaf litter on the forest floor of *Spathodea* novel forests (3.9 Mg ha^{-1}) compared to all the insular forests that they studied. Abelleira Martínez and Lugo (2008) also found low litter accumulation on the forest floor of alluvial *Spathodea* forests. Leaf litter does not accumulate in these forests because of its fast decomposition. Leaf litter accumulates when decomposition is slowed down by the low chemical quality of the decomposing materials as illustrated by leaf litter with lower chemical quality found in mature forests (Table 4).

It is possible that the leaf decomposition process slows down as the novel forest is enriched with late successional native species with leaf litter of lower chemical quality than that of *Spathodea*. Our findings support management interventions aimed at enriching *Spathodea* novel forests with late-successional tree species, which are largely absent in these novel forests. Late successional tree species are likely to have high rates of nutrient return to the forest soil and contribute to increasing SOM accumulation through slower decomposition rates. Such management interventions can increase the species richness of novel forests and increase the delivery of ecosystem services (Hobbs et al., 2013).

We hypothesize that as the novel forest matures, the elemental gap between soil and native tree species is reduced by the high nutrient return through litterfall and root mortality of introduced species. Closing the elemental gap between soil and native tree species would imply that the establishment of successional native tree species under the canopy of introduced tree species occurs in the absence of an organic soil horizon or a humus organic layer below the litter layer. Such establishment of native species is achieved through mobilization and fast re-cycling of nutrients through the decomposing of high quality leaf litter. These released nutrients restore stoichiometric conditions that are more amenable to the growth requirements of native tree species or of other organisms such as mychorrizal fungi, than possible on degraded soil after land abandonment. The scenario we just described is consistent with our observations in novel *Spathodea* forests and with the results of this study that suggest a scenario of rapid nutrient mobilization due to fast decomposition of high chemical quality *Spathodea* leaves.

5. Conclusions

The fast decomposition rate of *Spathodea* leaves does not result in SOM accumulation in degraded lands, which have low organic matter and nitrogen concentrations and lack a humus layer. The decomposition of *Spathodea* leaves concentrates and mobilizes nutrients (including nitrogen) on the forest floor, making them available to microbial and plant species. This rapid mobilization of plant nutrients on highly degraded soils facilitates the establishment of native tree species that cannot colonize degraded lands but regenerate under the canopy of *Spathodea*-dominated forests. The possibility of improving soil humus formation by establishing native late-successional tree species in novel *Spathodea* forests should be assessed because the addition of tree species lowers the chemical quality of litter, reduces the rate of decomposition, and increases SOM accumulation.

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Declaration of interests

None.

Data Availability Statement

Appendix Tables contain the analysis of mass, macro, and micro-elements and the original mass and chemistry data.

Appendix A

(See Tables A1–A6).

Table A1
Slopes (K_{16}, K_L, and K_{ALL}), t statistic (T), number of samples (n), and significance (p) of exponential regressions of carbon (C) and ash concentration (conc) and quantity remaining through the decomposition of *Spathodea campanulata* leaves in three locations on volcanic (Perchas), karst (Pugnado), and alluvial (Cibuco II) geological substrates within the subtropical moist forest life zone of Puerto Rico. Time of decomposition was 585 days for K_{ALL}, 16 days for K_{16}, and 51 to 585 days for K_L (see methods for exceptions). No significance (NS) is for $p > .05$. Empty cells correspond to NS relationships. The unit for K's is 1/day. Some values were rounded.

