

Soil Chemistry Modulates the Stoichiometry of Puerto Rican Novel Forests Dominated by *Spathodea* *campanulata* on Alluvial and Karst Substrates

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Cover Photograph: Group of highschoolers who harvested *Spathodea campanulata* trees to study its allometry. On the felled tree stem (left to right) are the authors, Oscar Abelleira Martínez and Ariel E. Lugo, and Carlos Torrens, who felled the tree with Carlos Estrada (extreme right on the ground). On the extreme left is Professor Josefina Arce of the University of Puerto Rico and co-principal Investigator of the National Science Foundation grant that funded the study. Photograph © La Alianza para el Aprendizaje de Ciencias y Matemáticas (AlACiMa).

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Soil Chemistry Modulates the Stoichiometry of Puerto Rican Novel Forests Dominated by *Spathodea campanulata* on Alluvial and Karst Substrates

Ariel E. Lugo^{1,2,*} and Oscar J. Abelleira Martínez³

Abstract - We studied the stoichiometry of 6 forest stands dominated by *Spathodea campanulata* (African Tulip Tree; hereafter *Spathodea*) on alluvial ($n = 3$) and karst ($n = 3$) substrates in the north-central region of Puerto Rico. The stands were on lands previously used for *Saccharum officinarum* (Sugar Cane) cultivation, subsistence agriculture, and grazing, and are representative of novel forest emergence and secondary succession in the study region. The functioning of these novel forests is poorly understood, and we sought to improve our understanding by studying the stoichiometry of forest stands in relation to substrate characteristics. Specifically, we were interested in any differences between the stoichiometry of canopy leaves, litterfall, and standing-litter forest components on alluvial and karst geological substrates, and the role of soil chemistry on regulating the stoichiometry of forest components. We also explored which stoichiometric attributes of *Spathodea* contribute to its role as a pioneer species in novel Puerto Rican forests and how ecosystem-level structure and processes vary with the stoichiometry of trees and soils. On each site, we established line-transects where we collected (1) 5 soil-core samples at 0–15 cm depth and another 5 at 15–30 cm depth for bulk density and chemical analyses; (2) adult fresh *Spathodea* green leaflets from the top of the forest canopy; (3) recently fallen and fresh yellow *Spathodea* leaves, representative of senesced leaves; (4) litterfall for almost 2 years; and (5) standing litter in July 2005 and March 2006. We chemically analyzed all vegetation and soil samples for total carbon, nitrogen, and sulfur, and concentrations of aluminum, calcium, iron, potassium, magnesium, manganese, phosphorus, sodium, and sulfur and estimated molar element ratios (hereafter, element ratios) for all samples. We also measured ash concentration in plant samples and loss on ignition on soil samples. Our results show a significant influence of geological substrate type and soil properties on stoichiometric relationships among the sampled forest ecosystem compartments and fluxes. Variations in soil aluminum, calcium, nitrogen, and phosphorous content combined with soil pH variation among sites exerted an influence on the stoichiometry of canopy leaves, litterfall, and standing litter, more so than geological substrate type. Discriminant function analysis of stoichiometric ratios of soils and forest components revealed that sites were clustered according to substrate type except for 1 site, Juan Nieves, that presented distinct soil properties and consequent element ratios of forest components. The onset of flowering coincided with peaks on carbon content and spikes of the C:N ratio in adult leaves. Peaks of phosphorus and nitrogen concentration, and peaks in the ratios of C:N and C:P, in adult leaves coincided with leaf expansion following leaf drop (younger leaves with high ratio of area:mass). The

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ratios of C:N and C:P in standing leaf litter tended to be higher for *Spathodea* senesced leaves, reflecting translocation, and lower for fragmented leaves, reflecting decomposition. The retranslocation percent for phosphorus (28% vs 44%) and nitrogen (39% vs 47%) was higher on *Spathodea* leaves on stands on alluvial vs karst substrate. Nitrogen and phosphorus retranslocation reached a peak rate coinciding with a peak in their concentrations in adult leaves. Element ratios of C:P, C:N, N:P, and Ca:P in *Spathodea* adult leaves, in litterfall and standing litter differed among sites on alluvial and karst substrates due to differences in these element ratios in the soil compartment. Sites on karst were more efficient in retaining phosphorus relative to fallen *Spathodea* leaf mass, but no differences were observed for other elements. All sampled forest compartments tended to have higher ratios of N:P and C:P at karst than alluvial sites, but the magnitude of those element ratios were low compared to those of historic successional and mature forests. The storage to 30 cm depth of soil nitrogen, phosphorus, and calcium correlated negatively with rates of *Spathodea* and total leaf-litter fall (leaffall; nitrogen and phosphorus), total litterfall rates (phosphorus and nitrogen), rates of calcium and phosphorus return in leaffall (nitrogen and calcium, respectively), and phosphorus storage to 30 cm depth (calcium). Soil pH correlated with soil element concentrations, soil element ratios, element ratios of *Spathodea* adult leaves, element ratios of *Spathodea* leaffall, element ratios of fragmented leaves in standing litter, and soil element storage of carbon, calcium, aluminum, iron, manganese, and phosphorus to a depth of 30 cm. These results illustrate a tight coupling between soil and forest compartments and fluxes of elements, with little nutrient limitations to the growth of *Spathodea* stands. However, *Spathodea* stands at karst sites are limited in phosphorous relative to those on alluvium. Our results also show that novel *Spathodea* forests are among the tropical forests subject to the lowest nutrient limitations on processes related to tree growth and standing-litter biomass accumulation, especially on alluvial substrates. Soil properties, including pH, are better predictors of stoichiometric differences in ecosystem structure and fluxes from canopy to soil than geological substrate type among novel *Spathodea* forests in Puerto Rico.

Introduction

Like other Caribbean islands, the forests of Puerto Rico have undergone a dramatic transformation in both land cover and species composition (Lugo and Helmer 2004). Land-cover changes preceded the species transformation, as the island was deforested when its human population expanded, used the land for agricultural purposes, and exploited existing forests as a source of fuelwood. At the turn of the 20th century, Murphy (1916) estimated that at the rate of wood consumption that he observed, the remaining forest area could supply fuelwood for only 12 years. A forested island at the time of its discovery by Europeans, Puerto Rico reached a historic low forest cover of 6% in the 1940s (Birdsey and Weaver 1982). After that low point, large-scale land abandonment, concentration of population in cities, urbanization, industrialization, and intensive use of fossil fuels in place of fuelwood resulted in the emergence of secondary forests on a landscape that had been highly degraded by erosion because of agricultural overuse and exposure of soils to heat, wind, and rain.

At the peak of agricultural activity, about half of the agricultural soils in Puerto Rico had lost over 75% of their topsoil (Picó 1969). This level of change in soil structure and fertility influenced forest regeneration on abandoned agricultural lands and resulted in secondary forests emerging from successional pathways that

were contingent on the land-use history, climate, geological substrate, and spatial characteristics of the site (Chinae 2002, Helmer et al. 2018, Lugo and Helmer 2004, Thompson et al. 2002). Periodic island-wide forest inventories established the differences in species composition between forest lands that escaped deforestation and the secondary forests that emerged after agricultural land abandonment (Birdsey and Weaver 1982, Brandeis and Turner 2013, Brandeis et al. 2007, Franco et al. 1997, Marcano Vega 2017). Notably, native species, with a few exceptions, failed to pioneer the post-agricultural succession, and naturalized tree species did so instead thereby becoming dominant in the emerging forests that are prevalent in the current Puerto Rican landscape (Martinuzzi et al. 2013). Out of the more than 100 introduced tree species that have become naturalized in Puerto Rico (Francis and Liogier 1991), *Spathodea campanulata* P. Beauv. (African Tulip Tree; hereafter *Spathodea*) became the most dominant tree in Puerto Rico (Fig. 1) after its introduction at the beginning of the 20th century. *Spathodea* is a pioneer species native to equatorial Africa, where it ranges from the lowlands to ~1200 m elevation in moist to wet conditions, often dominating riparian forests (Francis 2000).

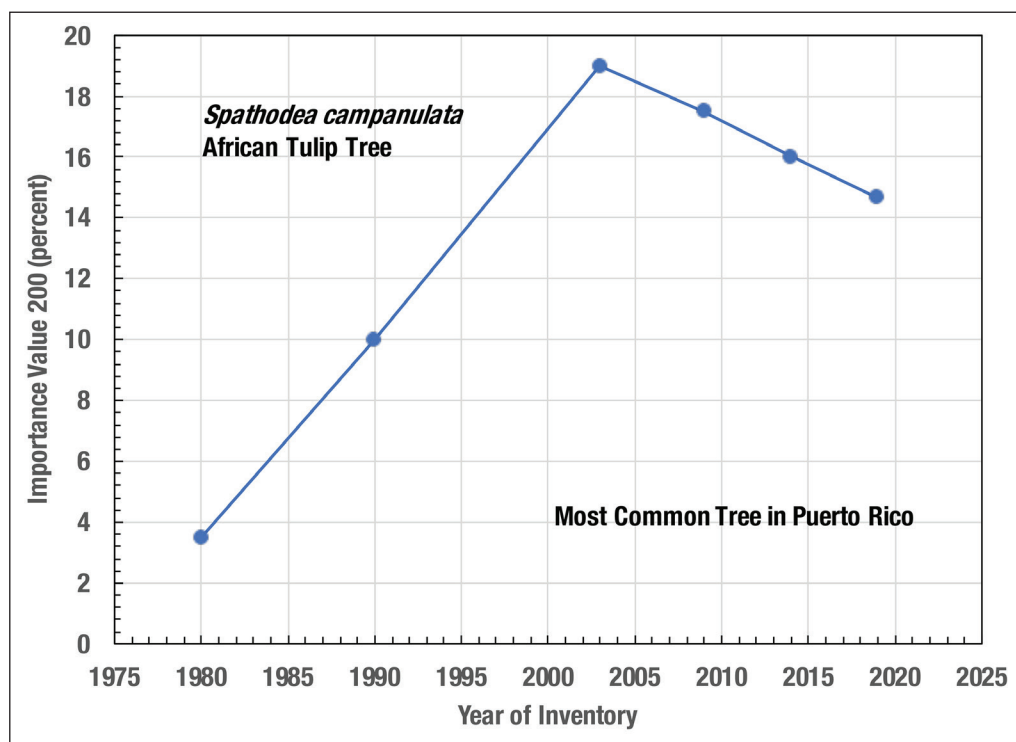


Figure 1. Importance Value-200 index of *Spathodea campanulata* among all species tallied in island wide forest inventories of Puerto Rico. The index, which adds to 100, is based on the relative basal area and relative density of the species with a minimum diameter at breast height of ≥ 12.5 cm. Data are from Birdsey and Weaver (1982), Franco et al. (1997), Brandeis et al. (2007), Brandeis and Turner (2013), Marcano Vega (2019) and H. Marcano Vega (USDA Forest Service, International Institute of Tropical Forestry, Río Pedras, PR, USA, unpubl. data from after Hurricane María).

Human agency is responsible for the presence of secondary forests dominated by naturalized tree species. However, all other aspects of their functioning are outside of anthropogenic control (Higgs 2017). Such forests are termed novel forests (Hobbs et al. 2006) and represent a forest type with ascending representation on landscapes throughout the world (Ellis 2015). Although novel forests on the continental tropics are dominated by native species, introduced tree species that have become naturalized dominate novel forests in Puerto Rico and the Caribbean islands (Lugo et al. 2020). In Puerto Rico, Martinuzzi et al. (2013) mapped novel forests and showed that they cover most of the island. Brandeis et al. (2009) demonstrated that novel forests in Puerto Rico respond to climatic controls as do historic forests, and Erickson et al. (2014) showed that novel forests had nutritionally enriched loose-litter compartments at comparatively higher levels than historical forests. There is a growing body of research related to the ecosystem structure and species composition of novel forests, but much less work has been conducted on the ecosystem function and process rates of these forests and how they compare to historic forests in Puerto Rico (Martinuzzi et al. 2013).

In the Archipelago of Puerto Rico, *Spathodea* stands grow on a variety of soil types on volcanic, alluvial, and karst geological substrates in the moist and wet regions (Abelleira Martínez 2019, Abelleira Martínez et al. 2010, Helmer et al. 2018). These geological substrates differ in the physical and chemical properties of soils that derive from the local parent materials and overlay the substrates, in the slopes of the terrain (e.g., 0° on alluvial and $>0\text{--}70^\circ$ on karst and volcanic substrates), and in flooding regime (e.g., severe on alluvial, moderate on karst, and none on volcanic) amongst other factors that affect tree growth and forest-ecosystem function (Beinroth et al. 2003, Gould et al. 2017, Miller and Lugo 2009, Monroe 1976). Alluvial and karst substrates in northern Puerto Rico lie near each other and share similar climate, disturbance regime, land-use history, and soil-weathering processes. These conditions provide the opportunity to evaluate the effects that geological substrate type and the physical and chemical properties of soils may have on the ecosystem functioning of novel forests. They also provide a glimpse of the ecosystem services that novel forests provide and insight as to whether they vary according to the heterogeneous geology of Puerto Rico.

Abelleira Martínez (2009) contrasted the ecological attributes of *Spathodea* novel forests on volcanic, alluvial, and karst geological substrates in north-central Puerto Rico. He found significant differences in understory tree species composition, litterfall rates, and seasonality among sites on alluvial and karst substrates, despite similar climate and dominant species (Abelleira Martínez 2010, 2011; Abelleira Martínez et al. 2010). A higher frequency of periodic flooding resulted in higher bi-weekly litterfall rates and annual litterfall mass on *Spathodea* stands on alluvial compared to karst sites, suggesting geological substrate can modify ecosystem process rates and function of novel forests (Abelleira Martínez 2011). Given the expanding global importance of novel forests and the lack of understanding of their ecological functioning, we further explored the effect of geological substrate type on the ecosystem function of novel *Spathodea* forests with a particular focus

on how the stoichiometry of forest compartments vary with the chemical properties of soils. We asked the following 3 questions:

- (1) Are there any differences between *Spathodea* stands on alluvial and karst substrates in terms of the stoichiometry of forest ecosystem compartments of canopy foliage, standing litter, and soil, and in fluxes of litterfall?
- (2) What chemical characteristics of soil are related to the stoichiometry of compartments of canopy foliage, standing litter, and litterfall fluxes on *Spathodea* stands?
- (3) How do forest ecosystem-level structure and processes vary with the stoichiometry of canopy foliage and standing-litter compartments, litterfall fluxes, and soils?

We expected that the elemental composition and molar ratios of canopy foliage, litterfall, and standing-litter components of *Spathodea* stands would vary according to differences in soil chemistry among alluvial and karst geological substrates that provide the parent material for these soils. We also expected that differences in the molar ratios of elements, especially of C:N, C:P, and N:P, which indicate constraints to plant growth, would vary among soils on alluvial and karst substrates. We expected higher C:N, C:P, and N:P in soils, canopy foliage, litterfall, and standing litter components of *Spathodea* forest stands on karst compared to alluvial sites due to higher nutrient (i.e., nitrogen and phosphorus) availability in the deep, fertile soils found on flat alluvial valleys and from inputs from flooding by major rivers (i.e., >4th order) over soils on alluvial substrates. We expected that higher values of C:N, C:P, and N:P in canopy foliage, litterfall, and standing-litter compartments would be associated with lower primary productivity rates, and hence lower stored dry mass per compartment. We therefore expected that higher C:N, C:P, and N:P in soil and forest compartments would be related to higher litterfall and standing-litter mass, and higher basal area (m²/ha) and biomass (Mg/ha) values that have been previously estimated for these stands (Abelleira Martínez et al. 2010, Lugo et al. 2011). We were also interested in exploring how elemental concentrations and ratios varied along the progression from the soil to canopy foliage, where most nutrients from root uptake are transported to and utilized, to return in litterfall and standing-litter components atop the forest floor that feedback into the soil through decomposition by microorganisms. In this study, we highlight the stoichiometric attributes of *Spathodea* that contribute to its role as a pioneer species in novel Puerto Rican forests. We shed light on the importance of edaphic factors on forest functioning and compare the stoichiometry of novel and historic tropical forests developing under a variety of climatic and edaphic conditions.

Methods

Study sites

The study was conducted on the north-central lowlands of Puerto Rico where we located 6 forest stands, 3 each on karst and alluvial substrates (Fig. 2). All stands were dominated by *Spathodea*. We identified the sites as Cibuco I (CI),

Cibuco II (CII), Paso del Indio (PI), Ollas y Calderas (OC), Pugnado (P), and Juan Nieves (JN). The first 3 were located on alluvial substrates, and the other 3 on karst substrates. Our study sites have a similar climate as they are all in the subtropical moist forest life zone sensu Holdridge (1967). The mean annual rainfall and mean annual temperature for the period 1971–2000 in nearby climatic stations (Fig. 2) varied, respectively, from 1443 to 1905 mm and from 21.5 to 25 °C (Abelleira Martínez 2009).

All stands were young forests with high basal areas, low tree species richness, and high dominance of nonnative tree species (Table 1). Tree species richness was

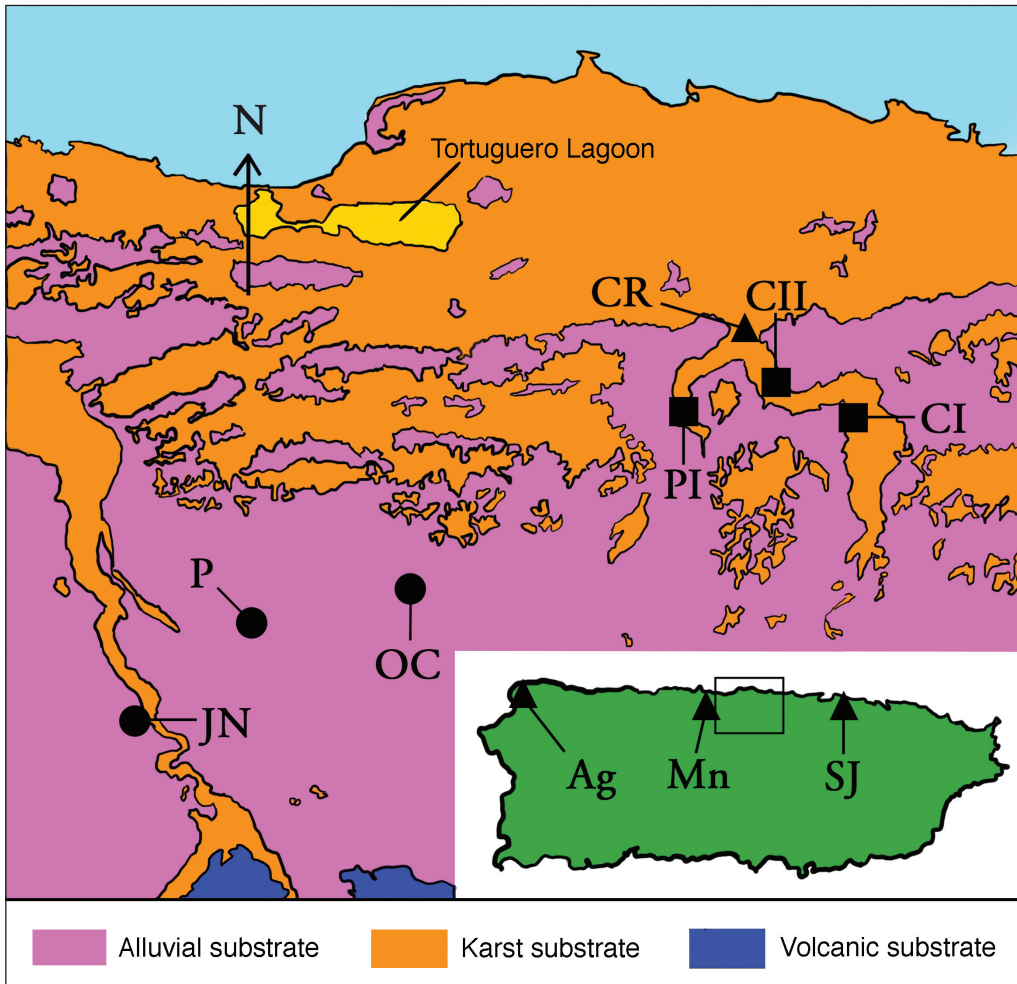


Figure 2. Map with the location of study sites, climate stations (Aguadilla [Ag], Manatí [Mn], and San Juan [SJ]), and Cibuco river discharge station (CR) in the north-central portion of Puerto Rico (Abelleira Martínez 2009). The identification of sites is: Cibuco I (CI), Cibuco II (CII), Paso del Indio (PI), Ollas y Calderas (OC), Pugnado (P), and Juan Nieves (JN). The box in the insular map delimits the study area. Tortuguero Lagoon is in yellow. The orange background is karst substrate, purple is alluvial substrate, and blue is volcanic substrate at higher elevation.

higher among small trees compared to large, canopy trees, and karst sites had higher tree species richness and lower dominance of *Spathodea* than alluvial sites. Soils in the karst sites were not exclusively derived from karst substrates and were mixed with sedimentary materials from the uplands (Bawiec et al. 2001). Alluvial sites had 0% slopes and karst sites were on 7–50% slopes. The soil orders and soil series for each of the study sites were as follows: CI = Inceptisol, Coloso silty clay; CII = Mollisol, Toa silty clay loam; PI = Mollisol, Toa silty clay loam; OC = Mollisol San Sebastian gravel clay; P = Mollisol San Sebastian gravel clay; and JN = Entisol San Germán gravel clay loam (Tables 1, 2). Acevido (1982) studied and mapped the soils of the area where we conducted our study and noted that the series aligned topographically with Coloso at a lower position than Toa in floodplains, while San Sebastián and San Germán are upland soils found on karst depressions; all are considered fertile soils (Table 2).