Location (element)	K_{16}	T (n)	p	K_L	T (n)	p	K_{ALL}	T (n)	p
Perchas (C_{conc})	NS			NS			NS		
Cibuco II (C_{conc})	NS			−0.001	6.6 (12)	.0001	−0.001	12.9 (32)	.0001
Pugnado (C_{conc})	NS			NS			−0.002	4.2 (31)	.0003
Perchas ($C_{quantity}$)	−0.02	15.4 (20)	.0001	−0.01	3.7 (11)	.0050	−0.01	14.4 (31)	.0001
Cibuco II ($C_{quantity}$)	NS			−0.01	4.9 (12)	.0007	−0.01	7.0 (32)	.0001
Pugnado ($C_{quantity}$)	−0.03	4.2 (19)	.0007	NS			−0.01	6.9 (31)	.0001
Perchas (Ash_{conc})	0.02	3.9 (20)	.0011	NS			0.004	4.4 (30)	.0002
Cibuco II (Ash_{conc})	0.02	6.5 (20)	.0001	0.001	4.3 (12)	.0015	0.002	7.3 (32)	.0001
Pugnado (Ash_{conc})	NS			NS			0.01	4.2 (29)	.0003
Perchas($Ash_{quantity}$)	NS			NS			−0.004	3.5 (30)	.0016
Cibuco II ($Ash_{quantity}$)	NS			−0.01	2.7 (12)	.0241	−0.003	2.9 (32)	.0071
Pugnado ($Ash_{quantity}$)	NS			NS			NS		

Table A2
Chemical and weight data by site and time of collection. Empty cells = missing data. Dry weight (DW) is in mg and all elements except %N, %C, and %Ash are in mg/g.