We ordered our study sites by flooding regime based on the topographic position of the soil series (Acevido 1982), the topographic position of stands, and our field observations and measurements. Starting with the longest hydroperiod, the ranking was: PI, CI, CII, JN, P, and OC; we never observed any flooding at OC. The deepest flooding we measured was 0.7 m at P, but the hydroperiods were longer in the floodplains (CI, CII, and PI), whereas flooding was shallow with sharp peaks of deeper water at P because the site is on a depression that drains through a ~30-cm-

Table 1. Ecological attributes of *Spathodea campanulata* forests of this study and attributes of the study sites. Cibuco I (CI), Cibuco II (CII), and Paso del Indio (PI) are on alluvial substrates, while Ollas y Calderas (OC), Pugnado (P) and Juan Nieves (JN) are on karst substrates. Data are from Abelleira Martínez (2009). Age corresponds to when the samples were collected. Large, small, and juvenile trees correspond to trees with a diameter at breast height of >10 cm, >2.5 to 10 cm, and <2.5 cm, respectively.

Attribute	Study site					
	CI	CII	PI	OC	P	JN
Number of large tree species	4	3	3	6	9	8
Basal area (m ² /ha)	73	99	80	55	72	37
Age (yr)	24	38	24	31	24	38
Elevation (m)	10	10	10	140	170	30
Slope (%)	0	0	0	25–50	7–15	8–15
Soil order	Inceptisol	Mollisol	Mollisol	Mollisol	Mollisol	Entisol*
Soil series	Coloso	Toa	Toa	San Sebastián	San Sebastián	San Germán
Number of large tree species	4	3	3	6	9	8
Number of small tree species	14	5	6	15	15	18
Number of juvenile tree species	8	19	14	26	24	33
% introduced large tree species	100	67	67	50	22	25
% introduced small tree species	29	40	17	20	20	11
% introduced juvenile tree species	13	37	21	19	17	9
% dominance of <i>Spathodea</i>	90	91	92	74	78	82

*The San Germán series was reclassified from an entisol (Beinroth et al. 2003) to a mollisol (Muñoz et al. 2018) during the time span between data collection and reporting.

wide sinkhole into the subsoil, and at times the sinkhole is blocked by organic matter, resulting in sharp flooding peaks that remain while the water filters through. In contrast, flooding at alluvial sites covered a larger proportion of the site due to a flat slope and berms next to the river channels that kept surface water contained on the site. Flood waters were stagnant in some sections of the forests but not in others where we observed sheet flow.

Field sampling

During July 2005, we collected 5 soil samples from along a 100-m transect within each forest stand. At each point, we made 2 borings with a soil corer with a diameter of 4.79 cm. One boring was to 15 cm depth, and the other was between 15 and 30 cm depth. We oven dried all the soil within each core at 100 °C to constant weight to determine the bulk density in g/cm³. We conducted additional sampling at the 2 depths to collect soil samples for chemical analysis. We placed these samples in cloth bags and air dried them in the laboratory prior to chemical analysis. The presence of rocks in some karst locations reduced the number of samples, particularly of soil from the 15–30-cm depth cores. We measured soil pH in water and KCl solutions. We made 55 bulk-density determinations, 54 pH measurements, and collected 54 soil samples for chemical analysis.

We collected adult *Spathodea* leaves from the top of the forest canopy on a bi-weekly basis between March 2006 and May 2007 at all study sites. On each sampling date, we used a slingshot and rocks from each site to down 18 adult

Table 2. Attributes of the soil series encountered in this study (from Acevido [1982] except for taxonomic classification, from Muñoz et al. [2018]).

Soil series	Depth (cm)	Clay <2 mm (%)	Moist bulk density (g/cm ³)	Soil reaction pH	Organic matter (%)	Depth to rock (cm)	Taxonomic classification
Coloso	0–18	40–55	1.30–1.35	5.6–7.3	2–4	>152	Fine, mixed, active, isohyperthermic Vertic Dystrudepts
	18–152	45–55	1.25–1.30	5.6–7.3			
Toa	0–46	28–40	1.35–1.55	5.1–7.3	1–4	>152	Fine, mixed, active, isohyperthermic Fluventic Hapludolls
	46–160	29–35	1.35–1.50	5.1–7.3			
San Sebastián	0–15	45–50	1.35–1.50	7.4–8.4	1–4	>152	Clayey-skeletal, carbonatic, isohyperthermic Calcic Argiudolls
	15–140	45–60	1.40–1.50	7.4–8.4			
San Germán	0–8	27–35	1.40–1.50	7.4–8.4	2–4	13–36	Clayey-skeletal, mixed, superactive, isohyperthermic Lithic Haplustolls
	8–25	27–35	1.40–1.50	7.4–8.4			

green leaflets from 6 randomly selected trees per site ($n = 3$ leaflets per tree). We did not include the rachis of the compound leaves in the sample and discarded leaflets that were broken or had evidence of herbivory, pathogens, or senescence. Adult green leaves were less available on dates (June–July 2006) corresponding to near-complete leaf loss and canopy opening (Abelleira Martínez 2011), resulting in a total of 25–29 adult leaf collections per site, which we took to the laboratory for chemical analysis.

We collected senesced yellow *Spathodea* leaflets from the forest floor at the time of litterfall collections on dates that corresponded to canopy leaf senescence and fall. We took special care to collect 18 yellow leaflets that were fresh and recently fallen, with no signs of withering, herbivory, pathogens, breakage, or drying (i.e., brown sections). These collections, which totaled 120 samples for chemical analysis, were representative of senesced adult leaves at the time of leaf excision.

We made litterfall collections on 44 occasions at the 6 study sites between 10 January 2006 and 31 October 2007 (659 days). Each sampling consisted of collection of all materials inside 6 litterfall baskets per site, and the time interval between collections was 2 weeks. The square baskets were constructed of 1-mm-mesh screen, elevated at 1 m above the forest floor, had an area of 0.25 m², and were randomly placed along line transects on each site (Abelleira Martínez 2011). Details of the methods used for litterfall measurements and results for mass fall from the first year of collections were reported by Abelleira Martínez (2011). We transported the content of each basket individually to the laboratory for processing, including chemical analysis. We separated litterfall materials into leaf, fine wood, reproductive parts, and miscellaneous components in the laboratory. We separated leaf components into *Spathodea* leaves and leaves of other species and further separated *Spathodea* leaves into brown and green leaves. This separation was made to distinguish potentially senesced from fresh leaf-litter fall (leaffall), as the differences in these colors were readily apparent and were indicative of mature (i.e., green) *Spathodea* leaves and senesced (i.e., yellow) leaves that turn brown in color. There were 1584 samples available for sorting and chemical analysis in the laboratory.

We conducted standing loose-litter collections in July 2005 and in March 2006 at 5 random points along a 100-m transect on each study site. On each point, we collected paired samples using a 0.25 m by 0.25 m (0.0625 m²) frame. We haphazardly located the frame each time and collected all the litter within the frame. We placed each category of loose litter (below) in a separate paper bag for transport to the laboratory. The date of standing-litter sampling in summer (i.e., July) coincided with full canopy opening of the deciduous *Spathodea* forest canopy in north-central Puerto Rico (Abelleira Martínez 2011). We focus on results from the July 2005 sampling date because it contains all the *Spathodea* leaffall that is produced (and shed) within a year and is therefore more representative of primary productivity rates and the chemical content of leaves that undergo the full process of leaf development from formation to maturity and then to senescence, including nutrient retranslocation and excision. Since *Spathodea* leaves decompose in a year or less,

the sampling date of July exclusively contains all *Spathodea* leaf material formed within the last growing season (i.e., a year; Lugo and Abelleira Martínez 2018).

We separated loose-litter collections in 2005 in the field into fine wood (hereafter, wood), fragmented leaves, recently fallen leaves, old leaves, humus, and miscellaneous. We further classified recently fallen and old leaves as *Spathodea* leaves and leaves of other species. We separated loose litter collected in 2006 in the laboratory into *Spathodea* leaves, other species of leaves, wood, flowers and fruits, and detritus. Detritus was the leftover small particle materials after the separation of the main litter compartments in the laboratory. Humus was present at the litter–soil interface, had to be collected by hand, as done in 2005, and was organic rather than particulate. There were 120 loose-litter collections in the field, resulting in 840 samples available for chemical analysis. However, not all categories were found in all samples, resulting in fewer samples analyzed chemically.

We measured the leaf-area index (LAI) of the 6 *Spathodea* stands using a Decagon Accupar LP-80 leaf-area meter (Meter Group, Pullman, WA, USA). We collected LAI samples between 9 a.m. and 12 p.m. on overcast or completely sunny days during February and March 2006. On each site, we collected 8 inner canopy readings of photosynthetic active radiation along the same line transects where litterfall baskets were placed. We estimated LAI based on the difference in PAR between readings taken in the inner canopy and in clearings outside the forest canopy immediately (i.e., <5 minutes) before conducting sampling on the line transects inside the forest stands (Meter Group, Inc. 2024). The time of LAI sampling coincided with full canopy closure of *Spathodea*'s fully deciduous canopy in the climate of north-central Puerto Rico (Abelleira Martínez 2011).

Laboratory analyses

We separated the contents of each litterfall basket in the laboratory into the following components: wood, miscellaneous, flowers and fruits, leaves of species other than *Spathodea*, and leaves of *Spathodea*, which were subclassified by appearance into brown and green leaves. We included the rachis of the compound *Spathodea* leaf with the woody litter and its leaflets, in the leaf category. The 6 litterfall categories, resulted in a possible 9504 samples for chemical analysis. However, missing collections at PI, insufficient sample for chemical analysis, and the fact that not all litterfall categories occurred every time the litterfall was collected, reduced the number of samples that were analyzed chemically.

After sorting, we oven-dried all samples of adult *Spathodea* leaves, recently fallen *Spathodea* yellow leaves, litterfall, and loose litter at 65 °C to constant weight, recorded their dry weight, and then ground them through a 20-mesh (0.85-mm mesh) sieve with a Wiley mill. We used the ground material for chemical analysis. We air-dried soil samples and passed them through a 20-mesh sieve prior to chemical analysis.

We assessed precision by analyzing duplicate samples every 10 determinations. To assess elemental recovery after extraction, we determined reference materials with known chemical composition in every batch of 40 samples. These

materials included *Prunus persica* (L.) Batsch (Peach) leaves (NIST-1547) and *Pinus* (pine) needles (NIST 1575a) obtained from the National Institute of Standards and Technology (Gaithersburg, MD, USA). The reference materials used in the total carbon, nitrogen, and sulfur determinations included *Nicotiana* (tobacco) leaves, orchard leaves, and *Medicago sativa* L. (Alfalfa) obtained from the LECO Corporation (St. Joseph, MI, USA). For soils, we utilized certified reference materials purchased from the LECO Corporation: Part No. 502-814, Part No. 502-309, Part No. 502-697, Part No. 502-308, and Part No. 502-062. In addition, we purchased other certified soil reference materials from Elemental Microanalysis (represented in the USA by EA Consumables, Marlton, NJ.), including, among others: Chalky Soil, Loamy Soil, Clay Soil, Silty Soil, Sandy Soil, Peat Soil, High Organic sediment, Medium Organic Soil, Low Organic Soil, and standard reference material Montana soil 2711.

Chemical analysis

We digested all samples using an open block digester and performed the elemental analyses using a Spectro Ciros ICP Emission Spectrophotometer (SPECTRO Analytical Instruments, Kleve, Germany; Isaac and Johnson 1998, Luh Huang and Schulte 1985). The analyses included aluminum, calcium, iron, potassium, magnesium, manganese, phosphorus, sodium, and sulfur. Extractions followed the method recommended by Luh Huang and Schulte (1985). Before analysis, we used concentrated HNO_3 , 30 % H_2O_2 , and concentrated HCl to digest the material. For the total carbon, total nitrogen, and total sulfur in soils and plant components analyzed before June 2007, we utilized the LECO CNS-2000 Analyzer at 1450 °C. For analyses after June 2007, we used the LECO TruSpec CN Analyzer (at 950 °C), and the LECO TruSpec S Analyzer (at 1450 °C). In both instruments, we used the dry-combustion method in a stream of ultrapure oxygen (99.99%; LECO Corp. 2003a, b; 2005a, b; 2008; 2009a).

We used the moisture factor to correct the chemical analysis results for each sample. We also determined ash (plant) or loss on ignition (LOI; on soil) by retrieving a representative subsample that was oven dried at 105 °C for 24 hours and determined the moisture-factor correction gravimetrically. We ignited the same sample in a muffle furnace at 490 °C for ~6–7 hours. The next day, we removed the samples from the muffle furnace and cooled them in a desiccator. We reweighed them after reaching room temperature with an analytical balance to obtain ash content, expressed in percent (Wilde et al. 1979). After 2009, we determined all the moisture-factor results (at 105 °C), LOI (soils at 490 °C), and ash (plant components at 490 °C) using the automated LECO Thermogravimetric Analyzer TGA701 (LECO Corp. 2009b).

We analyzed aluminum, calcium, iron, potassium, magnesium, manganese, sodium, phosphorus, carbon, sulfur, nitrogen, and ash in all samples. We analyzed a total of 1808 samples of litterfall from the 6 sites. For each site and date of collection, we separated and analyzed 6 components of litterfall: *Spathodea* green leaves, *Spathodea* brown leaves, non-*Spathodea* leaves, flowers and fruits, wood, and miscellaneous. We also chemically analyzed senesced *Spathodea* yellow

leaves from the forest floor when available. In addition, we chemically analyzed 161 samples of adult *Spathodea* leaves for concentration of carbon, sulfur, nitrogen, and ash and 67 samples for total element concentrations. We collected 278 litter samples and chemically analyzed 167 of them; the difference was due to excluding samples with insufficient material for chemical analysis. We chemically analyzed 60 soil samples.

Data analysis

We expressed concentration data in mg/g, percent, and mmol/kg, calculating the molar concentration by dividing the mg/g concentration by the molecular weight of the element. We used element molar concentrations to estimate molar element ratios (hereafter, element ratios) of collected vegetation and soil samples. For litterfall and leaffall calculation of element fluxes, we assigned a zero when the litterfall component did not appear on a sample for a particular collection. For element concentration data, we based the mean of each element on the measured values for each of the analyses conducted.

We estimated the retranslocation of nitrogen and phosphorus of canopy *Spathodea* leaves by subtracting the concentration in *Spathodea* yellow leaves collected from the ground from the corresponding concentration in adult canopy leaves. We expressed the resulting mg of element per gram dry weight retranslocated as a percentage of the element concentration in adult leaves.

We based the estimate of the mass or element content of standing loose litter on each site on the means for all sampling points by component. We made this estimate only for the 2005 loose-litter collections because dry-weight data for the 2006 loose-litter collections were unavailable. We expressed loose-litter concentration data in kg/ha. We converted the dry weight data for each litterfall component to litterfall rate in g/m²•day by dividing by 0.25 m² and the interval between collections in days. We based estimates of soil storage of mass or elements on the concentration of organic matter or individual elements multiplied by the soil bulk density and the depth of the soil layer. The mean pH was the arithmetic mean, which differed slightly from the log mean.

We statistically analyzed data using Excel spreadsheets (Microsoft Corp., Redmond, WA, USA) for basic statistics and StatPlus:mac Pro version 7.3.3.0 (AnalystSoft, Inc., Brandon, FL, USA) for testing the differences between mean values and performing discriminate function analysis (DFA) on values of elemental concentrations and molar ratios in selected compartments of soils, adult leaves, leaf-fall, and leaf-loose litter among alluvial and karst sites. We report the results for the DFA on element concentrations in the supplemental tables (see Supplemental File 1, available online at <https://www.eaglehill.us/CANAonline/suppl-files/C249-Lugo-s1>) but do not discuss them in the manuscript because the results for the molar element ratios yield the same patterns. We tested the data for normality with a variety of tests including the Shapiro–Wilk W test. If the data were normal, we used one-way ANOVA and post hoc comparison of means at $P \leq 0.05$. We used the Scheffe test to determine significantly different mean values. If the data were not normal, we log-transformed and tested them again for normality before performing

parametric tests. We analyzed data that were not normal (e.g., loose-litter and litter-fall data) with the Kruskal–Wallis non-parametric ANOVA test, using $P \leq 0.05$ for determining significance. For the DFA, we used the Wilk’s lambda for determining significance at $P \leq 0.05$. For the analysis of element ratios, we verified that the log transformation of data yielded the same results as non-transformed data, as suggested by Isles (2020), who recommended log-transforming large metadata datasets that are much more heterogeneous than ours.

We used linear regressions to evaluate relationships of *Spathodea* forest ecosystem structure (e.g., LAI, tree basal area, standing-litter biomass, *Spathodea* stem-wood biomass) and function (e.g., leaf and litterfall rates) to soil chemistry (pH, percent LOI, LOI mass, and percent clay). We used tree basal area and stem-wood biomass values from Abelleira Martínez (2011) and Lugo et al. (2011), respectively. We also regressed soil pH against the chemistry and stoichiometry of soil (including element storage), adult *Spathodea* leaves, *Spathodea* leaffall, and fragmented leaf litter.

We report results for 11 elemental concentrations and 17 element ratios on all sampled canopy leaves, litterfall, and standing loose-litter components, and soil. We focus our discussion on the element concentrations and element ratios most relevant for ecosystem function. We also focus on foliage components of canopy leaves (adult and senescent), and litterfall and standing loose-litter compartments, which constitute the plant parts where most processes relevant for ecosystem function occur (e.g., photosynthesis and transpiration) and therefore concentrate most elements that may be limiting for rates of ecosystem processes.

Results

All the mean ash and element-concentration data for soil, forest canopy foliage, and litterfall and standing loose-litter compartments by site are contained in Supplemental Tables S1 and S2, and corresponding data (except for soil) by date of collection are contained in Supplemental Table S3 (see Supplemental File 1).

Soils

The soils on all sites had low bulk density, but soils at alluvial sites were heavier than at karst sites (Table 3). The difference was mostly due to the low values in JN on karst, particularly in the soil from a depth of 15–30 cm (see Supplemental Table S1 in Supplemental File 1). Loss on ignition and concentrations of potassium, sodium, and especially magnesium were higher at alluvial sites (Table 3). The carbon and nitrogen content of soils at 0–15 cm depth were higher at karst sites, and pH was higher at karst sites for soils of the 2 sampled depths when combined. No significant difference was detected in phosphorus and calcium concentration at any depth, although concentrations of both elements tended to be higher at karst sites on both sampling depths. Most element concentrations decreased with depth except for aluminum and iron (Table 3; see also Supplemental Table S1 in Supplemental File 1). Among all sites, JN had high concentrations of soil phosphorus, manganese, iron, and aluminum, and higher concentrations of magnesium relative to other karst

Table 3. Mean element concentration data for soil, adult, and senesced *Spathodea campanulata* (Sc) leaves, and components of litter fall and loose litter of forests dominated by *Spathodea* on alluvial and karst substrates. Loss on Ignition for soil is reported under “Ash”. Soil pH and bulk density are also included. “**” indicate significant differences at $P \leq 0.05$. “-” indicate data were not available, or humus not found in alluvial sites. [Table continued on following 2 pages.]

Variable/ Substrate	C (%)	N (%)	S (%)	Al (mg/g)	Ca (mg/g)	Fe (mg/g)	K (mg/g)	Mg (mg/g)	Mn (mg/g)	Na (mg/g)	P (mg/g)	Ash (%)	pH in H ₂ O	pH in KCl	Bulk density (g/cm ³)
Soil 0–15 cm															
Alluvial	3.1*	0.30*	0.03	32.20	11.8	47.9	0.9*	8.40*	1.20	0.20*	0.80	16.8*	7.12	6.16	1.15*
Karst	5.5*	0.40*	0.04	34.70	38.6	48.9	0.7*	2.20*	1.30	0.10*	1.20	19.0*	7.33	6.65	0.92*
Soil 15–30 cm															
Alluvial	2.2	0.20	0.03	32.60	19.5	48.7	0.8*	8.40*	1.20	0.20*	0.70	15.2*	6.52	5.92	1.15*
Karst	3.7	0.30	0.03	36.10	33.5	51.0	0.7*	2.20*	1.20	0.10*	1.10	16.7*	7.04	6.32	0.92*
Sc adult leaves															
Alluvial	43.5	2.11*	0.36*	0.19	33.2*	0.10*	13.5	4.17	0.02*	0.18*	2.31*	11.2			
Karst	43.2	1.93*	0.33*	0.20	37.8*	0.08*	11.9	4.06	0.03*	0.11*	1.92*	11.5			
Sc senesced (yellow) leaves															
Alluvial	46.6	1.10*	0.47*	0.28	43.5*	0.15*	9.7*	4.54	0.02	0.63*	1.63*	13.4			
Karst	46.7	1.00*	0.40*	0.31	48.2*	0.12*	7.7*	4.28	0.09	0.25*	1.00*	14.0			
Sc brown leaffall															
Alluvial	47.1	1.60*	0.36*	0.35	41.8*	0.21*	5.5*	3.62	0.03*	0.41*	1.75*	12.4*			
Karst	47.0	1.52*	0.33*	0.36	49.0*	0.13*	4.8*	3.59	0.04*	0.28*	1.26*	13.4*			
Sc green leaffall															
Alluvial	48.4	2.14*	0.39	0.20*	31.1*	0.12*	9.3*	3.35	0.02*	0.39*	1.85*	11.9*			
Karst	48.0	1.95*	0.38	0.28*	40.5*	0.14*	7.6*	3.78	0.03*	0.25*	1.57*	13.1*			
Sc leaffall															
Alluvial	47.9*	1.79*	0.37*	0.30*	38.2*	0.18*	6.8*	3.53	0.02*	0.40*	1.78*	12.2*			
Karst	47.5*	1.66*	0.35*	0.34*	46.2*	0.14*	5.7*	3.65	0.03*	0.27*	1.36*	13.3*			
Other species leaffall															
Alluvial	49.2*	1.89	0.43*	0.36*	38.2*	0.19*	8.3*	3.26*	0.06*	0.70*	1.76*	12.3*			
Karst	50.7*	1.92	0.32*	0.30*	34.7*	0.13*	5.3*	3.03*	0.08*	0.32*	1.15*	10.8*			
Fine wood fall															
Alluvial	48.2	0.68*	0.11*	0.17	21.7*	0.09	8.1*	2.33*	0.01*	0.45*	2.09*	7.1			
Karst	48.6	0.75*	0.13*	0.19	24.9*	0.09	5.2*	2.14*	0.03*	0.31*	1.19*	7.3			

Table 3 continued.

Variable/ Substrate	C (%)	N (%)	S (%)	Al (mg/g)	Ca (mg/g)	Fe (mg/g)	K (mg/g)	Mg (mg/g)	Mn (mg/g)	Na (mg/g)	P (mg/g)	Ash (%)	pH in H ₂ O	pH in KCl	Bulk density (g/cm ³)
Flower and fruit fall															
Alluvial	49.9*	1.99	0.22	0.14	12.6	0.12	13.4*	2.41	0.02	0.29*	2.40*	6.7*			
Karst	50.6*	2.08	0.24	0.13	13.2	0.09	9.8*	2.30	0.04	0.24*	2.00*	5.9*			
Miscellaneous fall															
Alluvial	48.8*	2.31*	0.36	0.53	35.5	0.83	7.0*	3.13*	0.05	0.48*	2.38*	10.9			
Karst	49.4*	2.43*	0.35	0.50	37.0	0.55	5.6*	2.97*	0.05	0.34*	1.87*	10.8			
Loose litter 2005															
Sc recently fallen leaf litter															
Alluvial	46.8	1.40	0.46	1.12	31.4*	1.20	8.6	3.48	0.04	0.28	1.13	14.9			
Karst	45.2	1.50	0.44	3.11	37.8*	4.50	6.3	3.25	0.13	0.14	1.33	20.9			
Other species recently fallen leaf litter															
Alluvial	44.9	2.13	0.54	2.68	3.8	3.18	5.1	2.68	0.09	0.12	0.12	-			
Karst	50.4	1.61	0.27	1.19	29.4	0.50	4.7	1.80	0.06	0.52	0.58	-			
Sc old leaf litter															
Alluvial	44.3	1.53	0.32*	3.02	37.7*	3.77	3.3*	3.35	0.11	0.15	1.21	19.4			
Karst	43.0	1.47	0.24*	3.42	53.0*	4.43	1.7*	2.39	0.14	0.14	0.89	21.5			
Other species old leaf litter															
Alluvial	44.3	1.80	0.31	4.20	27.8	5.60	2.5	3.60	0.17	0.21	1.09	12.0			
Karst	50.4	1.60	0.25	0.81	39.5	0.62	1.31	2.88	0.06	0.15	0.62	12.6			
Fragmented leaf litter															
Alluvial	33.9*	1.73	0.21	10.70*	30.8*	15.60*	1.3*	3.80*	0.38	0.13	1.21	34.5*			
Karst	40.9*	1.89	0.22	6.70*	47.0*	9.60*	0.9*	1.80*	0.28	0.13	1.16	24.4*			
Fine wood litter															
Alluvial	47.4	0.74	0.11	3.53	13.0*	5.10	0.8*	1.50*	0.14	0.07*	0.67	12.2			
Karst	47.5	0.89	0.16	3.54	19.9*	5.20	1.4*	1.10*	0.13	0.13*	0.93	12.1			
Miscellaneous litter															
Alluvial	48.4	-	0.15	2.80	7.4	3.70	4.8	1.80	0.09	0.08	1.50	10.6			
Karst	52.1	-	0.15	0.20	5.4	0.20	9.8	1.16	0.004	0.118	0.28	3.7			

Table 3 continued.

Variable/ Substrate	C (%)	N (%)	S (%)	Al (mg/g)	Ca (mg/g)	Fe (mg/g)	K (mg/g)	Mg (mg/g)	Mn (mg/g)	Na (mg/g)	P (mg/g)	Ash (%)	pH in H ₂ O	pH in KCl	Bulk density (g/cm ³)
Humus															
Alluvial	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Karst	22.7	0.14	1.70	15.80	17.2	22.40	0.9	1.80	0.85	0.14	0.84	53.4			
Loose litter 2006															
Sc leaf litter															
Alluvial	41.9*	1.64	3.03*	2.92	41.4*	3.60*	4.0	3.58	0.10	0.33	1.85*	16.2			
Karst	43.6*	1.70	2.50*	1.93	54.5*	1.60*	3.3	3.95	0.06	0.25	1.27*	15.5			
Other species loose litter															
Alluvial	46.0	1.70	2.57	1.38	35.3	1.80	5.3*	3.80*	0.09	0.50*	1.50*	12.9			
Karst	47.0	1.90	2.05	2.12	35.1	1.90	3.0*	2.80*	0.09	0.30*	1.00*	12.0			
Fragmented leaf litter															
Alluvial	37.3*	1.90*	2.35	7.77	34.9*	11.00*	3.7*	4.80*	0.28	0.27*	1.74*	25.1*			
Karst	42.1*	2.20*	2.37	5.72	47.8*	5.80*	2.5*	2.90*	0.18	0.19*	1.46*	19.2*			
Fine wood litter															
Alluvial	44.5	1.00*	1.10*	2.70	19.6*	3.80	3.7	2.30*	0.10	0.25	1.50	10.4			
Karst	45.5	1.20*	1.30*	3.20	29.1*	3.69	2.7	1.60*	0.10	0.19	1.10	11.4			
Flower and fruit litter															
Alluvial	44.0	2.10	1.75	2.71	13.0	4.20	10.1	3.10*	0.11*	0.26	2.10	12.0*			
Karst	46.0	2.00	1.71	2.00	16.9	2.70	7.4	2.40*	0.06*	0.24	1.80	8.4*			
Detritus litter															
Alluvial	18.0*	1.10*	1.41*	20.80*	22.8*	32.40*	2.8*	6.90*	0.79*	0.20*	1.50	58.0*			
Karst	32.0*	2.00*	1.98*	14.30*	36.1*	17.20*	2.0*	2.30*	0.41*	0.17*	1.50	35.0*			

sites (see Supplemental Table S1 in Supplemental File 1). Calcium concentration was notably high on PI, OC, and P, and lowest on JN.

Differences in soil element ratios among sites (Table 4; see also Supplemental Table S4 in Supplemental File 1) were many, especially in soils from a depth of 0–15 cm. At the 0–15-cm depth, N:S, N:K, N:Mg, Ca:Mg, and Ca:K were higher at karst sites, and Mg:P was the only ratio that was higher at alluvial sites (Table 4). At the 15–30-cm depth, the same differences and patterns were found for N:K, N:Mg, Ca:Mg, and Mg:P only (Table 4). The stoichiometric ratios of soils at JN, especially at a depth of 0–15 cm, were distinct from all other sites and characterized by the lowest C:N, C:P, N:P, K:P, and Mg:P, and highest N:Ca. Among karst sites, N:Mg was lowest on JN, with a value closer to alluvial sites. When soil element ratios were subjected to DFA, we found that alluvial sites clustered together, and JN separated from the other 2 karst sites as an extreme outlier (Fig. 3; see also Supplemental Tables S5 and S6 in Supplemental File 1).

In the top 15 cm of soil, karst sites stored more nitrogen than alluvial sites, which stored more potassium, magnesium, and sodium than karst sites (Table 5; see also Supplemental Table S7 in Supplemental File 1). The differences among alluvial and karst soil-element storage increased at the 15–30-cm depth, where

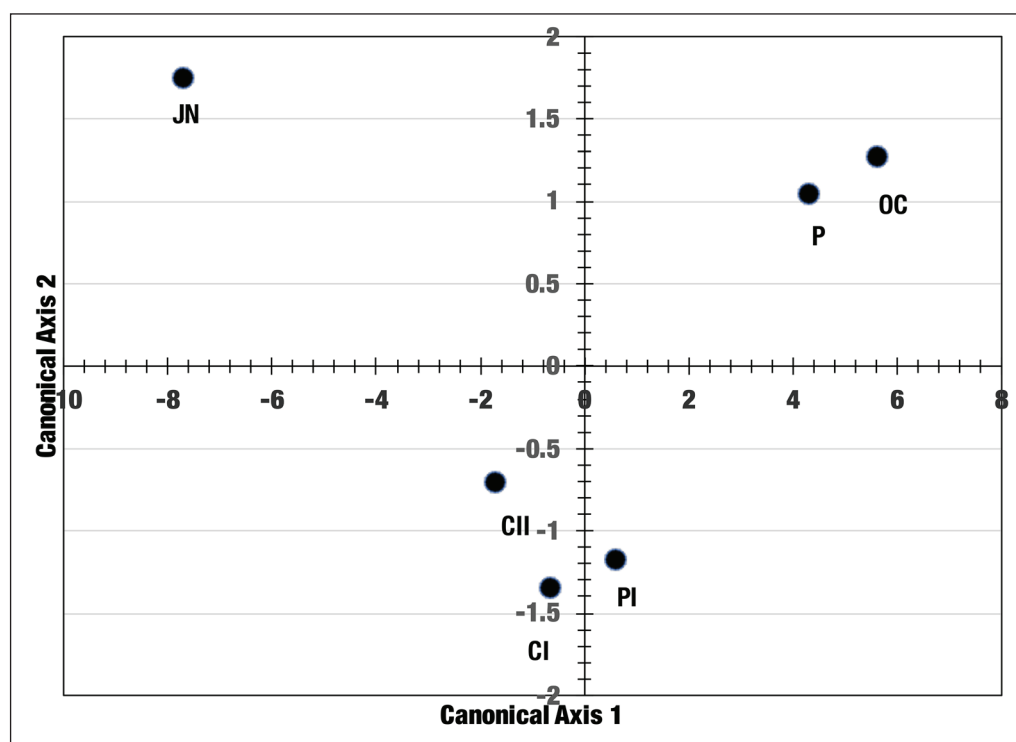


Figure 3. Discriminant function analysis of molar element ratios of soils of 6 *Spathodea campanulata* forest stands. Three of the forests were on alluvial substrates (Cibuco I [CI], Cibuco II [CII], and Paso del Indio [PI]) and 3 were on karst substrates (Ollas y Calderas [OC], Pugnado [P], and Juan Nieves [JN]). See Supplemental Tables S5 and S6 (in Supplemental File 1), respectively, for the centroids for each variable and the statistical results.

Table 4. Mean molar element ratios for soils, adult canopy leaves, and litterfall and loose litter components of forests dominated by *Spathodea campanulata* (*Sc*) in alluvial (A) and karst (K) substrates. “*” indicates statistical differences between alluvial and karst sites at $P \leq 0.05$. [Table continued on following page.]

Compartment/ substrate	Mean molar elemental ratios																
	C:N	C:S	C:P	N:S	N:P	N:K	N:Mg	N:Ca	S:P	Ca:Mg	Ca:Al	Ca:P	K:P	Mg:P	Al:P	Ca:K	Fe:Mn
Soil																	
0–15 cm																	
A	13	262	102	20*	8	9*	0.6*	0.8	0.4	0.9*	0.3	12	0.9	14.0*	47	14*	40
K	14	424	240	28*	15	18*	3.4*	0.9	0.5	12.0*	1.3	58	0.8	4.0*	37	65*	37
15–30 cm																	
A	12	240	85	20	7	8*	0.5*	0.7	0.4	1.6*	0.5	24	1.0	16.0*	55	27	40
K	13	436	191	30	13	13*	2.6*	0.9	0.4	10.5*	1.0	56	1.2	4.0*	81	56	45
Canopy adult leaves																	
Sc leaves																	
A	24*	336*	534*	14	22*	5*	9	2.0*	1.7*	5.0*	124*	12*	4.4*	2.4*	0.10*	3*	7*
K	27*	370*	678*	14	26*	6*	9	1.6*	2.0*	6.0*	134*	17*	5.3*	2.8*	0.14*	4*	3*
Sc yellow leaves on the ground																	
A	51*	275*	749*	6	15*	4*	4.4	0.75*	2.0*	5.9*	112	21*	4.8*	3.6*	0.21*	5*	7*
K	54*	323*	1470*	6	28*	6*	4.7	0.65*	4.3*	7.6*	116	44*	8.2*	5.9*	0.41*	11*	4*
Litter fall																	
Sc brown leaffall																	
A	35	383*	728*	11	21*	10*	8	1.2*	1.2*	7.2*	91*	19*	2.5*	2.7*	0.23	9*	7*
K	36	415*	1132*	11	32*	12*	8	1.0*	1.9*	9.0*	103*	33*	3.7*	3.9*	0.36	13*	3*
Sc green leaffall																	
A	27*	343	703	13	26*	7*	11*	2.2*	1.2*	5.6*	106*	13*	4.0	2.4*	0.13*	4*	7*
K	29*	346	716	12	31*	9*	10*	1.6*	2.8*	6.8*	113*	22*	4.5	3.2*	0.22*	7*	4*
Leaffall of other species																	
A	31	409	782*	13	26*	8*	11*	1.6*	1.8*	7.4	82*	18*	3.9	2.5*	0.25*	6*	4*
K	31	448	1362*	15	44*	13*	12*	1.7*	3.6*	7.2	92*	27*	4.3	3.9*	0.32*	8*	2*
Flower and fruit fall																	
A	31	650	588*	22*	19*	6*	15*	5.0	0.6*	3.2*	71	4*	4.6*	1.4*	0.07*	1*	8*
K	29	614	752*	20*	26*	8*	16*	4.8	1.4*	3.6*	73	6*	4.2*	1.5*	0.09*	2*	5*

Table 4, continued Compartment/ substrate		Mean molar elemental ratios																
		C:N	C:S	C:P	N:S	N:P	N:K	N:Mg	N:Ca	S:P	Ca:Mg	Ca:Al	Ca:P	K:P	Mg:P	Al:P	Ca:K	Fe:Mn
Fine wood fall		90*	1210*	689*	13*	8*	3*	5.3*	1.0	0.6*	5.7*	95*	9*	3.2*	1.6*	0.10*	3*	12*
Miscellaneous fall		83*	1131*	1956*	12*	25*	6*	7.1*	1.0	1.9*	7.7*	97*	27*	6.4*	3.5*	0.31*	7*	7*
Loose litter 2005		25*	384	553*	15	22*	11*	13*	2.0	1.5*	7.2*	53*	12*	2.4	3.7	0.26*	6*	12*
Fragmented leaf litter		24*	392	791*	16	33*	16*	14*	1.9	2.2*	7.8*	70*	18*	3.1	2.3	0.31*	9*	7*
Fine wood litter		84	1233*	2052	15	25	27	9*	1.7*	1.7	11.0*	3*	16*	1.0*	3.1	7.0*	16	37
Loose litter 2006		68	957*	2296	15	33	24	14*	1.3*	2.7	6.0*	10*	27*	1.9*	2.4	4.0*	18	34
Sc leaf litter		30	387*	605*	13	13	12*	7	1.2*	1.6*	6.0*	14*	18*	1.7	3.0*	2.0	11*	34*
Other species leaf litter		30	478*	954*	16	16	18*	8	0.9*	2.1*	9.0*	22*	36*	2.4	4.0*	2.0	21*	25*
Fragmented leaf litter		32	513	815*	17*	28*	33*	8*	1.5	1.6	6*	19	19*	1.1*	3	1.1	23*	23
Loose litter 2005		31	646	1330*	22*	46*	21*	13*	1.6	2.1	8*	18	29*	2.6*	4.0	2.5	14*	20
Sc leaf litter		24	431	563*	18*	24*	15*	7*	15.0*	1.3*	5.0*	6	16*	1.7	3.7*	6.0	10*	36
Other species leaf litter		23	476	794*	21*	35*	26*	14*	1.0*	1.7*	10*	8	26*	1.4	2.6*	5.0	21*	37
Flower and fruit litter		25	702	578	29	24	7	12*	5.0*	0.9	3.0*	5	5*	4.0	2.0	1.7	1	39
Loose litter 2006		28	762	800	27	28	11	100*	4.0*	1.0	4.0*	8	9*	3.0	2.0	1.4	2	47
Fine wood litter		57*	1188*	917*	22	18*	9*	8*	1.5	0.8*	5.0*	7	12	2.0	2.2*	2.0*	6*	37
Detritus litter		46*	967*	1297*	22	29*	17*	30*	1.3	1.4*	27.0*	10	26	2.0	0.9*	4.0*	14*	41
Loose litter 2005		20	366	330*	18*	17*	12*	3*	1.4	0.9*	2.0*	0.8*	12*	1.5*	6.0*	17.0	8*	41
Sc leaf litter		19	434	630*	23*	33*	32*	15*	1.7	1.5*	10.0*	2.2*	21*	1.2*	2.0*	14.0	20*	46

alluvial soils stored more sulfur, aluminum, iron, potassium, magnesium, manganese, and sodium than karst sites. The difference in magnesium was notable and attributed to the high storage in the alluvial sites CI and CII. There were no differences in LOI or element concentrations for the pooled 0–30-cm depth. Among individual sites, carbon and nitrogen storage were highest on OC and lowest on JN, and phosphorus storage was lowest in P and highest in JN, which was also the site with the lowest storage of calcium.