Days	DW	N	P	K	Ca	Mg	Al	Fe	Mn	Na	Ash	C	C/N	C/P	N/P
Perchas															
0	6.086	1.11	1.43	4.06	39.64	7.00	1.33	6.24	0.10	0.19	13.4	44.2	47	800	17
0	5.226	1.12	1.27	2.88	37.98	6.04	0.92	1.47	0.10	0.20	13.5	44.2	46	901	20
0	5.075	1.06	1.49	4.83	41.91	8.31	1.03	7.59	0.10	0.35	13.7	43.6	48	756	16
1	5.424	1.18	1.30	2.40	32.63	5.08	1.02	1.79	0.17	0.23	15.0	44.3	44	882	20
1	4.981	1.23	1.35	2.31	38.76	6.24	0.94	1.51	0.10	0.20	13.5	45.0	43	862	20
1	4.579	1.18	1.36	2.99	36.16	6.54	1.25	2.54	0.12	0.22	14.3	43.8	43	829	19
2	5.306	1.17	1.61	2.01	38.35	5.71	1.27	2.39	0.14	0.19	15.2	44.0	44	705	16
2	4.907	1.14	1.30	3.32	43.61	7.51	0.53	0.34	0.05	0.26	13.2	44.0	45	875	19
2	4.513	1.14	1.29	2.56	45.56	6.43	0.66	0.49	0.06	0.16	13.3	44.6	46	890	20
4	4.052	1.30	1.14	1.21	43.29	5.06	1.09	1.75	0.11	0.10	14.8	44.0	40	999	25
4	4.648	1.27	1.16	1.21	42.72	5.44	1.11	1.78	0.11	0.10	14.8	44.0	40	977	24
4	4.232	1.30	1.29	1.91	38.22	5.93	0.79	1.28	0.26	0.13	12.7	45.2	41	908	22
4		0.93	0.95	1.73	27.55	5.71	5.35	15.14	0.55	0.11	36.3	31.2	39	843	22
8	4.444	1.35	1.06	1.22	36.50	4.39	1.34	2.87	0.17	0.10	15.6	45.2	39	1099	28
8	4.48	1.32	1.40	1.61	41.27	5.33	1.94	4.12	0.19	0.11	19.2	42.1	37	775	21
8	4.141	1.39	1.37	1.62	47.70	5.82	1.13	1.65	0.10	0.11	15.4	44.2	37	836	23
16	4.226	1.53	1.42	1.24	45.31	4.55	2.18	5.00	0.28	0.12	22.7	40.7	31	740	24
16	3.411	1.75	1.47	1.26	40.58	4.68	1.50	3.41	0.17	0.11	16.5	44.9	30	786	26
16	3.567	1.44	1.13	1.17	45.16	3.87	2.60	6.07	0.38	0.12	23.0	41.0	33	939	28
51	3.558	1.67	1.29	1.19	31.42	6.17	5.94	11.61	0.45	0.12	30.8	35.2	25	706	29
51	1.82	1.66	1.00	0.86	43.64	4.34	3.29	6.34	0.29	0.09	25.0	40.2	28	1036	37
51		1.13	1.00	0.86	44.48	4.16	3.33	6.55	0.29	0.09	51.9	23.5	24	610	25
51		1.10	1.05	1.32	18.76	6.28	10.18	22.34	0.85	0.15	51.6	23.0	24	562	23
71	2.566	1.67	1.41	1.31	27.67	5.62	6.92	15.76	0.63	0.24	36.0	33.6	23	618	26
71	2.336	1.81	1.18	1.13	36.01	3.98	3.47	15.13	0.35	0.15	23.7	41.5	27	903	34
71	3.577	1.60	1.57	1.25	30.33	5.76	6.65	14.51	0.57	0.14	39.6	30.7	22	506	23
129	3.481	1.92	1.31	1.15	27.03	4.37	4.40	9.55	0.57	0.32	29.8	37.2	23	734	32
129	1.763	1.90	1.71	1.05	36.91	5.49	6.71	11.46	0.48	0.32	32.9	36.2	22	546	25
129	1.351	1.61	1.26	1.18	34.97	5.33	8.06	16.81	0.63	0.17	40.5	30.5	22	626	28
255	0.203	1.26										22.1	20		
255	0														
585		1.60										24.0	17		
Cibuco II															
0	4.922	1.45	2.71	14.36	39.19	4.00	0.61	0.58	0.04	0.48	13.4	44.4	36	422	12
0	2.316	1.48	2.65	14.28	39.78	4.01	0.58	0.57	0.04	0.47	13.4	44.4	35	433	12
0	5.427	1.18	2.25	8.94	50.17	3.87	0.59	0.34	0.03	0.32	14.0	44.2	44	507	12
0		1.18	2.77	12.18	45.09	3.83	0.56	0.24	0.02	0.35	13.8	44.2	44	411	9
1	4.620	1.27	2.64	11.12	41.40	3.71	0.48	0.30	0.02	0.21	13.0	44.6	41	436	11
1	5.173	1.09	2.28	9.82	48.55	4.59	0.56	0.30	0.03	0.21	14.6	43.6	47	494	11
1	4.579	1.21	2.55	11.31	47.25	4.05	0.65	0.50	0.03	0.27	13.7	44.6	43	451	11
2	4.726	1.43	2.11	5.63	48.13	3.66	0.52	0.29	0.03	0.32	13.0	44.9	37	550	15
2	5.265	1.16	2.08	7.95	48.85	3.92	0.56	0.26	0.03	0.20	13.9	44.2	45	548	12
2	5.209	1.21	2.18	11.19	45.78	4.29	0.51	0.26	0.02	0.34	14.1	44.1	42	522	12
4	2.971	1.27	2.46	4.84	49.95	3.15	0.64	0.43	0.03	0.20	13.2	45.1	41	473	11
4	4.688	1.35	2.31	3.12	44.14	3.38	0.54	0.33	0.03	0.20	11.9	45.5	39	509	13
4	4.751	1.35	2.18	2.98	41.12	3.30	0.47	0.32	0.03	0.20	11.9	45.5	39	538	14
4		1.28	2.34	2.63	48.34	3.05	1.00	1.19	0.06	0.15	14.1	44.4	40	489	12
8	3.974	2.32	1.88	1.86	45.37	2.90	0.92	1.21	0.06	0.21	13.1	46.0	23	632	27
8	4.597	1.49	1.86	2.09	47.64	3.15	0.56	0.35	0.03	0.11	12.6	46.5	36	647	18
8	4.458	1.63	2.01	4.80	46.54	3.85	0.63	0.55	0.04	0.22	13.7	45.4	32	583	18
16	3.077	1.54	1.26	1.62	50.26	2.54	1.36	4.49	0.30	0.13	18.9	43.8	33	897	27
16	3.873	1.73	1.14	1.28	50.20	2.39	2.44	4.58	0.11	0.14	20.1	43.0	29	970	33
16	3.732	1.60	1.16	1.28	45.72	2.36	2.48	4.40	0.11	0.15	19.7	43.5	32	967	30
51	2.889	1.90	1.35	1.17	37.44	3.25	4.58	9.97	0.29	0.09	27.2	38.9	24	743	31
51	3.200	2.01	2.01	1.28	51.86	2.93	1.88	2.80	0.10	0.17	17.8	44.3	26	570	22
51		2.16	1.77	1.09	47.05	3.14	2.77	5.62	0.20	0.14	21.2	42.5	23	621	27
51		2.19	1.64	1.00	44.04	2.87	2.46	5.10	0.18	0.13	20.6	43.0	23	679	30
71	2.513	2.00	1.59	1.08	45.60	3.56	3.65	7.40	0.24	0.07	23.0	41.8	24	679	28
71	2.723	2.11	1.91	1.53	40.38	3.63	4.76	10.32	0.31	0.07	24.3	40.4	22	546	24
71	2.063	2.30	2.07	1.93	40.32	3.96	4.41	9.68	0.28	0.08	26.2	38.9	20	483	25
129	0.325	2.34	1.74	0.92	43.15	3.93	3.17	6.75	0.23	0.13	23.4	41.6	21	619	30
129	0.809	2.57	1.74	0.91	39.84	3.94	3.14	6.82	0.23	0.13	23.6	41.8	19	622	33
129	1.537	2.25	1.83	1.05	50.30	4.08	3.78	6.78	0.20	0.16	23.8	41.6	22	586	27
255	0.627	2.01	1.62	1.42	28.11	5.30	7.28	16.77	0.45	0.10	35.7	32.6	19	519	27
255	1.080														
585		1.73									35.7	23.9	16		