Adult *Spathodea campanulata* leaves

Spathodea adult leaves on alluvial substrate had higher nitrogen, sulfur, iron, sodium, and phosphorus concentration than those on karst (Table 3). Leaves on karst had higher calcium and manganese concentration than those on alluvial substrates. There were no significant differences in the mean concentration of aluminum, potassium, magnesium, carbon, and ash in adult *Spathodea* leaves from alluvial and karst sites. The concentrations of ash, aluminum, calcium, magnesium, and phosphorous were higher, and of potassium and sodium lower, at JN relative to all other sites (see Supplemental Table S1 in Supplemental File 1). In turn, N:K and Al:P were higher, and N:P, N:K, N:Mg, N:Ca, and K:P lower on *Spathodea* adult leaves at JN than on the other sites (see Supplemental Table S4 in Supplemental File 1).

The temporal change in the concentration of phosphorus in adult *Spathodea* leaves exhibited a sharp peak associated with leaf out between the end of July to mid-September (Fig. 4A). The high concentrations of phosphorus in adult leaves better than tripled at JN, reaching 5.9 mg/g, during late July–August (Fig. 4A). At this time, all sites exhibited an increase in phosphorus concentration in adult *Spathodea* leaves, with JN exhibiting the highest peak. The nitrogen concentration in adult *Spathodea* leaves was more variable and tended to decrease through July,

Table 5. Storage of elements in soils of alluvial and karst forests dominated by *Spathodea campanulata*. All values in Mg/ha. “*” indicates significant differences between alluvial and karst soils at $P \leq 0.05$.

Variable	Soil depth/type					
	0–15 cm		15–30 cm		0–30 cm	
	Alluvial	Karst	Alluvial	Karst	Alluvial	Karst
LOI	258	253	263	224	520	455
Carbon	47	74	38	53	85	125
Nitrogen	4.3*	5.8*	3.8	4.3	8.1	9.7
Sulfur	0.48	0.48	0.44*	0.33*	0.90	0.80
Aluminum	49	45	57*	44*	106	86
Calcium	18	55	34	47	52	106
Iron	73	63	85*	61*	158	119
Potassium	1.4*	0.9*	1.4*	0.9*	2.8	1.8
Magnesium	13.0*	2.9*	15.0*	2.7*	28.0	6.0
Manganese	1.8	1.6	2.1*	1.5*	3.9	3.0
Sodium	0.27*	0.18*	0.3*	0.17*	0.60	0.40
Phosphorus	1.2	1.5	1.2	1.1	2.4	2.5

peaked in September, and declined for the rest of the year (Fig. 4B). Juan Nieves and CII reached the highest calcium concentration peak among study sites. Like phosphorous and calcium (not shown), the concentration of carbon peaked in August, and like that of nitrogen, remained variable through the year. However, the adult leaf carbon concentration exhibited a steady decline between the end of July and mid-September, and a sharp drop after November (Fig. 4C).

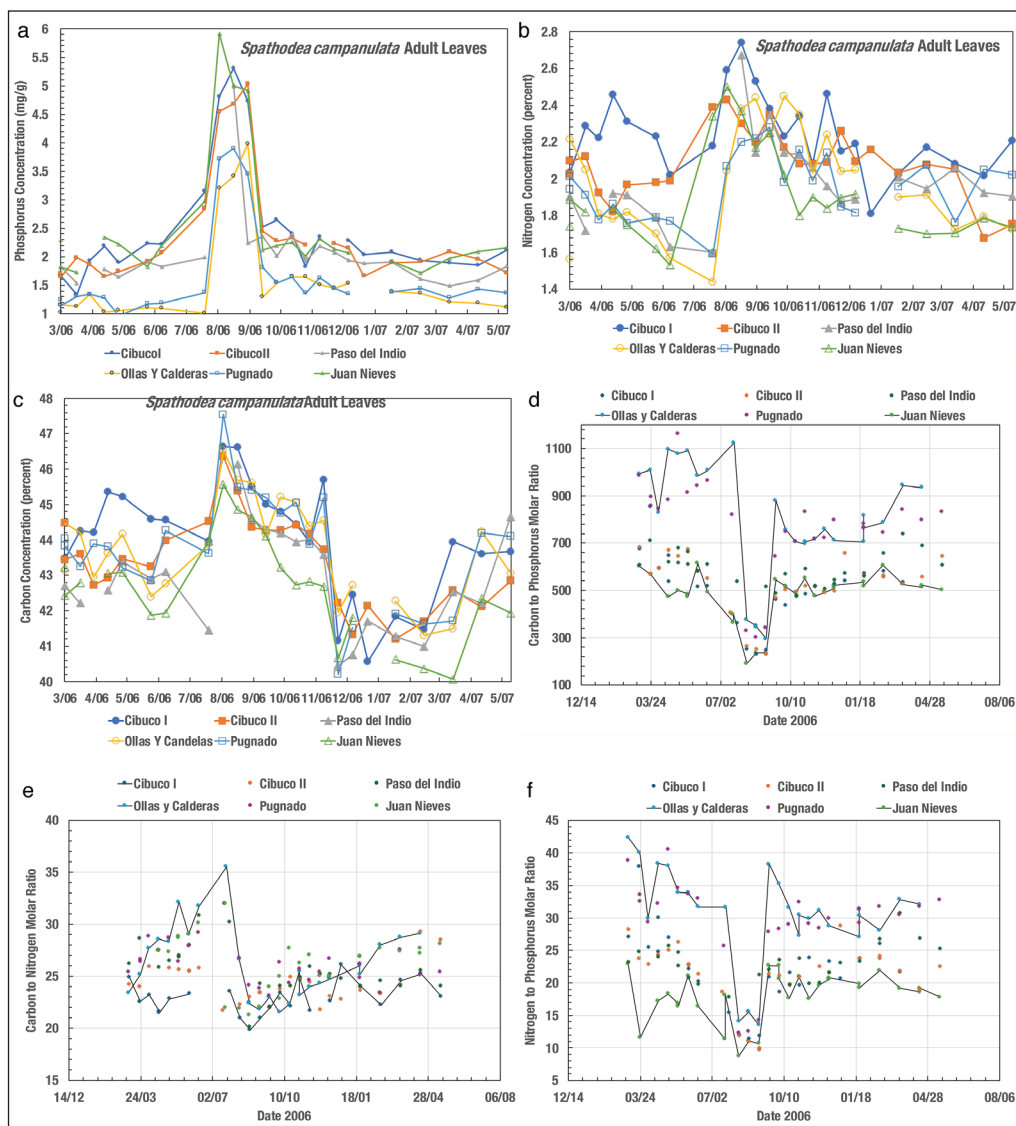


Figure 4. The temporal variation in the concentration of (A) phosphorus, (B) nitrogen, and (C) carbon; and the element molar ratios (D) C:P, (E) C:N, and (F) N:P of adult *Spathodea campanulata* leaves in 6 stands in north-central Puerto Rico. Three stands are on alluvial substrates (Cibuco I, Cibuco II, and Paso del Indio), and 3 are on karst substrates (Ollas y Calderas, Pugnado, and Juan Nieves). The 2 lines for the elemental-ratio pattern include the high and low value series in each graph.

Elemental ratios were very dissimilar among adult *Spathodea* leaves from alluvial and karst substrates (Table 4). Among the ratios that were different among substrate types, C:N, C:S, C:P, N:P, N:K, S:P, Ca:Mg, Ca:Al, Ca:P, K:P, Mg:P, Al:P, and Ca:K were all higher at karst sites, and only S:P and Fe:Mn were higher at alluvial sites. The only elemental ratios that were not different among alluvial and karst substrates were N:S and N:Mg, which had the same mean values among substrates. Like elemental concentrations, the DFA for elemental ratios showed that JN was an outlier site relative to karst and alluvial sites (Fig. 5A; see also see Supplemental Tables S5 and S6 in Supplemental File 1).

The temporal changes in the elemental ratios of C:P, C:N, and N:P of adult *Spathodea* leaves were all characterized by a dip in values during August–September of 2005 (Fig. 4D, E, F). The dip on the ratio of C:N was less apparent and was also characterized by a preceding peak on most sites. The 3 ratios tended to be lower in *Spathodea* adult leaves at alluvial sites among all sampling dates. However, *Spathodea* adult leaves at JN had the lowest values of C:P and especially, N:P, among most sampling dates, and the temporal variation in these ratios was closer to that of alluvial sites than the other 2 karst sites.

Senescent *Spathodea campanulata* leaves

Senescent *Spathodea* leaves (yellow leaves) had higher nitrogen, sulfur, iron, potassium, sodium, and phosphorus concentrations at alluvial sites, higher calcium concentration at karst sites, and no differences in carbon, aluminum, magnesium, manganese, and ash concentrations among substrate types (Table 3). Similar to adult *Spathodea* leaves, elemental ratios were very dissimilar among substrate types, with C:N, C:S, C:P, N:P, N:K, S:P, Ca:Mg, Ca:P, K:P, Mg:P, Al:P, and Ca:K higher at karst sites, only N:Ca and Fe:Mn higher at alluvial sites, and no differences in N:S, N:Mg, and Ca:Al (Table 4). As with soils and adult *Spathodea* leaves, DFA for element ratios in *Spathodea* senesced leaves showed that JN was an outlier site relative to the other 2 karst sites and the alluvial sites, which grouped together according to substrate type (Fig. 5B; see also see Supplemental Tables S5 and S6 in Supplemental File 1).

Senescent *Spathodea* leaves had contrasting element concentrations when compared with adult *Spathodea* leaves of the same sites (Table 3; see also Supplemental Table S2 in Supplemental File 1). The most significant difference was the lower nitrogen and phosphorus concentrations and the higher calcium concentration in senescent *Spathodea* leaves compared to adult leaves. Except for the lower potassium and similar magnesium concentrations, all other elements and ash had higher concentrations in *Spathodea* senescent leaves than in adult leaves. On the other hand, C:N, C:P, and Ca:P tended to be higher for *Spathodea* senesced than adult leaves, and N:Ca tended to be higher for *Spathodea* adult than senesced leaves (Table 4).

Litterfall

Concentrations of ash and elements: alluvial vs karst. There were significant differences in the mean concentration of ash and elements in litterfall components estimated for all sampling dates among alluvial and karst sites (Tables 3; see also

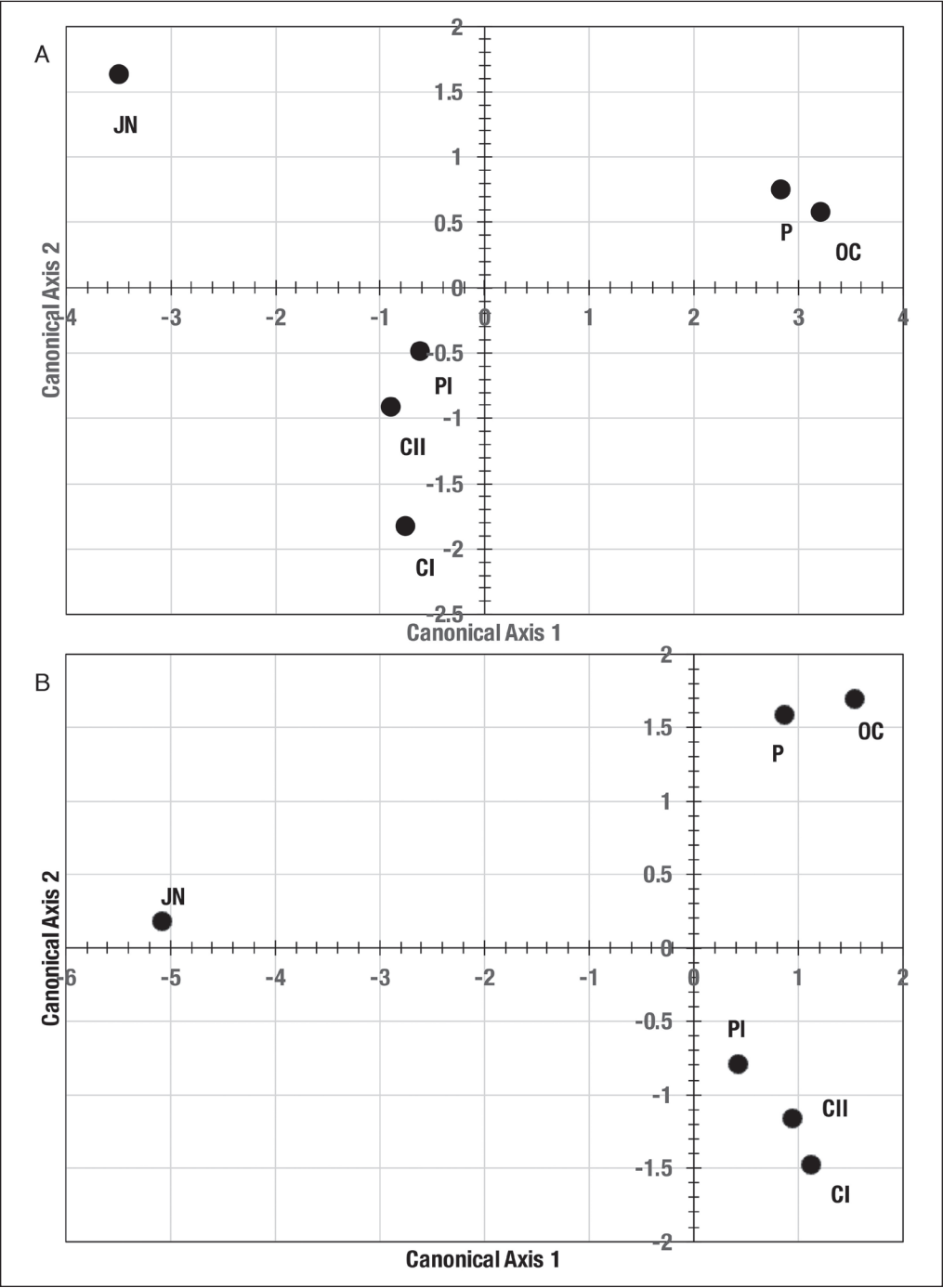


Figure 5. Discriminant function analysis of molar element ratios of (A) *Spathodea campanulata* (Sc) adult leaves and (B) Sc yellow leaves of 6 Sc forest stands. Three stands are on alluvial substrates (Cibuco I, Cibuco II, and Paso del Indio), and 3 are on karst substrates (Ollas y Calderas, Pugnado, and Juan Nieves). See Supplemental Tables S5 and S6 (in Supplemental File 1), respectively, for the centroids for each variable and the statistical results.

Supplemental Table S1 in Supplemental File 1). Most of these differences were found in foliage as leaf fall of *Spathodea* or of other species. Ash content, concentrations of aluminum, calcium, and manganese were higher in *Spathodea* leaf fall at karst sites; carbon, nitrogen, iron, potassium, sodium, sulfur, and phosphorus concentrations were higher in *Spathodea* leaf fall of alluvial sites; and magnesium was the only element with the same concentration in *Spathodea* leaf fall among alluvial and karst sites. These differences were also found among the components of *Spathodea* leaf fall except for nitrogen, sulfur, and aluminum of *Spathodea* brown leaf fall, and carbon, sulfur, and iron of *Spathodea* green leaf fall, which were not different among *Spathodea* stands on alluvial or karst substrates. On the other hand, the concentration of magnesium was higher on *Spathodea* brown leaf fall at alluvial sites and higher on *Spathodea* green leaf fall at karst sites, being the only element with a different pattern among brown and green *Spathodea* leaf fall components.

Among the element concentrations of leaf fall of other species, only the concentration of manganese was higher at karst sites, and the concentrations of ash, sulfur, aluminum, calcium, iron, potassium, magnesium, sodium, and phosphorus were all higher at alluvial sites (Table 3; see also Supplemental Table S1 in Supplemental File 1). Like *Spathodea* leaf fall, there was only 1 element with the same concentrations in leaf fall of other species among alluvial and karst sites, in this case the concentration of nitrogen. Wood fall at alluvial sites had higher potassium, magnesium, and sodium concentrations but lower nitrogen, sulfur, calcium, and manganese concentrations than wood fall at karst sites (Table 3; see also Supplemental Table S1 in Supplemental File 1). Flower and fruit fall at alluvial sites had higher concentrations of ash, potassium, sodium, and phosphorus but lower concentration of carbon than flower and fruit fall at karst sites. Miscellaneous litter fall at alluvial sites had higher concentrations of sodium, phosphorus, potassium, and magnesium, and lower concentrations of carbon and nitrogen, than miscellaneous fall at karst sites. All components of leaf fall tended to have higher ash, sulfur, aluminum, calcium, iron, magnesium, and manganese, and lower phosphorous content than wood and flower and fruit fall components (Table 3; see also Supplemental Table S1 in Supplemental File 1). Element concentrations in miscellaneous fall were at times similar to those in leaf fall, as for calcium and magnesium, but higher for many other elements including nitrogen, aluminum, iron, and phosphorous.

Element ratios: alluvial vs karst. Like the ash and elemental concentrations, we found many differences in elemental ratios in litter fall among alluvial and karst sites (Table 4; see also Supplemental Table S4 in Supplemental File 1). However, differences in elemental ratios were evident among all litter fall components and not, as was the case with concentrations, just foliage. As with adult-leaf chemistry, *Spathodea* leaf fall at karst sites had higher ratios of calcium to other elements, and, with a few exceptions, higher ratios of carbon and nitrogen to other elements when compared to alluvial sites. Patterns in elemental ratios were not entirely the same among brown and green *Spathodea* leaf fall. The elemental ratios of C:S, C:P, N:P, N:K, S:P, Ca:Mg, Ca:Al, Ca:P, K:P, Mg:P, Al:P, and Ca:K were all higher on *Spathodea* brown leaf fall at karst sites, and only N:Ca and Fe:Mn was higher at

alluvial sites. On the other hand, the ratios of C:N, N:P, N:K, S:P, Ca:Mg, Ca:Al, Ca:P, Mg:P, Al:P, and Ca:K were higher in *Spathodea* green leaffall at karst sites, and N:Mg, N:Ca, and Fe:Mn were higher at alluvial sites. Among alluvial and karst sites, no differences in C:N, N:S, N:Mg, and Al:P were found in *Spathodea* brown leaffall, and no differences were found in C:S, C:P, N:S, and K:P of *Spathodea* green leaffall. At karst sites, the C:P of brown leaffall was much higher than that of *Spathodea* green leaffall.

Leaffall of other species had higher ratios of C:P, N:P, N:K, N:Mg, N:Ca, S:P, Ca:Al, Ca:P, Mg:P, Al:P, and Ca:K at karst sites, with only the ratio of Fe:Mn being higher at alluvial sites (Table 4; see also Supplemental Table S4 in Supplemental File 1). No differences were found in C:N, C:S, N:S, Ca:Mg, and K:P of leaffall of other species among alluvial and karst sites. Among litterfall of all other components, C:P, N:P, N:K, S:P, Ca:Mg, Ca:P, Al:P, and Ca:K were all higher at karst sites and, like leaffall, only Fe:Mn was higher at alluvial sites. Compared to the foliage components of litterfall, wood fall and flower and fruit fall had low S:P. Flower and fruit fall had high N:S and K:P, and low Al:P, compared to most other litterfall components, and their C:P was low. Flower and fruit fall had the lowest Ca:P and Ca:Mg element ratios. Wood fall had the highest C:N and C:S element ratios, and these ratios for miscellaneous fall were among the lowest of litterfall components. Flower and fruit fall had the highest N:Ca ratio, and wood fall the lowest. Wood fall also had the lowest N:K element ratios, and flower and fruit and miscellaneous fall had the highest.

The DFA of elemental ratios of *Spathodea* leaffall grouped JN with alluvial sites, and the other 2 karst sites as outliers from the group and separated from each other (Fig. 6A; see also Supplemental Tables S5 and S6 in Supplemental File 1). The same pattern was found for *Spathodea* green leaves (Fig. 6B), which was also like that of *Spathodea* adult and senesced leaves. However, for *Spathodea* brown leaffall, the pattern was somewhat different (Fig. 6C) with OC and P clustered together, and JN located closer to the alluvial sites, which were also clustered together.

Fluxes of mass and elements. Mean daily values of total litterfall rates were higher at alluvial than at karst sites (Table 6). Half or more of the litterfall on both alluvial and karst sites was in the form of leaffall. Daily rates of leaffall of *Spathodea* brown leaves, of all *Spathodea* leaffall, and of total leaffall of all species were also higher at alluvial than at karst sites. Daily rates of wood fall were also higher at alluvial sites, and no differences were found among the other components. There were lower daily rates of *Spathodea* brown leaves and all *Spathodea* leaffall at OC compared to the other sites.