(*continued on next page*)

Table A2 (*continued*)

Days	DW	N	P	K	Ca	Mg	Al	Fe	Mn	Na	Ash	C	C/N	C/P	N/P
Pugnado															
0	5.323	1.17	0.897	11.312	42.344	2.287	0.539	0.535	0.040	0.115	12.7	45.1	45	1298	29
0	5.205	1.11	0.816	5.482	51.589	2.401	1.916	25.145	0.203	0.176	16.6	43.8	46	1385	30
0	5.199	1.13	0.802	5.443	52.295	2.361	1.948	12.056	0.123	0.176	16.1	43.1	44	1387	31
0		1.12	0.894	7.736	52.569	2.423	0.622	0.212	0.044	0.264	14.6	44.3	46	1278	28
1	5.343	1.10	0.805	7.639	46.994	2.682	0.577	0.189	0.041	0.143	13.8	44.7	47	1433	30
1	5.145	1.36	0.911	8.056	43.529	1.849	1.013	19.271	0.159	0.238	13.6	45.6	39	1293	33
1	4.880	1.24	0.866	5.711	52.220	1.912	0.592	0.275	0.045	0.209	13.4	45.8	43	1367	32
2	5.102	1.23	0.858	9.179	48.757	2.312	0.502	0.200	0.051	0.144	13.5	45.4	43	1366	32
2	5.031	1.22	0.828	6.831	48.730	2.250	0.593	0.203	0.045	0.207	13.6	45.4	44	1417	33
2	5.168	1.11	0.786	5.789	51.748	3.180	0.609	0.212	0.045	0.190	13.9	44.6	47	1465	31
4	4.850	1.25	0.874	3.995	54.460	2.062	0.953	0.657	0.063	0.149	15.0	44.4	41	1313	32
4	4.729	1.27	0.804	3.637	51.780	1.790	1.602	7.199	0.103	0.116	14.9	45.1	41	1447	35
4	4.814	1.39	0.899	4.133	51.056	1.964	0.733	0.419	0.050	0.138	13.4	45.9	39	1317	34
4		1.41	0.869	4.056	51.261	1.903	0.694	0.392	0.049	0.128	13.3	45.9	38	1363	36
8	4.343	1.38	0.877	1.731	52.460	1.555	0.661	0.329	0.049	0.072	13.4	46.1	39	1356	35
8	4.375	1.60	0.922	1.742	56.983	1.859	0.895	0.615	0.066	0.104	14.7	45.3	33	1267	38
8	4.167	1.57	0.841	2.218	56.552	1.820	0.677	0.234	0.050	0.137	14.5	46.2	34	1419	41
16	3.738	1.62	0.906	1.019	70.261	1.070	1.879	2.035	0.113	0.087	21.9	42.6	31	1213	39
16	3.940	1.69	1.041	1.251	55.241	1.347	1.284	1.304	0.084	0.085	16.9	44.6	31	1106	36
16	3.770	1.62	0.938	1.325	63.304	1.881	0.914	0.325	0.062	0.101	16.5	45.3	33	1245	38
51	2.726	2.18	1.170	1.039	61.922	1.932	1.374	1.139	0.078	0.054	17.3	45.7	24	1007	41
51	2.848	2.10	1.358	3.718	67.383	2.530	1.444	1.229	0.116	0.051	18.9	43.8	24	833	34
51	2.583	2.13	0.943	0.923	59.323	1.431	0.874	0.358	0.058	0.038	15.1	46.7	26	1278	50
71	2.649	1.97	0.985	1.489	62.934	1.686	1.576	1.584	0.105	0.140	18.6	43.2	26	1131	44
71	3.222	1.77	1.018	1.557	67.259	1.747	1.646	1.605	0.106	0.143		38.0	25	963	38
71	2.363	1.80	1.103	1.214	62.644	2.029	3.917	6.464	0.233	0.064		38.4	25	899	36
71		2.11	1.027	0.972	63.926	2.206	1.098	0.449	0.076	0.092	16.4	46.5	26	1170	45
129	2.123	2.20	1.204	0.745	82.302	1.869	4.097	5.933	0.240	0.109		38.0	20	814	40
129	0.803	2.49	1.144	0.840	60.165	1.811	1.494	1.592	0.126	0.219	16.9	46.2	22	1042	48
129	1.539	2.41	1.189	1.015	52.038	2.158	1.710	2.526	0.153	0.217	17.8	45.3	22	984	45
255	1.820	2.13	1.138	1.169	65.437	2.112	5.137	8.710	0.328	0.114		35.8	20	812	41
255	0.422														
585													18		