Daily rates of litterfall mass illustrate that peaks in rates were independent of substrate type (Fig. 7). For example, a peak in daily rates of total litterfall occurred during March–April of 2006 at karst sites OC and P but not at the other sites. Likewise, a peak in total litterfall occurred around November of 2007 at alluvial sites CI and CII (Fig. 7A), and the karst site JN (Fig. 7B), but not at the other sites. There was insufficient data among sites collected between June and August 2007 to indicate whether the observed peak in litterfall occurred only at a subset of sites.

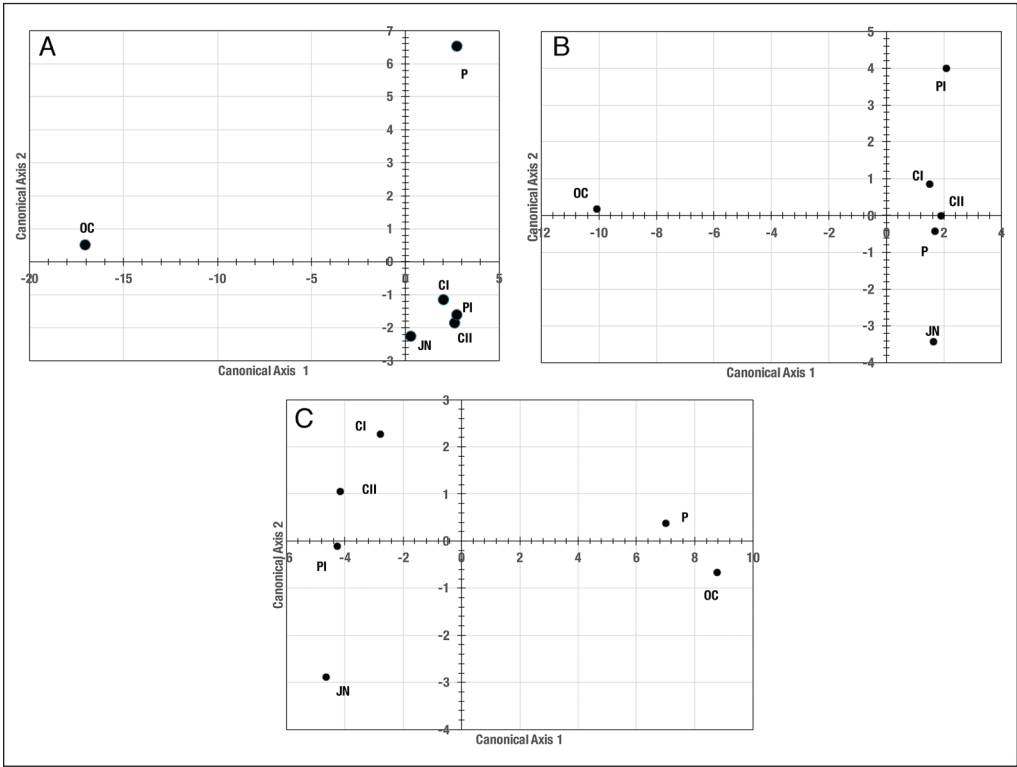


Figure 6. Discriminant function analysis of molar element ratios of (A) *Spathodea campanulata* (Sc) leaffall, (B) *Sc* green leaffall, and (C) *Sc* brown leaffall of 6 *Sc* forest stands. Three of the forests were on alluvial substrates (Cibuco I [CI], Cibuco II [CII], and Paso del Indio [PI]), and 3 were on karst substrates (Ollas y Calderas [OC], Pugnado [P], and Juan Nieves [JN]). See Supplemental Tables S5 and S6 (in Supplemental File 1), respectively, for the centroids for each variable and the statistical results.

Table 6. Mean litterfall rates (g/m²•day) by compartment in 6 *Spathodea campanulata* (*Spathodea*) novel forests in northwestern Puerto Rico. The alluvial sites were Cibuco I (CI), Cibuco II (CII), and Paso del Indio (PI). Karst sites were Ollas y Calderas (OC), Pugnado (P), and Juan Nieves (JN). “*” indicated values for karst and alluvial rows that are statistically different at $P \leq 0.05$. Values in rows with the same superscript letter are not statistically different. Values were rounded and the totals were calculated separately. To convert to Mg/ha•yr, multiply by 3.65.

Compartment	Sites						Alluvial (n = 3)	Karst (n = 3)
	CI	CII	PI	OC	P	JN		
<i>Spathodea</i> brown leaves	1.96 ^A	1.53 ^A	1.98 ^A	1.17 ^B	1.60 ^A	1.66 ^A	1.83*	1.48*
<i>Spathodea</i> green leaves	0.23 ^A	0.09 ^A	0.17 ^A	0.09 ^A	0.08 ^A	0.12 ^A	0.16	0.10
<i>Spathodea</i> total leaffall	2.14 ^A	1.63 ^A	2.15 ^A	1.25 ^B	1.68 ^A	1.78 ^A	1.98*	1.57*
Other species	0.37 ^A	0.39 ^A	0.23 ^B	0.43 ^A	0.36 ^A	0.31 ^A	0.33	0.37
Total leaffall	2.51 ^A	2.01 ^{AB}	2.38 ^A	1.68 ^B	2.04 ^{AB}	2.10 ^A	2.31*	1.82*
Flowers and fruits	0.61 ^A	0.53 ^A	0.62 ^A	0.65 ^A	0.62 ^A	0.58 ^A	0.59	0.62
Fine wood	1.36 ^A	0.82 ^A	1.20 ^A	0.76 ^A	1.03 ^A	0.77 ^A	1.13*	0.86*
Miscellaneous	0.26 ^A	0.21 ^A	0.22 ^A	0.23 ^A	0.23 ^A	0.23 ^A	0.23	0.23
Total litterfall	4.74 ^A	3.57 ^A	4.42 ^A	3.32 ^A	3.92 ^A	3.66 ^A	4.25*	2.97*

Despite the pulsed variation in adult-leaf element concentrations, leaffall element concentrations remained relatively constant throughout the year (Fig. 8).

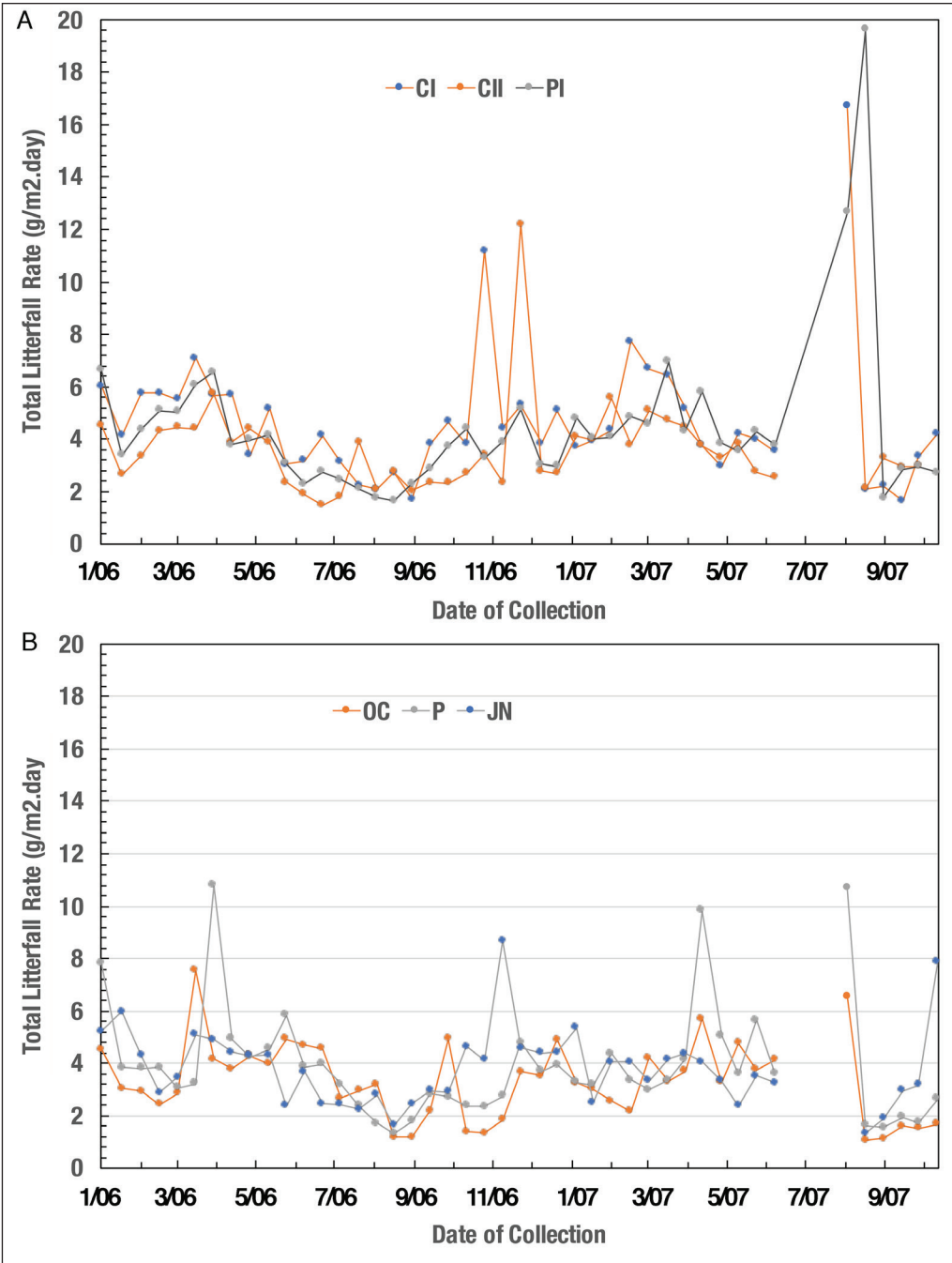


Figure 7. Temporal rate of total litterfall in forests of *Spathodea campanulata* growing on (A) alluvial and (B) karst substrates in north-central Puerto Rico. The alluvial sites were Cibuco I (CI), Cibuco II (CII), and Paso del Indio (PI). Karst sites were Ollas y Calderas (OC), Pugnado (P), and Juan Nieves (JN).

The rate of litterfall did not appear to relate to variations in the element ratios of *Spathodea* leaffall (Fig. 9) and other litterfall components in general (data not shown). Except for sulfur and manganese, the return of ash and elements on *Spathodea* brown leaffall was higher at alluvial than karst sites (Table 7). These differences were not found for *Spathodea* green leaffall except for iron, sodium, and phosphorous, which were higher at alluvial sites as well. When *Spathodea* brown and green leaffall are grouped together, all these differences disappear. The return

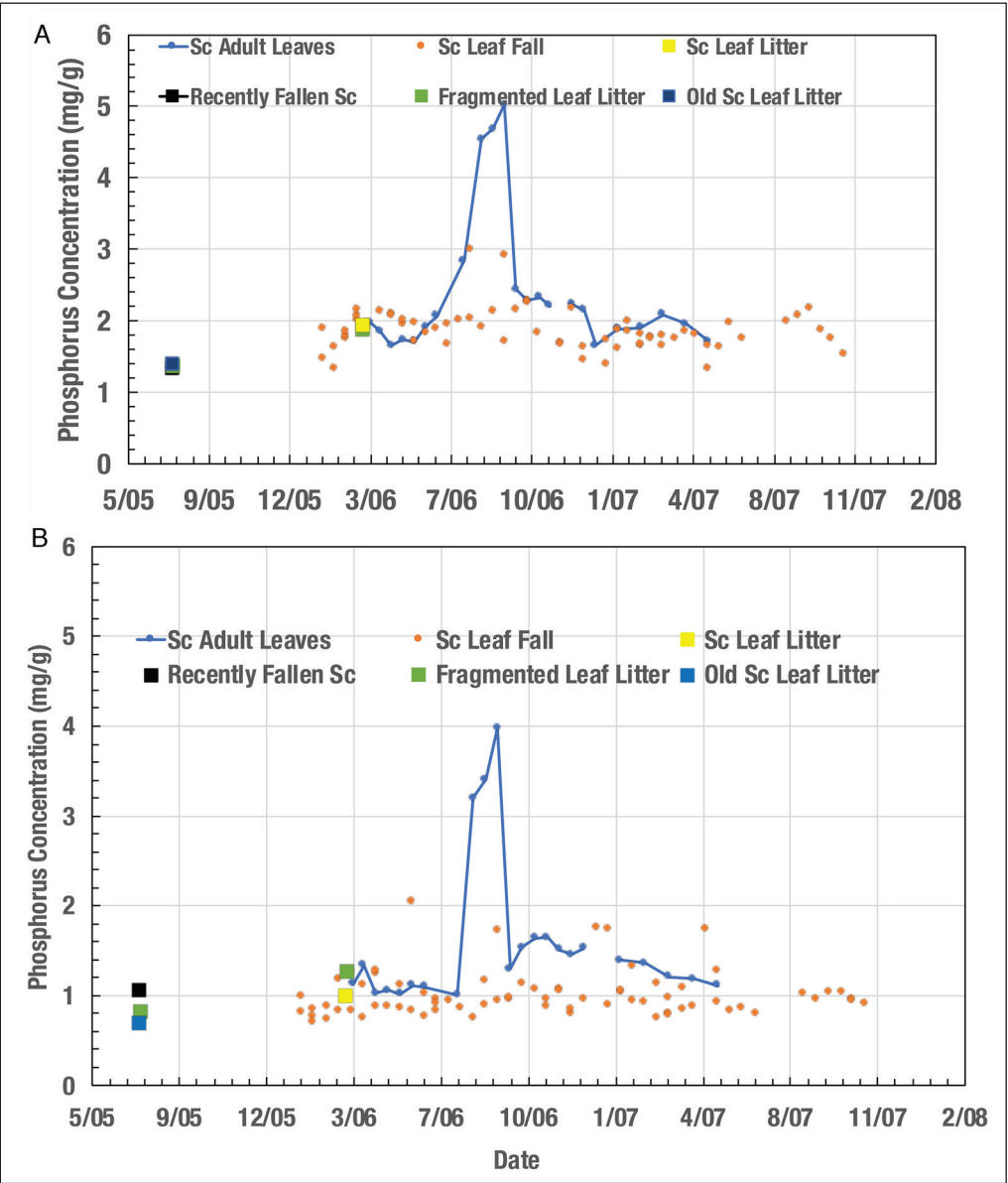


Figure 8. Temporal variation in the phosphorus concentration of adult and dead leaves of *Spathodea campanulata* in litterfall and loose litter in forest stands in (A) alluvial (Cibuco II) and (B) karst (Ollas y Calderas) substrates in north-central Puerto Rico.

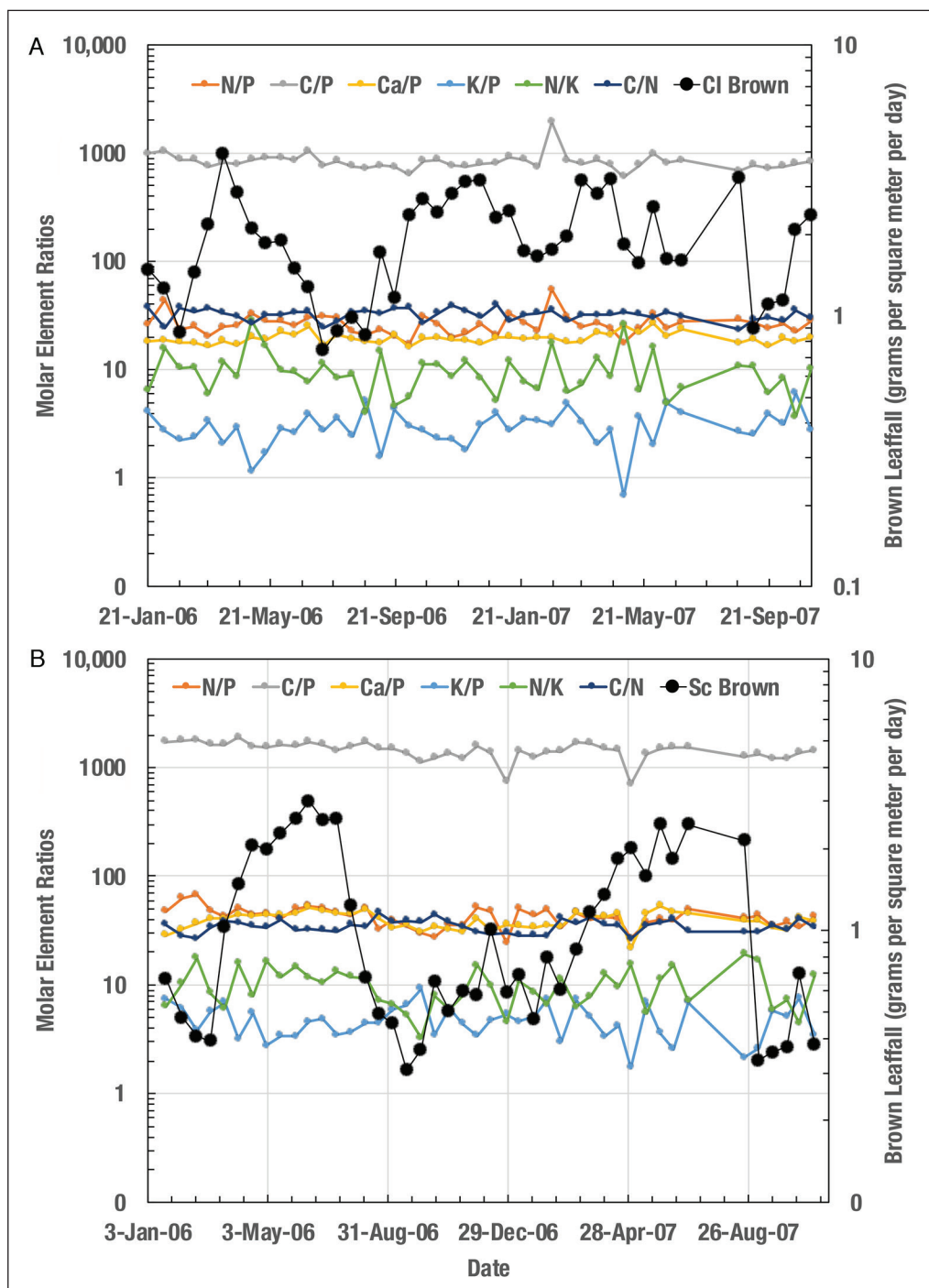


Figure 9. Temporal variation in leaffall mass of *Spathodea campanulata* and of 6 molar element ratios of leaffall in (A) an alluvial site (Cibuco I) and (B) a karst site (Ollas y Calderas) in north-central Puerto Rico. Note the logarithmic scales of both primary and secondary vertical axes. Leaffall mass (black dots) is on the secondary axis.

of iron, potassium, sodium, and phosphorous in leaf fall of other species was higher at alluvial sites, and their return of manganese higher at karst sites. There was no difference in the return of ash and any elements via flowers and fruits components of litter fall among alluvial and karst sites (Table 7; see also Supplemental Table S8 in Supplemental File 1). The return of ash and elements in wood fall was higher at alluvial than at karst sites except for manganese, which was higher at karst sites, and nitrogen, aluminum, and calcium, which were mostly the same among sites. There was a cyclical (i.e., yearly) pattern in the ratios of N:P and K:P, with peaks and dips that occurred during January and May, respectively, at alluvial sites that flood (e.g., CII), but these variations were absent at OC, the site that does not flood (Fig. 9).

Loose litter

Ash and element concentrations: alluvial vs karst. The calcium concentration at karst sites was higher than at alluvial sites in recently fallen and old leaf litter

Table 7. Mean ash and element return (kg/ha•yr) by litterfall compartments in alluvial and karst forests dominated by *Spathodea campanulata* (Sc). Means are based on all biweekly data from 22 sampling months (January 2006–October 2007). “*” indicate alluvial and karst values that are statistically different a $P \leq 0.05$. Values were rounded to the nearest kg or 0.1 kg. Sc leaf fall is the sum of the means of brown and green leaf fall, and total litter fall is the sum of litter fall compartments; they were not subject to statistical analysis.