Table A3

Slopes (K_{16}, K_L, and K_{ALL}), t statistic (T), number of samples (n), and significance (p) of exponential regressions of concentration (conc) of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) in remaining mass through the decomposition of *Spathodea campanulata* leaves in three locations on volcanic (Perchas), karst (Pugnado), and alluvial (Cibuco II) geological substrates within the subtropical moist forest life zone of Puerto Rico. Time of decomposition ranged from 129 to 255 days for K_{ALL}, 16 days for K_{16}, and 51 to 255 or 129 days for K_L (see methods). No significance (NS) is for $p > .05$. Empty cells correspond to NS relationships. The unit for K's is 1/day. Some values were rounded.

Location (element)	K_{16}	T (n)	p	K_L	T (n)	p	K_{ALL}	T (n)	p
Perchas (N_{conc})	0.02	8.4 (20)	.0001	0.0006	4.2 (12)	.0020	0.001	6.4 (32)	.0001
Cibuco II (N_{conc})	0.02	3.0 (20)	.0072	NS			NS		
Pugnado (N_{conc})	0.02	7.1 (19)	.0001	NS			0.001	2.1 (31)	.0492
Perchas (P_{conc})	0.01	3.8 (20)	.0014	NS			0.002	5.3 (31)	.0001
Cibuco II (P_{conc})	−0.04	8.8 (20)	.0001	NS			−0.002	2.5 (31)	.0201
Pugnado (P_{conc})	NS			NS			NS		
Perchas (K_{conc})	−0.15	4.6 (20)	.0002		NS		−0.15	4.6 (31)	.0001
Cibuco II (K_{conc})	−0.24	6.1 (20)	.0001		NS		−0.24	6.8 (31)	.0001
Pugnado (K_{conc})	−0.11	4.0 (19)	.0010	NS			−0.01	2.9 (29)	.0071
Perchas (Ca_{conc})	0.02	5.9 (20)	.0001	NS			0.001	3.7 (31)	.0009
Cibuco II (Ca_{conc})	NS			NS			−0.001	3.1 (31)	.0040
Pugnado (Ca_{conc})	NS			NS			−0.002	2.4 (29)	.0234
Perchas (Mg_{conc})	−0.03	4.0 (20)	.0009	NS			NS		
Cibuco II (Mg_{conc})	−0.03	6.4 (20)	.0001	0.002	8.2 (11)	.0001	0.001	3.0 (31)	.0053
Pugnado (Mg_{conc})	−0.03	4.3 (19)	.0005	NS			NS		

Table A4
Slopes (K_{16}, K_L, and K_{ALL}), t statistic (T), number of samples (n), and significance (p) of exponential regressions of quantity of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) in remaining mass through the decomposition of *Spathodea campanulata* leaves in three locations on volcanic (Perchas), karst (Pugnado), and alluvial (Cibuco II) geological substrates within the subtropical moist forest life zone of Puerto Rico. Time of decomposition ranged from 129 to 255 days for K_{ALL}, 16 days for K_{16}, and 51 to 255 or 129 days for K_L (see methods). No significance (NS) is for $p > .05$. Empty cells correspond to NS relationships. The unit for K's is 1/day. Some values were rounded.

Location (element)	K_{16}	T (n)	p	K_L	T (n)	p	K_{ALL}	T (n)	p
Perchas ($N_{cquantity}$)	NS			−0.004	2.6 (11)	.0307	−0.003	6.3 (31)	.0001
Cibuco II ($N_{quantity}$)	NS			−0.01	4.3 (12)	.0016	−0.004	3.6 (32)	.0010
Pugnado ($N_{quantity}$)	NS			NS			−0.005	4.1 (31)	.0003
Perchas ($P_{quantity}$)	−0.01	4.5 (20)	.0003	NS			−0.01	7.8 (32)	.0001
Cibuco II ($P_{quantity}$)	−0.05	5.0 (20)	.0001	−0.01	3.8 (11)	.0046	−0.003	5.4 (31)	.0001
Pugnado ($P_{quantity}$)	−0.03	4.1 (19)	.0121	NS			−0.01	4.4 (29)	.0002
Perchas ($K_{quantity}$)	−0.17	4.6 (20)	.0002	NS			−0.17	5.4 (31)	.0001
Cibuco II ($K_{quantity}$)	−0.22	4.5 (20)	.0003	−0.01	3.1 (11)	.0126	−0.22	5.6 (31)	.0001
Pugnado ($K_{quantity}$)	−0.20	4.6 (19)	.0003	NS			−0.20	4.8 (29)	.0001
Perchas ($Ca_{quantity}$)	NS			NS			−0.01	8.0 (31)	.0001
Cibuco II ($Ca_{quantity}$)	NS			−0.01	4.1 (11)	.0027	−0.01	6.0 (31)	.0001
Pugnado ($Ca_{quantity}$)	−0.01	2.0 (19)	.0587	NS			−0.01	7.0 (29)	.0001
Perchas ($Mg_{quantity}$)	−0.06	5.1 (20)	.0001	NS			−0.01	4.8 (31)	.0001
Cibuco II ($Mg_{quantity}$)	−0.04	3.2 (20)	.0047	−0.01	3.6 (11)	.0055	−0.01	4.6 (31)	.0001
Pugnado ($Mg_{quantity}$)	−0.06	5.5 (19)	.0001	NS			−0.01	4.6 (29)	.0001

Table A5
Slopes (K_{16}, K_L, and K_{ALL}), t statistic (T), number of samples (n), and significance (p) of exponential regressions of concentration (conc) of aluminum (Al), iron (Fe), manganese (Mn), and sodium (Na) in remaining mass, through the decomposition of *Spathodea campanulata* leaves in three locations on volcanic (Perchas), karst (Pugnado), and alluvial (Cibuco II) geological substrates within the subtropical moist forest life zone of Puerto Rico. Time of decomposition ranged from 129 to 255 days for K_{ALL}, 16 days for K_{16}, and 51 to 255 or 129 days for K_L (see methods). No significance (NS) is for $p > .05$. Empty cells correspond to NS relationships. The unit for K's is 1/day. Some values were rounded.