Compartment/ substrate	Elements											
	Ash	C	N	S	Al	Ca	Fe	K	Mg	Mn	Na	P
Sc brown leaf fall												
Alluvial	2.2*	3181*	108*	22	2.4*	283*	1.4*	35*	24*	0.2	3.0*	12*
Karst	1.9*	2582*	86*	19	2.0*	275*	0.8*	24*	20*	0.2	1.4*	7*
Sc Green leaf fall												
Alluvial	0.2	268	11	2	0.2	21	0.1*	4	2	0.0	0.3*	1*
Karst	0.2	181	7	1	0.1	16	0.0*	2	2	0.0	0.1*	1*
Sc leaf fall												
Alluvial	2.4	3449	119	24	2.6	304	1.5	39	26	0.2	3.3	13
Karst	2.1	2763	93	20	2.1	291	0.8	26	22	0.2	1.5	8
Other species leaf fall												
Alluvial	0.4	590	23	4	0.5	48	0.3*	10*	415	0.1*	0.9*	2*
Karst	0.4	677	25	4	0.4	48	0.2*	7*	409	0.1*	0.5*	2*
Flower and fruit fall												
Alluvial	0.6	1146	42	5	0.3	26	0.3	40	574	0.0	0.8	6
Karst	0.5	1152	43	5	0.3	28	0.2	28	534	0.1	0.7	5
Fine wood fall												
Alluvial	0.7*	2025*	26	3*	0.6	75	0.4*	29*	841*	0.0*	1.5*	8*
Karst	0.6*	1543*	20	3*	0.6	71	0.4*	14*	604*	0.1*	0.8*	3*
Miscellaneous fall												
Alluvial	0.3	411	19	3	0.4*	30	0.5*	6*	264	0.0	0.4*	2*
Karst	0.3	413	20	3	0.5*	33	0.6*	5*	262	0.0	0.3*	1*
Total litter fall												
Alluvial	4.4	7621	229	39	4.4	483	2.9	125	2121	0.4	6.9	31
Karst	3.9	6548	202	35	3.8	471	2.1	80	1831	0.5	3.7	19

of *Spathodea*, fragmented leaf litter, and fine wood litter (Table 3). Old leaf litter of *Spathodea* had higher potassium, and sulfur concentration at alluvial sites than at karst sites. Fragmented leaf litter at alluvial sites had higher concentration of aluminum, potassium, magnesium, iron, and ash and lower concentration of carbon and calcium than fragmented leaf litter at karst sites. Wood litter at alluvial sites had higher magnesium concentration and lower potassium and sodium concentration than wood litter at karst sites. There were no differences in ash and element concentrations in miscellaneous litter and other species recently fallen leaf and old leaf litter. The ash and element concentrations in humus at karst sites was notable for its high levels of ash, aluminum, manganese, iron, and sulfur and low potassium, nitrogen, and carbon.

Element ratios: alluvial vs. karst. All analyzed elemental ratios in fragmented leaves sampled in loose litter on July 2005 were higher at karst than at alluvial sites except for N:S, which was not different, and N:Ca, K:P, Mg:P, Al:P, and Fe:Mn, which were higher at alluvial sites (Table 4). In contrast, all elemental ratios in wood of loose litter sampled on July 2005 were similar among sites except for C:S, N:Ca, AL:P, and Ca:Mg, which were higher at alluvial sites, and N:Mg, Ca:Al, Ca:P and K:P, which were higher at karst sites.

The DFA of *Spathodea* leaf litter in 2005 (Fig. 10A) and 2006 (Fig. 10B) showed both similarities and differences. Leaf litter in both years had JN separate from the other sites, and P and OC in similar positions both times. The 3 alluvial sites were clustered together in 2005, but in 2006, CII approached the space of JN, and OC and P flipped positions. Fragmented leaf litter in 2006 (Fig. 11) had all alluvial sites clustered together as well as OC and P, with JN as an extreme outlier.

Mass, ash, and element content and distribution. The litter mass on the floor of alluvial and karst sites was similar except for wood, which was higher in alluvial forests compared to karst forests (Table 8; see also Supplemental Table S9 in Supplemental File 1). Fine wood litter at alluvial sites also stored more ash, carbon, aluminum, iron, magnesium, manganese, and sodium than fine wood litter at karst sites. Miscellaneous litter stored more aluminum, and total litter stored more aluminum, iron, magnesium, and manganese at alluvial than at karst sites. The amount of sulfur, nitrogen, potassium, and phosphorus in all litter compartments showed no difference at alluvial vs karst sites. Aluminum, iron, and manganese concentrated in humus (Table 3).

Leaf area index

The LAI of *Spathodea* forest stands at alluvial sites was higher than at karst sites (Table 9). The highest LAI was sampled on the *Spathodea* stand at CII. The *Spathodea* stands at JN and OC shared the lowest LAI values sampled.

Retranslocation of nitrogen and phosphorus in *Spathodea* foliage

The mean retranslocation of nitrogen and of phosphorus of *Spathodea* foliage were both higher in *Spathodea* stands was higher at karst compared to alluvial sites (Table 10). *Spathodea* foliage at all study sites had similar nitrogen retranslocation rates except CII, whose low rates caused the lower mean for alluvial sites. Mean

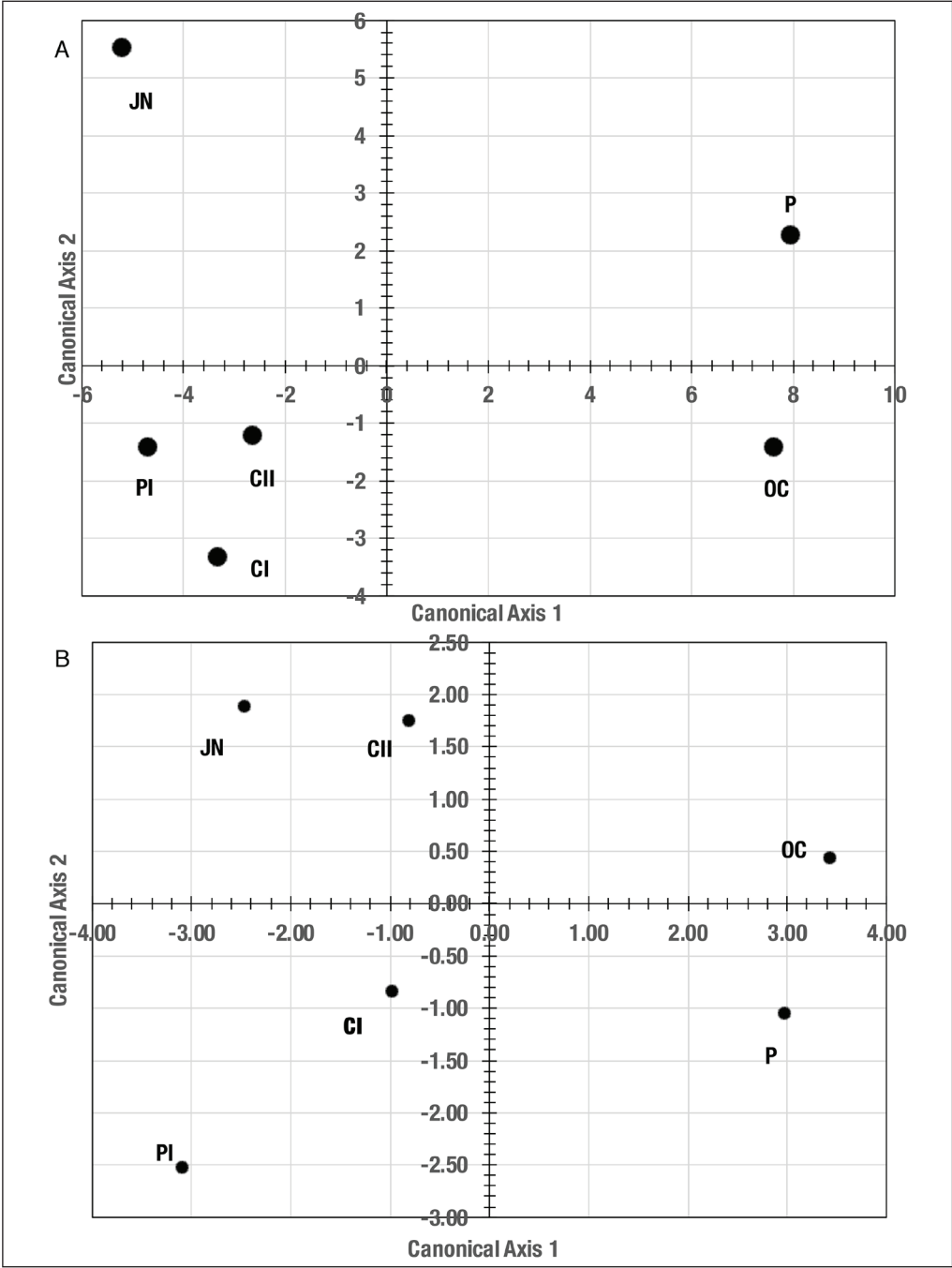


Figure 10. Discriminant function analysis of molar element ratios of (A) *Spathodea campanulata* (Sc) leaf litter of July 2005, regardless of state, (B) Sc leaf litter of March 2006 of 6 Sc forest stands. Three of the forests were on alluvial substrates (Cibuco I [CI], Cibuco II [CII], and Paso del Indio [PI]), and 3 were on karst substrates (Ollas y Calderas [OC], Pugnado [P], and Juan Nieves [JN]). See Supplemental Tables S5 and S6 (in Supplemental File 1), respectively, for the centroids for each variable and the statistical results.

retranslocation of phosphorous was highest at the karst site OC (50%) and lowest at the alluvial site PI (20%). The temporal pattern of retranslocation in foliage was similar at all sites (data shown for 2 sites, CII and OC; Fig. 12). For nitrogen, the pattern was a descendent rate until July, with higher values after August (Fig. 12A). For phosphorus, the pattern included a peak rate of translocation in August, with lower values before and after the peak (Fig. 12B). The highest values for nitrogen retranslocation were 67% and 64% at PI and OC, respectively, and the highest rates for phosphorus retranslocation were 68% and 95% at CI and OC, respectively.

Soil chemistry, stoichiometry, and ecosystem function

We found no significant relationships between soil chemistry (pH, clay concentration, LOI and LOI mass) and parameters of ecosystem structure and function including leaf-litter mass, total litter mass, stand basal area, stem-wood biomass, LAI, leaffall rate, total litterfall rate, and phosphorus and nitrogen retranslocation. One of 2 exceptions was a negative correlation between percent soil LOI and tree basal area ($R^2 = 0.43$, $P \leq 0.05$). The other exception was a positive correlation between percent clay and phosphorus retranslocation ($R^2 = 0.43$, $P \leq 0.05$).

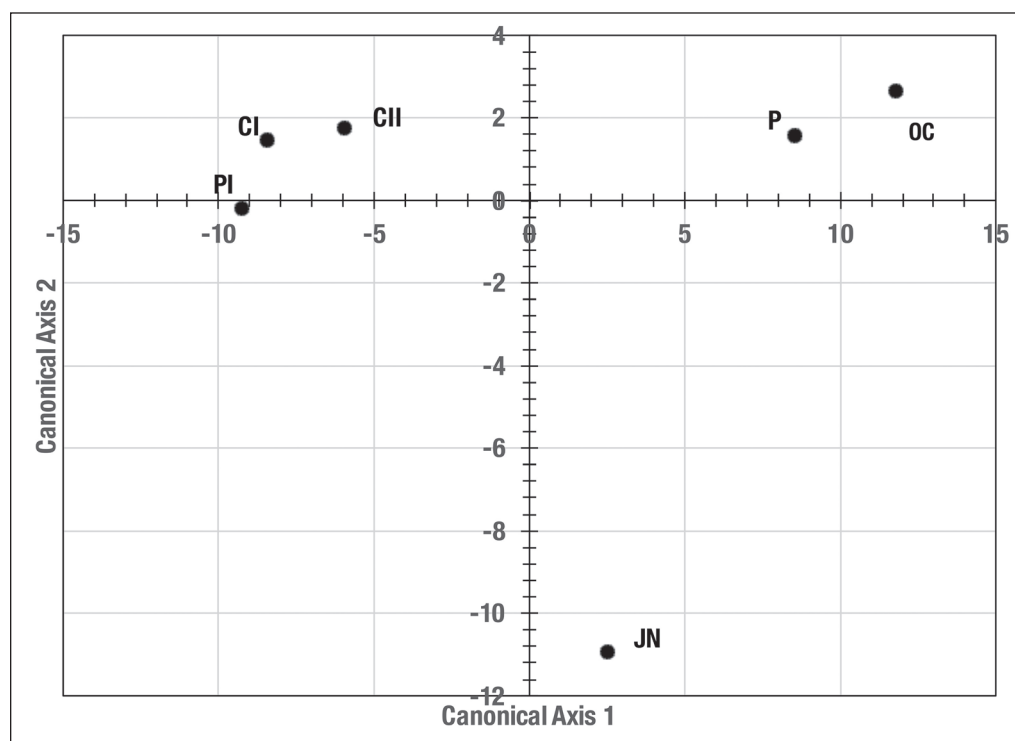


Figure 11. Discriminant function analysis of molar element ratios of fragmented leaves in loose litter of March 2006 of 6 *Spathodea campanulata* (Sc) forest stands. Three of the forests were on alluvial substrates (Cibuco I [CI], Cibuco II [CII], and Paso del Indio [PI]), and 3 were on karst substrates (Ollas y Calderas [OC], Pugnado [P], and Juan Nieves [JN]). See Supplemental Tables S5 and S6 (in Supplemental File 1), respectively, for the centroids for each variable and the statistical results.

Table 8. Storage of mass and elements in loose litter components of *Spathodea campanulata* forests on alluvial and karst substrates. “*” indicates significant differences between alluvial and karst sites at $P \leq 0.05$. “-” indicates that data were not available. All values are in kg/ha and have been rounded to the nearest kg or 0.1 kg. Data are for July 2005.

Compartment	Mass	Ash	Elements										
			C	S	N	Al	Ca	Fe	K	Mg	Mn	Na	P
Alluvial													
Fragmented leaves	1040	359		2.4	19.4	10.6	31.6	15.5	1.3	3.9	0.4	0.1	1.3
Recently fallen <i>Spathodea</i> leaves	19	-	9	0.1	0.3	0.0	0.5	0.0	0.0	0.1	-	0.0	0.0
Recently fallen other leaves	3	-	-	0.0	0.0	-	0.1	0.0	0.1	0.0	-	-	0.0
Old <i>Spathodea</i> leaves	62	13	27	0.2	0.9	0.2	2.4	0.3	0.2	0.2	0.0	0.0	0.1
Old other leaves	28		12	0.1	0.5	0.1	0.8	0.2	0.1	0.1	0.0	0.0	0.0
All leaves	1153	374	423	2.8	21.1	10.9	35.3	16.0	1.7	4.2	0.4	0.2	1.4
Fine wood	3400*	421*	1613*	3.9	25.8	12.0*	44.5	17.3*	2.9	5.1*	0.5*	0.2*	2.3
Miscellaneous	217	17	107	0.2	2.0	0.4*	1.5	0.6	1.0	0.2	-	0.0	0.1
Total	4767	812	2143	6.9	48.9	23.3*	81.3	33.9*	5.6	9.6*	0.9*	0.4	3.9
Karst													
Fragmented leaves	1123	280	-	2.5	21.7	6.2	53.1	8.1	1.1	2.0	0.3	0.1	0.8
Recently fallen <i>Spathodea</i> leaves	65	--	29	0.2	0.9	0.3	2.5	0.4	0.3	0.2	-	0.0	0.1
Recently fallen other leaves	8	-	--	0.0	0.1	-	0.2	0.0	0.0	0.0	-	-	0.0
Old <i>Spathodea</i> leaves	200	41	88	0.5	2.9	0.5	10.4	0.7	0.5	0.5	0.2	0.0	0.1
Old other leaves	39		20	0.1	0.6	0.5	1.4	0.0	0.0	0.1	0.0	0.0	0.0
All leaves	1437	337	613	3.4	26.3	7.1	67.6	9.2	1.9	2.8	0.3	0.2	1.0
Fine wood	1497*	155*	727*	2.4	13.0	3.7*	29.8	5.1*	2.2	1.6*	0.1*	0.2*	0.9
Miscellaneous	80	4	41	0.0	0.5	0.0*	0.4	0.0	0.8	0.1	-	0.0	0.0
Total	3070	512	1395	6.0	40.7	11.7*	98.8	15.6*	4.8	4.6*	0.5*	0.4	2.0

We found that total litterfall rate correlated negatively with both nitrogen and phosphorus storage to 30 cm depth of soil and that *Spathodea* leaffall correlated negatively with soil nitrogen storage (Fig. 13). In the case of total litterfall to soil nitrogen, the relationship only held when JN, a site with low soil nitrogen, was excluded as an outlier. We also found negative correlations between soil element storage and leaffall mass and element return. Soil calcium storage to 30 cm depth negatively correlated ($r = 0.8$, $P \leq 0.05$) with leaffall phosphorus return and with soil phosphorus storage to 30 cm depth ($r = 0.8$, $P \leq 0.05$). Soil nitrogen storage to 30 cm negatively correlated with leaffall calcium return ($r = 0.9$, $P \leq 0.01$), leaffall phosphorus return ($r = 0.8$, $P \leq 0.05$), and leaffall mass ($r = 0.7$, $P \leq 0.10$).

Soil pH correlated negatively with soil storage phosphorous and exponentially with soil calcium storage (Fig. 14A, Table 11). Also, soil pH correlated negatively with *Spathodea* adult-leaf molar element concentration of phosphorus and magnesium (Fig. 14B). Soil pH had no correlation with rate processes, such as those associated with litterfall, but we found high correlations with soil element

Table 9. Mean leaf area index values of forest stands dominated by *Spathodea campanulata* on alluvial and karst substrates in northcentral Puerto Rico. The alluvial sites were Cibuco I, Cibuco II and Paso del Indio. Ollas y Calderas, Pugnado, and Juan Nieves were the karst sites. Values with the same superscript letter were not statistically different at $P \leq 0.05$. For the combined data set (alluvial vs karst) mean, “*” indicate a difference was statistically significant at $P \leq 0.05$. Data represent 2 measuring dates in February and March 2006, when the forest canopies were closed.

Site	Leaf area index (m ² /m ²)
Cibuco I	6.5 ^{AD}
Cibuco II	7.9 ^B
Paso del Indio	7.2 ^{AB}
Ollas y Calderas	5.5 ^C
Pugnado	6.3 ^{DC}
Juan Nieves	5.5 ^C
Alluvial	7.2*
Karst	5.8*

Table 10. Percent retranslocation of nitrogen and phosphorous estimated from mature *Spathodea campanulata* (*Spathodea*) leaves from the canopy and recently fallen senesced leaves collected from the forest floor in 6 forest stands dominated by *Spathodea*. Forests grew on alluvial and karst substrates in northcentral Puerto Rico. Alluvial sites were Cibuco I (CI), Cibuco II (CII), and Paso del Indio (PI). Karst sites were Ollas y Calderas (OC), Pugnado (P), and Juan Nieves (JN). Different superscript letters and “*” denote statistical differences to $P \leq 0.05$ among sites and substrate types, respectively.