Location (element)	K_{16}	T (n)	p	K_L	T (n)	p	K_{ALL}	T (n)	p
Perchas (Al_{conc})	NS			0.01	3.7 (11)	.0049	0.01	8.4 (31)	.0001
Cibuco II (Al_{conc})	0.09	8.8 (20)	.0001	0.004	3.9 (11)	.0039	0.01	8.4 (31)	.0001
Pugnado (Al_{conc})	NS			NS			0.01	4.9 (29)	.0001
Perchas (Fe_{conc})	NS			0.01	3.7 (11)	.0049	NS		
Cibuco II (Fe_{conc})	0.19	13.2 (20)	.0001	0.005	3.9 (11)	.0035	0.01	8.0 (31)	.0001
Pugnado (Fe_{conc})	NS			NS			0.01	3.9 (29)	.0005
Perchas (Mn_{conc})	NS			0.01	4.6 (11)	.0013	0.01	7.9 (31)	.0001
Cibuco II (Mn_{conc})	0.14	5.0 (20)	.0001	0.004	3.5 (11)	.0070	0.01	7.0 (31)	.0001
Pugnado (Mn_{conc})	0.05	2.1 (19)	.0548	NS			0.01	4.8 (29)	.0001
Perchas (Na_{conc})	−0.06	3.7 (20)	.0017	NS			NS		
Cibuco II (Na_{conc})	−0.08	3.6 (20)	.0019	NS			−0.01	3.2 (31)	.0036
Pugnado (Na_{conc})	−0.08	3.3 (19)	.0045	0.01	3.5 (10)	.0085	−0.003	2.1 (29)	.0492

Table A6
Slopes (K_{16}, K_L, and K_{ALL}), t statistic (T), number of samples (n), and significance (p) of exponential regressions of quantity of aluminum (Al), iron (Fe), manganese (Mn), and sodium (Na) in remaining mass, through the decomposition of *Spathodea campanulata* leaves in three locations on volcanic (Perchas), karst (Pugnado), and alluvial (Cibuco II) geological substrates within the subtropical moist forest life zone of Puerto Rico. Time of decomposition ranged from 129 to 255 days for K_{ALL}, 16 days for K_{16}, and 51 to 255 or 129 days for K_L (see methods). No significance (NS) is for $p > .05$. Empty cells correspond to NS relationships. The unit for K's is 1/day. Some values were rounded.

Location (element)	K_{16}	T (n)	p	K_L	T (n)	p	K_{ALL}	T (n)	p
Perchas ($Al_{cquantity}$)	NS			NS			NS		
Cibuco II ($Al_{quantity}$)	0.08	6.7 (20)	.0001	NS			NS		
Pugnado ($Al_{quantity}$)	NS			NS			0.01	2.5 (29)	.0186
Perchas ($Fe_{quantity}$)	NS			NS			NS		
Cibuco II ($Fe_{quantity}$)	0.17	11.5 (20)	.0001	NS			NS		
Pugnado ($Fe_{quantity}$)	NS			NS			NS		
Perchas ($Mn_{quantity}$)	NS			NS			NS		
Cibuco II ($Mn_{quantity}$)	−0.04	3.2	.0047	−0.01	3.6 (11)	.0055	−0.01	4.6 (31)	.0001
Pugnado ($Mn_{quantity}$)	NS			NS			0.004	2.1 (29)	.0431
Perchas ($Na_{quantity}$)	−0.08	4.4 (20)	.0004	NS			−0.08	3.8 (31)	.0007
Cibuco II ($Na_{quantity}$)	−0.09	3.6 (20)	.0022	−0.02	2.5 (11)	.0351	−0.08	3.7 (31)	.0009
Pugnado ($Na_{quantity}$)	−0.14	4.1 (19)	.0008	NS			−0.14	2.7 (29)	.0107

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.07.059.

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