Site	Nitrogen	Phosphorous
CI	51.0 ^A	40.7 ^{ABC}
CII	19.9 ^B	23.2 ^{AC}
PI	48.5 ^A	20.1 ^C
OC	47.4 ^A	49.9 ^B
P	46.2 ^A	45.9 ^{AB}
JN	48.6 ^A	34.3 ^{ABC}
Alluvial	39.4*	27.9*
Karst	47.4*	43.5*

concentrations, element ratios in soil; element ratios in adult *Spathodea* leaves, leaffall, and fragmented leaf litter; and soil element storage to a depth of 30 cm

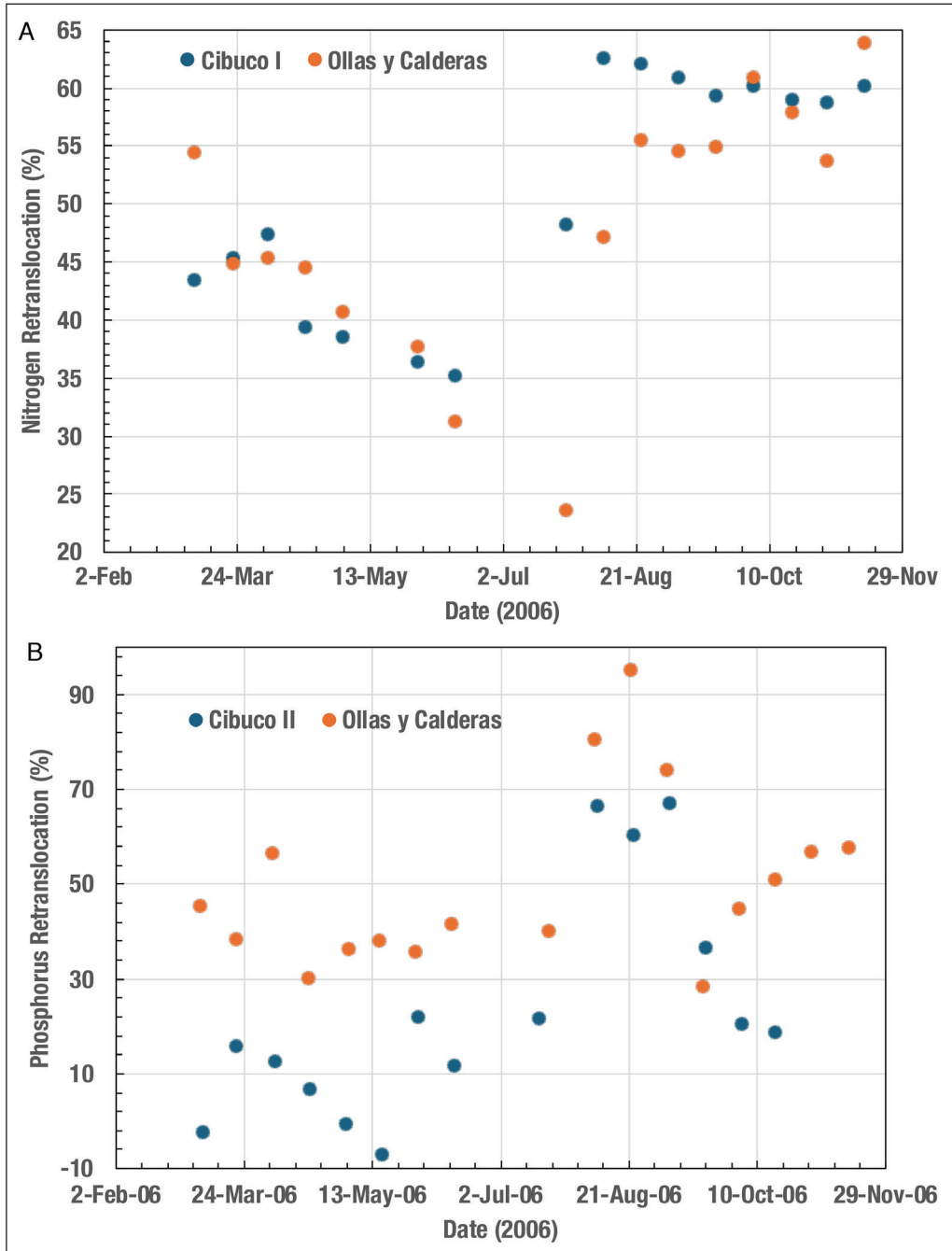


Figure 12. Temporal rate of (A) nitrogen and (B) phosphorus retranslocation on alluvial (Cibuco I) and karst (Ollas y Calderas) stands dominated by *Spathodea campanulata* (*Sc*) in north-central Puerto Rico. Adult and senescent (yellow) leaves of *Sc* were used to arrive at a translocation estimate.

(Table 11). Soil pH correlated with 7 element concentrations and 10 element ratios of soil. Aluminum, potassium, iron, manganese, and sodium concentrations had negative correlations with soil pH, and all others had positive correlations. Eight element ratios of *Spathodea* adult leaves, 4 of leaf fall, and 4 of fragmented leaf loose litter had positive correlations with soil pH. In addition, soil pH correlated with 6 soil element storages to a depth of 30 cm. All but carbon and calcium storage had negative relationships with soil pH.

Finally, we found that, in general, most elemental ratios and concentrations changed going from soil to *Spathodea* leaves in the canopy and litterfall but appeared to return in leaf components of standing litter to values more similar to those in the soil (Fig. 15).

Discussion

Our study clearly demonstrates that geological substrate type modifies local soil conditions in a way that affects the ecosystem function, namely the elemental

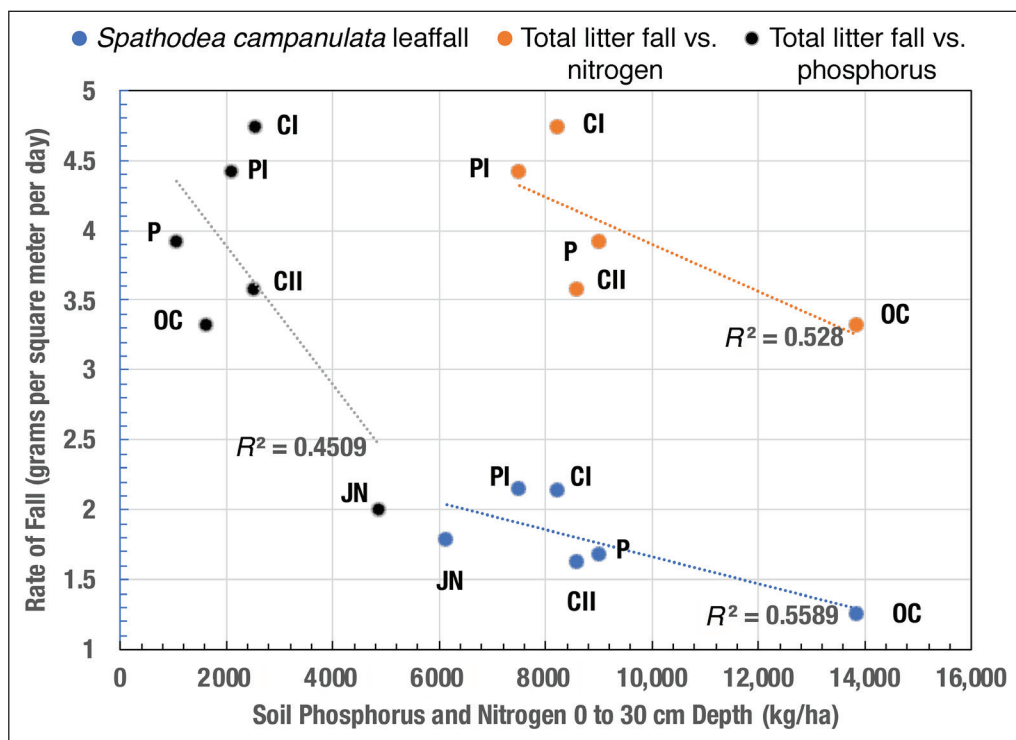


Figure 13. Relationship between total litter fall and *Spathodea campanulata* (*Sc*) leaffall with phosphorus or nitrogen stored to a soil depth of 30 cm in 6 *Sc* stands in north-central Puerto Rico. Total litterfall is correlated with both phosphorus and nitrogen storage, and *Sc* leaffall is correlated with nitrogen storage. Three stands are on alluvial substrates (Cibuco I [CI], Cibuco II [CII], and Paso del Indio [PI]), and 3 are on karst substrates (Ollas y Calderas [OC], Pugnado [P], and Juan Nieves [JN]). The Juan Nieves site was not included in the relationship between total litterfall and nitrogen storage because it was an outlier. All regressions are significant to $P \leq 0.05$.

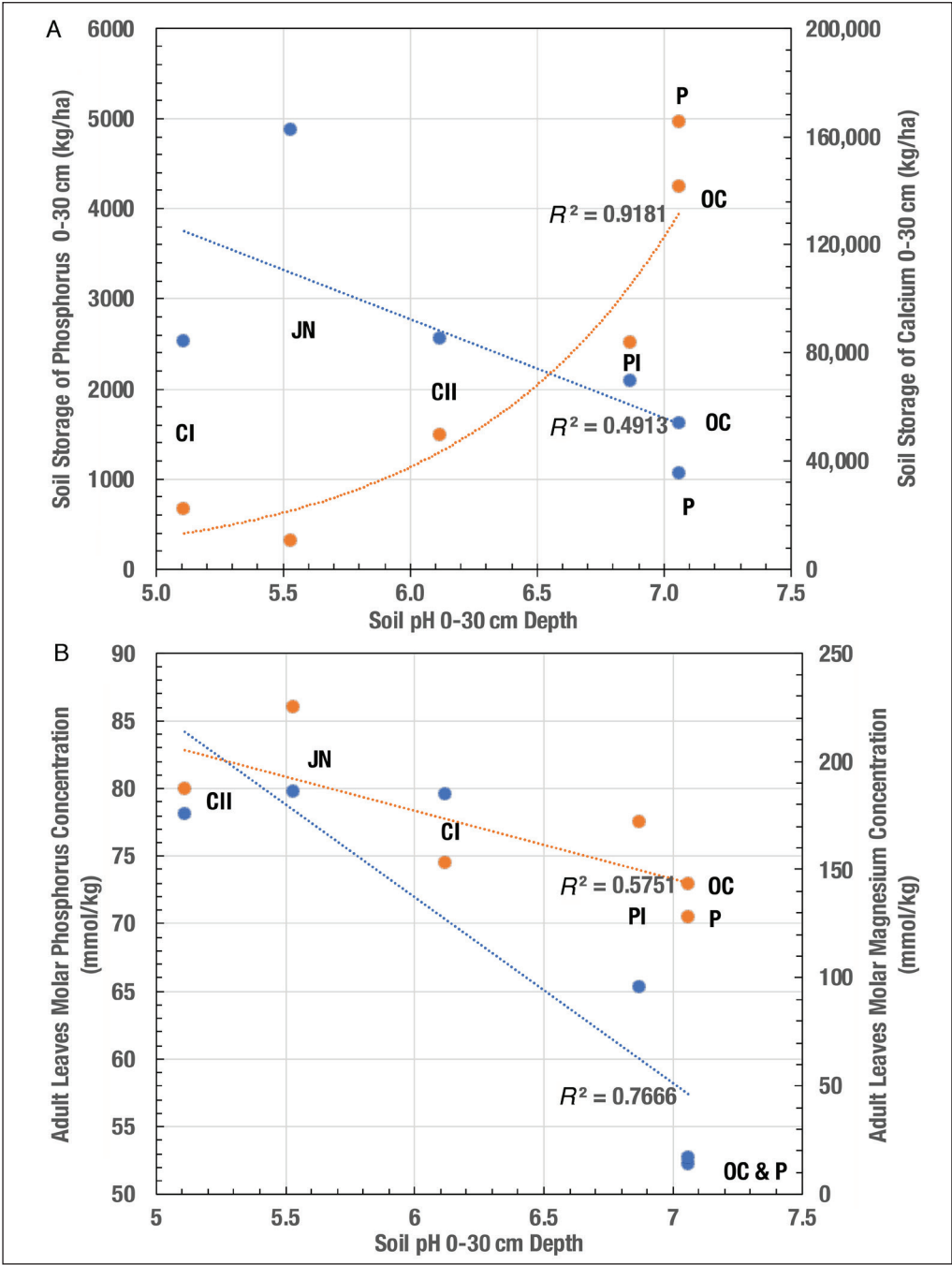


Figure 14. Relationship between (A) soil pH and soil storage of phosphorus and calcium to 30 cm depth and (B) soil pH and the concentration of phosphorus and magnesium in adult leaves of *Spathodea campanulata* (*Sc*). Data are for 6 *Sc* stands in north-central Puerto Rico. Three stands are on alluvial substrates (Cibuco I [CI], Cibuco II [CII], and Paso del Indio [PI]), and 3 are on karst substrates (Ollas y Calderas [OC], Pugnado [P], and Juan Nieves [JN]). All regressions are significant to $P \leq 0.05$.

Table 11. Correlation between soil pH and soil element concentrations, molar element ratios in soils, adult *Spathodea campanulata* (*Sc*) leaves and leaffall, fragmented leaf litter, and soil element storage to depth of 30 cm. Data are for 6 *Sc* forest stands in north-central Puerto Rico. We show correlations higher than 0.65 or $P \leq 0.16$. Correlations higher than 0.73 are significant at $P \leq 0.10$, and those higher than 0.80 are significant at $P \leq 0.05$.

Parameter	Linear correlation	Slope
Soil		
Aluminum	0.75	-
Potassium	0.71	-
Iron	0.76	-
Calcium	0.82	+
Manganese	0.79	-
Sodium	0.87	-
Carbon	0.77	+
C:S	0.78	+
C:P	0.76	+
N:S	0.74	+
N:P	0.76	+
N:K	0.65	+
N:Ca	0.85	+
S:P	0.73	+
Ca:Mg	0.68	+
Ca:Al	0.74	+
Ca:P	0.70	+
Adult <i>Sc</i> leaves		
Ca:P	0.69	+
Ca:Mg	0.66	+
N:P	0.68	+
C:P	0.71	+
S:P	0.71	+
K:P	0.70	+
Mg:P	0.65	+
Al:P	0.75	+
<i>Sc</i> leaffall		
K:P	0.69	+
Ca:P	0.70	+
N:P	0.69	+
C:P	0.71	+
Fragmented leaves loose litter		
C:N	0.80	+
C:P	0.68	+
Ca:Al	0.73	+
Ca:P	0.85	+
Soil element storage (depth of 0–30 cm)		
Carbon	0.80	+
Calcium	0.91	+
Aluminum	0.84	-
Iron	0.83	-
Manganese	0.73	-
Phosphorus	0.70	-

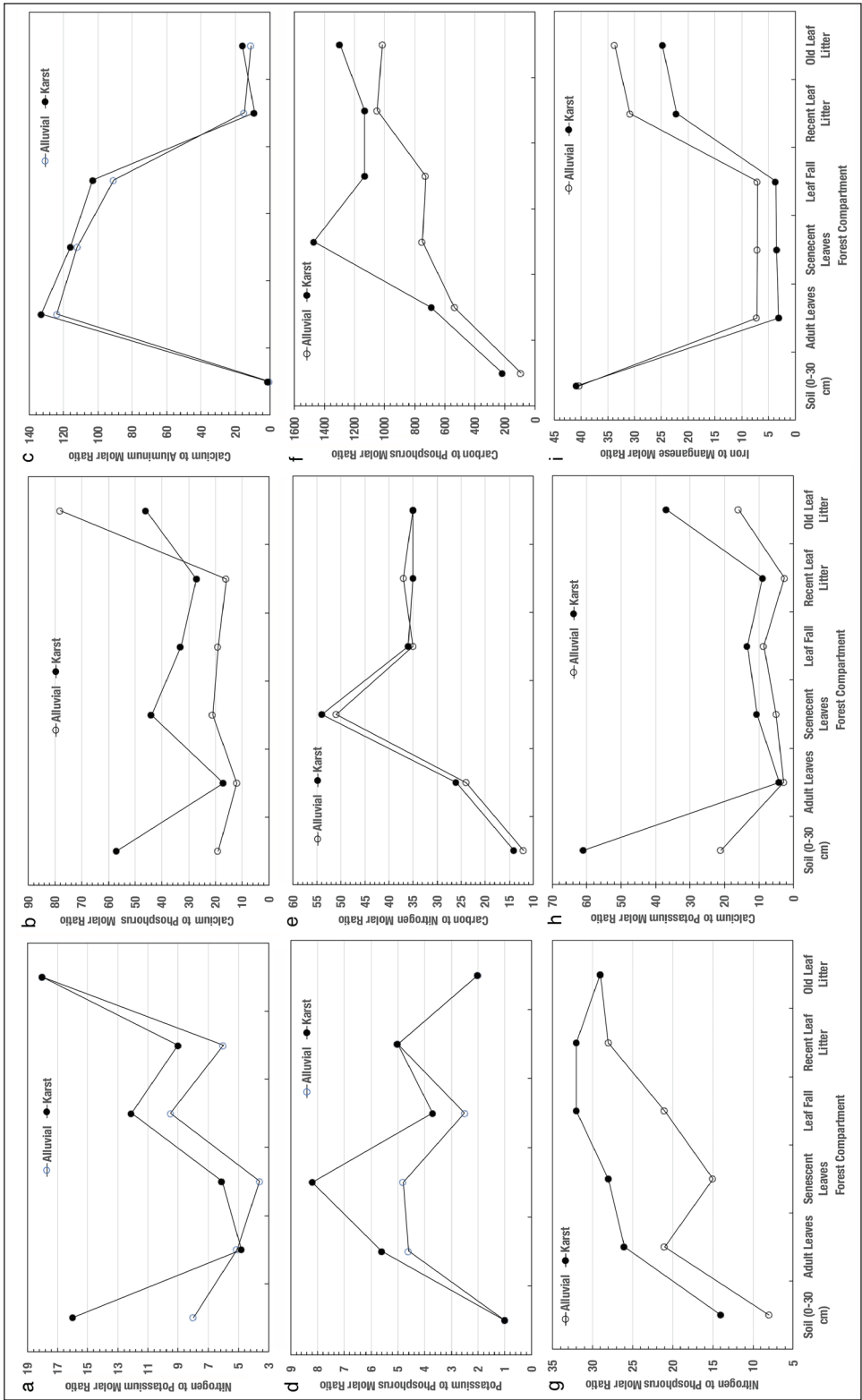


Figure 15. [See following page for caption.]

composition and stoichiometry of biomass transferred from canopy to soil, of novel *Spathodea* forests in northcentral Puerto Rico (Tables 3, 4). The differences in the chemistry and stoichiometry of soils among alluvial and karst sites included differences in the concentration of key elements required for plant growth and nutrition, such as nitrogen, potassium, and magnesium (Marschner 2012, Taiz and Zeiger 2002). Except for nitrogen and carbon, all these elements—especially magnesium—had higher concentrations on the soil of alluvial sites. The concentration of magnesium was 4 times higher on the soil of alluvial than karst sites. In turn, the ratios of N:Mg and Mg:P in the soil were notably different, being higher and lower, respectively, at karst vs alluvial sites. There were also differences in soil elemental concentrations that were not attributable to substrate type. For example, the karst site JN had the highest soil phosphorus and low soil nitrogen concentration, which, along with other differences in soil elemental concentrations, led to a distinct elemental ratio soil profile signature at JN compared to the other sites (Fig. 3).

The differences in soil chemistry and stoichiometry that we found among alluvial and karst sites translated into many more differences in the elemental concentrations and element ratios of canopy foliage, litterfall, and standing-litter components (Tables 3, 4; see also Supplemental Tables S1, S2, S3, and S4 in Supplemental File 1). *Spathodea* canopy foliage and leaf fall exhibited the most differences in chemistry and stoichiometry, which included higher contents and concentrations of nitrogen and phosphorous at alluvial sites, and higher N:P and Mg:P at karst sites. The differences in chemistry and stoichiometry due to substrate type mostly disappear in standing-litter components except for fragmented leaves, humus, and detritus, which in turn may be due to influence by the soil microbial community. In all, these findings indicate a relatively higher level of nutrient limitations, particularly phosphorus, on soils at karst compared to alluvial sites. These conclusions are supported by the higher retranslocation percentages for phosphorous from *Spathodea* foliar tissue from *Spathodea* stands at karst compared to alluvial substrate (Table 10, Fig. 12).

The previous answers to our first study question underscore that heterogeneity in local conditions that lead to differences in the pedogenesis and classification of soils, whether on alluvial or karst substrates, influence the chemistry and stoichiometry of soils, and in consequence, of forest ecosystem components of *Spathodea* stands. An illustrative example is the *Spathodea* stand at JN, which stood apart from stands at the other karst sites with regards to many aspects of the chemistry and stoichiometry of soil and forest compartments evaluated (Figs. 3, 5, 6, 10, 11; see also Supplemental Tables S1, S4, and S8 in Supplemental File 1). The soils of JN were distinct, initially classified as entisols (Tables 1, 2; Beinroth et al. 2003), a classification unlike the rest of soils at all other sites. The soils at this site were

Figure 15 (preceding page). Nine mean molar element ratios for soil, adult leaves, senesced leaves, leaf fall, and leaf litter of *Spathodea campanulata* stands on alluvial and karst substrates in north-central, Puerto Rico. The element ratios are: (A) N:K, (B) Ca:P, (C) Ca:Al, (D) K:P, (E) C:N, (F) C:P, (G) N:P, (H) Ca:K, and (I) Fe:Mn.

characterized by low bulk density and by element concentrations and some element ratios that were different from most, if not all, sites (Table 1, Fig. 3; see also Supplemental Tables S1 and S4 in Supplemental File 1). The low bulk density that we measured at JN was much lower than reported for the San Germán series in Table 2. Notably, soil aluminum, iron, and phosphorous concentrations were higher, and calcium concentration lower, at JN compared to all other sites, and soil magnesium concentration was higher and nitrogen concentration lower at JN vs the other karst sites. These results translated into even more differences in stoichiometry between JN and all other sites that were characterized by ratios of elements to phosphorous that were much lower than at the other sites, especially N:P (see Supplemental Table S4 in Supplemental File 1). In addition, the soils at JN were acid, with the lowest pH values along with those at CII, indicating greater immobilization and low availability of most nutrients (except for iron and manganese), including nitrogen in the form of nitrate ($-\text{NO}_3$; see Supplemental Table S1 in Supplemental File 1; Brady and Weil 2002). Indeed, soil N:P was positively related to soil pH (Table 11), indicating lower available nitrogen relative to phosphorus on sites with acid soils such as JN. This result strongly suggests a nitrogen limitation to plant growth on the soils of JN relative to all other sites (Sterner and Elser 2002, Vitousek 1984, Vitousek and Sanford 1986). This conclusion is also supported by the retranslocation of nitrogen in mature *Spathodea* leaves, which was amongst the highest at JN (Table 10), indicating higher supply of this nutrient from internal sources than from soil uptake. Accordingly, temporal values of N:P were low in *Spathodea* adult leaves at JN compared to all other sites along the sampled period, indicating a higher demand for nitrogen in the foliage and other internal components of the *Spathodea* stand on this site (Fig. 4). Since nitrogen is limiting at JN and not the other sites, the negative relationship among soil nitrogen storage and total litterfall production is only evident when this site is excluded (Fig. 13); the pattern is reversed when JN is included. In all, the concentrations of calcium, nitrogen, magnesium, and phosphorous, and the molar ratios that include these elements, were unique on soils at JN compared to the other sites.

The distinct chemistry and stoichiometry of soils at JN translated into corresponding differences in canopy foliage, litterfall, and standing litter relative to all other sites (Figs. 3, 4, 5, 6, 10, 11, and 13; see also Supplemental Table S1, S4, and S8 in Supplemental File 1). The concentrations of aluminum, magnesium, and phosphorous in *Spathodea* canopy adult leaves and leaffall compartments were highest at JN relative to all other sites. On the other hand, iron concentration in *Spathodea* adult leaf and leaffall compartments was no different at JN than at the other sites, and calcium concentrations were higher on these compartments at JN than all other sites in spite soil calcium being lowest at JN. Thus, the answer to our second study question is that differences in chemistry and stoichiometry of soils translate into corresponding differences in canopy foliage, litterfall, and standing-litter compartments of *Spathodea* forest stands. However, the resulting relationships may not be as expected, as for calcium, due to the interaction of this element with others (e.g.,

potassium, sodium, magnesium) during the process of uptake from soil and the incapacity of plants to remove calcium by nutrient retranslocation during leaf senescence (Aerts 1996, Killingbeck 1996, Marschner 2012, Niinemets and Tamm 2005). As a result of apparent nitrogen and calcium limitations in the soil of JN, the element ratios of N:Mg, N:Ca, and K:P in adult canopy leaves, senesced leaves, and brown and green leaf fall of *Spathodea* at JN is different from that of all other sites. These findings clearly show soil and leaf tissue chemistry are tightly coupled on the novel *Spathodea* forest stands that grow in north-central Puerto Rico.

The chemistry and stoichiometry of soils of JN stood apart from that of karst sites, at times being similar to alluvial sites, and this translated into elemental concentrations and element ratios of adult leaves, litter and litterfall that at times resembled that of alluvial sites as well (Tables 3, 4; Figs. 3, 4, 5, 6, 10, 11; see also Supplemental Table S1, S3, S4, S7, and S8 in Supplemental File 1). Soil phosphorous concentration at JN was higher than on all other sites, which resulted in canopy foliage, standing litter, and litterfall compartments that had a phosphorus content and ratios of other elements to phosphorous that were different from the other 2 karst sites and similar to the alluvial sites. Something analogous, but to a lesser degree, occurred with soils at CI, which are classified as inceptisols, also differently from all other sites. This difference in soil type influenced the chemistry and stoichiometry of litterfall, foliage, and litter compartments at CI, which at times differed from the other 2 alluvial sites. These findings are consistent with stands at JN and CI growing on soils that are classified differently from the other sites, underscoring the implications that pedogenesis and resulting soil properties, including chemistry and stoichiometry, may have on ecosystem structure and function (Tables 1, 2). In fact, JN and CI are the only sites in the study with soils that were not classified as mollisols according to Beinroth et al. (2003).

The San Germán soil series found in JN was reclassified from an entisol to a mollisol during the time span of this study (Muñoz et al. 2018). This update explains some of the affinities in soil chemistry and stoichiometry among JN and the other alluvial sites. Although the other 2 karst sites are also classified as mollisols, the classification of soils at JN is more akin to the mollisols of alluvial sites, being active to super active (i.e., shrink and expand based on water content) and characterized by minimum soil-horizon development (i.e., prefix hapl- in taxonomic group). In contrast, the mollisols of OC and P are carbonatic, meaning they contain a large proportion of calcium carbonate rocks, and display an argillic horizon (Tables 1, 2). The absence of carbonate rocks can explain the low soil calcium at JN. On top of this, *Spathodea* stands modify the soil by the return of litterfall characterized by forest ecosystem compartments that adjust some ratios (e.g., N:P, Mg:P, and N:Ca) to suit the metabolic requirements of plant tissue and respond to the mobility of elements (e.g., potassium vs. calcium). Forest stands, whether dominated or not by *Spathodea*, also influence pedogenesis and the formation of soil layers, especially the organic horizons, and feedback into soil classification in a process that takes longer than the time these forests took to grow after agricultural abandonment and up to maturity (i.e., 30 to 40 years;

Table 1). The high rates of growth and primary productivity of *Spathodea* forest stands may be accelerating this feedback to the soil (Abelleira Martínez 2019, Lugo and Abelleira Martínez 2018, Lugo et al. 2011).

Despite the heterogeneity in soil chemistry and stoichiometry among these sites, the effect of geological substrate is still evident in the differences in litterfall rates, tree basal area, and biomass of *Spathodea* stands on alluvial and karst substrates (Abelleira Martínez 2011, Abelleira Martínez et al. 2010, Lugo et al. 2011). In contrast, our study found that the mass of standing-litter components is not any different among *Spathodea* stands on alluvial and karst substrates except for fine wood (Table 8). This difference may be related to higher tree basal area, and hence woody material, at alluvial sites (Abelleira Martínez et al. 2011, Marengo Casul 2023).

However, the example of JN makes it clear that variation in soil chemistry and stoichiometry is reflected in tree foliage of *Spathodea* forest stands, and that this variation can be traced from adult canopy leaves all the way to standing-litter components. These variations can in turn be related to a lower canopy LAI, standing-litter mass, tree basal area, and biomass at JN compared to all other sites (Tables 1, 9 ; see also Supplemental Table S9 in Supplemental File 1; Abelleira Martínez 2011, Lugo et al. 2011). The apparent limitation of soil nitrogen at JN, which is evident on *Spathodea* adult leaf and leaffall material, also appears to translate to lower primary productivity, and hence lower canopy leaf area, mass of leaves in standing litter, thinner trees, and less accumulated biomass compared to other sites despite the same age since abandonment and onset of forest succession. Thus, the answer to the third question posed by our study is that soil chemistry and stoichiometry does influence ecosystem-level attributes and processes of *Spathodea* forest stands; only that it is diluted amongst other factors, such as flooding regime, that may be related to geological substrate type. For example, pulses in the rate of litterfall were dependent on flooding events that occurred independently on some alluvial and karst sites, and not others, and this affected the annual litterfall mass (Fig. 4, Table 6). This relationship is apparent in the litterfall peaks at P and JN, which were absent at the other karst site OC and that resulted in lower annual litterfall mass in the latter. These findings highlight that heterogeneity in local conditions that result from soil properties, geological substrate type, and other factors affect ecosystem function of novel *Spathodea* forests, with implications on concomitant services related to carbon storage and nutrient retention.

***Spathodea campanulata* phenology effects on soil and foliage chemistry and stoichiometry**

Among all tree compartments sampled, adult *Spathodea* leaves had the highest element ratios for Ca:Al (Fig. 15C), which buffer toxic effects of aluminum (Cronan and Grigal 1995). Senesced *Spathodea* leaves had the highest K:P, C:N, and C:P element ratios, consistent with the reabsorption or retranslocation of phosphorus and nitrogen associated with leaf senescence (Figs. 15D, E, and F, respectively.). The N:P ratio increased from soil to recently fallen leaves, followed by a decline in old leaf litter and a convergence of element ratios among karst and alluvial old

leaf litter (Fig. 15G). The increases in C:N and C:P from soil to senesced leaves reflect both the fixing of carbon in leaves and the translocation of phosphorus and nitrogen before leaf fall. We attribute the difference in the pattern of change (compare Fig. 15E with 15F) to nitrogen not being limiting in these forests, except for at JN, and to the differences in phosphorus concentration in falling *Spathodea* leaves on alluvial and karst substrates. The *Spathodea* stand at the karst site JN is also an exception to the latter, as this site exhibited the highest concentration of phosphorus in leaf tissue and the highest peak in concentration in *Spathodea* leaf fall (Fig. 4). Thus, higher foliar phosphorus concentration on *Spathodea* leaves on *Spathodea* stands, regardless of substrate, lowers the C:P in canopy foliage, litterfall, and standing-litter forest compartments (Fig. 15F). At karst sites, a higher retranslocation of phosphorus is translated into *Spathodea* brown (i.e., senesced) leaf fall that has much higher C:P than *Spathodea* green leaf fall (Tables 4, 10). This finding illustrates that *Spathodea* stands adjust foliar nutrient resorption processes in response to soil nutrient availability, and in turn this modifies the nutritional quality of *Spathodea* leaf tissue returned in litterfall to the soil.

Adult leaves of *Spathodea*, regardless of substrate, have similar and close to optimal Ca:K element ratios that contrast with the diverging and higher values in the soil the plant is growing in (Fig. 15H). This finding suggests metabolic selectivity for potassium uptake. Because the potassium ion is so mobile, the Ca:K ratio increases in senescent yellow leaves and leaf fall. In contrast, the Fe:Mn ratio remains constant from adult to leaf fall, increasing dramatically in the leaf-litter compartment (Fig. 15I).

The chemical changes that occur in the leaf-litter compartment as it ages have already been noted and discussed in other forest types on volcanic substrates (Lugo et al. 1990, 2022; Vitousek 2004). Our study confirms that as the forest compartments change from soil through the process of leaf development, fall, and decomposition, they develop their own nutritional dynamics as reflected in the changes in element ratios (Fig. 15). The element ratios of old *Spathodea* leaf litter are particularly notable. Element ratios for Ca:Al and K:P of old leaf litter are close to those of soil (Fig. 15C, D). For most of the other element ratios (N:K, Ca:P, C:N, C:P, N:P; Figs. 15A, B, E, F, G, respectively), old leaf litter maintains higher values than soil. We believe that these results reflect the metabolic activity of the microbial communities of leaf litter. Soil microorganisms have the capacity to alter the stoichiometry of falling leaves within the context of their own metabolism and environmental conditions. Accumulation of nitrogen leads to higher N:P, and leaching of potassium alters the N:K ratio. For Ca:P and C:P, these microbial communities are transforming the leaf fall materials in contrasting directions, with calcium increasing relative to phosphorus to a greater degree in the alluvial litter, while carbon is accumulating in the karst leaf litter relative to phosphorus.

Adult-leaf chemistry. *Spathodea campanulata* adult-leaf chemistry varied throughout the year (Fig. 4A–D) reflecting the difference between stands and their phenology. The phosphorus concentration peak was common to all study sites and

coincided with the production of new leaves (leaf-out) that followed complete canopy opening during late June and early July, when there were no leaves in *Spathodea* tree crowns (Fig. 4A; Abelleira Martínez 2011). Nitrogen (Fig. 4B), and carbon (Fig. 4C) concentrations in adult leaves increased as the canopy reached full closure. Then phosphorus, nitrogen, and carbon concentrations all decreased sharply during September, and nitrogen concentration continued to slowly decreased thereafter. In turn, molar ratios exhibited similar patterns. In particular, the strong temporal dip in C:P and N:P that occurred in *Spathodea* adult leaves coincided with leaf-out, suggesting a high rate of carbon fixation in newly formed leaves during this time. Our temporal element concentration results from *Spathodea* adult leaves reflect the aging of canopy leaves from young (following leaf-out) to adult (mature leaves) to old (prior to senescence and fall), as leaf-nutrient concentrations change with leaf age and are associated with changes in mass:area and element ratios (Medina 2024).

For carbon (Fig. 4C), the concentration peaked in early August, decreased slowly up to another peak or plateau during late October and early November, depending on site, and then decreased sharply in late November and December. The second peak and sharp drop in carbon concentration was most evident in adult leaves collected at CI and P and coincided with the onset of flowering on all sites (Fig. 4C; Abelleira Martínez 2011). Retranslocation of nutrients (Fig. 12C, B) peaked in August for phosphorus and was high from August onwards for nitrogen, coinciding with the onset of flowering. This process may move nutrients from leaves to flowering buds to support flower production and can be associated to this second peak in carbon concentration in adult leaves, and to drops in nitrogen and phosphorous concentrations observed at most sites in November. Flowering buds of *Spathodea* contain high concentrations of nitrogen and enzymes related to phosphorous metabolism (Charylulu and Rao 1990, 1995), and high demand may be supplied partly from leaves, especially canopy leaves that are close to the terminal flower panicles.

Litterfall chemistry. While the pulses in element concentrations in adult leaves are related to phenological processes, the absence of such pulses in litterfall materials relate to plant reabsorption of elements prior to litterfall (Figs. 4, 12). Some of these elements are more limiting in karst than alluvial sites (e.g., magnesium and phosphorous), and therefore there are much more differences in the elemental concentrations and element ratios among *Spathodea* brown leaffall, which has undergone some senescence, and *Spathodea* green leaffall of *Spathodea* stands at karst than alluvial sites (Tables 1, 4). The rate of litterfall, while it influences the quantity of element return to the forest floor, does not influence the element ratios of falling materials (illustrated for leaffall in Fig. 9). For both alluvial and karst sites, we observed pulses of leaffall, but the element ratios did not reflect the pulse in leaffall. Instead, variations in N:P and K:P in leaffall appeared to be related to other factors, such as internal processes of leaf senescence or responses to flooding. For example, the peaks in these ratios during January and May were mostly absent in OC, the only site that did not flood. The element ratios involving potassium exhibited more

temporal oscillations, but they were not timed to pulses in mass fall. These potassium element pulses appear to be related to the onset of leaf senescence during May–June, and leaf-out during August–September (Abelleira Martínez 2011).

Leaf-litter chemistry. The litter layer of *Spathodea* forests is characterized by its high element concentrations and low carbon concentrations compared to litter from mature historic forests (Erickson et al. 2014). The concentrations that we found reflect the composition of the litterfall input (discussed above). Here we emphasize the chemical transformation of *Spathodea* leaves from the canopy (adult leaf composition discussed above) to the leaf-litter layer. The chemical difference in *Spathodea* leaves from plants growing on karst substrates (high calcium concentration) and those from alluvial sites (high phosphorus concentration) is maintained in the litter layer, but the rest of the chemical signature of *Spathodea* leaves is homogenized (with few exceptions) in the litter layer. This finding is probably due to the functioning of the decomposer community in these forests. As the litter is fragmented and decomposed, nutrient concentrations change because of the uptake and retention by microbial communities and roots, leaching, and accumulation in longer-term storages such as humus. These processes alter the initial element concentrations in falling litter, but not sufficiently to alter the difference between alluvial and karst substrates in the elements phosphorus and calcium.

In the following sections, we discuss the ecosystem-level implications of our findings, with special attention to the effects of fine-scale differences. Finally, we compare our results with those of other similar studies on tropical forests to place *Spathodea* novel forest stands in ecological and biogeochemical context of historic and novel forests in Puerto Rico and elsewhere.

Ecosystem-level implications

The differences in chemistry and stoichiometry of brown and green *Spathodea* leaffall among alluvial and karst sites are for different element concentrations or element ratios, which indicate that different mechanisms are responsible for the differences observed at the aggregate level (i.e., *Spathodea* leaffall; Tables 3, 4). These mechanisms are related to nutritional requirements to support photosynthetic rates for green *Spathodea* leaffall, and to leaf senescence and retranslocation of nutrients from foliar tissue back to the tree. The nutritional requirements are higher for key elements (i.e., nitrogen, phosphorus) at alluvial vs karst sites, as indicated by higher concentration of those nutrients in adult leaves (Table 3). The physiological need for retaining those same elements is higher at karst sites, at least for phosphorus, as suggested by the lower content of this element, and hence higher retranslocation rates, on senesced leaves at karst compared to alluvial sites (Tables 3, 10). This conclusion is further indicated by higher N:P ratios on *Spathodea* adult, senesced leaves and leaffall, which were always higher at karst compared to alluvial sites in spite the absence of differences in this ratio in the soil among these sites (Table 4, Fig. 4). These findings, along with those indicating that soil nitrogen was limiting at JN, illustrate that tree ecosystem compartments of novel *Spathodea* forest stands adjust their chemistry and stoichiometry according to internal requirements, and that soils set the starting point for any necessary changes.

Likewise, the changes in stoichiometry and chemistry undergone in foliage, and the consequent inputs in leaf fall, disappear as leaves decompose into detritus and humus, and eventually into soil organic matter (Tables 3, 4; see also Supplemental Table S1, S2, S3, and S4 in Supplemental File 1). The element ratios of these standing-litter compartments, which have undergone significant decomposition, more closely resemble those of the soil compared to the others. The chemical and stoichiometric coupling of signatures of the canopy–litterfall–standing litter–soil relationship decreases with soil depth, indicating a limit to the effects of the establishment of novel *Spathodea* forest stands on lands previously deforested and used for agriculture. The limit of the feedback also occurs going from soil to canopy. For example, differences in element ratios of carbon to other elements in the soil, while very evident at JN relative to other sites, do not translate into the same differences among *Spathodea* adult, senesced, and fallen leaf material, unlike differences for element ratios with other elements as the numerator, which persist. Decomposition further normalizes carbon content to other elements among sites by the mobilization of nutrients necessary for microbial and plant growth.

Over the 659 days of this study, we observed similar temporal patterns and rates of litterfall as reported by Abelleira Martínez (2011) for the first 395 days. The main difference was that the peak rates of litterfall during August 2007 were higher for 2 alluvial sites, CI and CII, that were subject to the most frequent and extensive flooding events, and coincidentally experienced the highest litterfall rates in the study (almost 20 g/m²•day; Fig. 5; Pérez et al. 2012). That was the period when we lost the collection for an alluvial site, PI, due to excessive flooding. These peak events in litterfall are caused by the periodic atmospheric disturbances that forests in Puerto Rico must overcome, including floods due to heavy and/or prolonged rains, thunderstorms and hurricanes, as has been described for litterfall patterns for wetland forests on floodplains (Álvarez 1990, Euse and Aide 1999), historic forests on volcanic substrates at the Bisley sector of the Luquillo Mountains (Scatena et al. 1996), and novel forests of Utuado in the central mountains of Puerto Rico (Lugo et al. 2011). At Utuado, the rate of element return by litterfall is accelerated during and after disturbances such as hurricanes (Lugo et al. 2011). Flooding, combined with atmospheric low-pressure systems, had similar effects on alluvial novel *Spathodea* forests.

The results of our study provide an explanation to the observations of Erickson et al. (2014) that the loose litter of novel forests throughout the island are nutrient-enriched relative to the loose litter of historic forests. We found that litterfall in *Spathodea* forests function as a “nutrient-pump” by returning the highest quantities of elements per unit area/time measured so far in the island (Table 12). The high level of nutrient return occurs because of the low nutrient-use efficiency of leaf fall in these stands (Fig. 16). When compared to nutrient-use efficiencies reported by Vitousek (1984, 2004), Cuevas and Medina (1986), Medina and Cuevas (2000), Lugo et al. (1999), and others for other tropical and temperate forests (Table 13), the values for *Spathodea* forests are, by a large margin, the lowest reported, except for potassium in the Bisley watershed (Scatena et al. 1996). Except for nitrogen at JN, the nutrient use-efficiency of *Spathodea* forests in this study suggests an

Table 12. Comparison of mass and nutrient concentration and flux in litterfall, and nutrient concentration in loose litter and soil of various tropical forests arranged along a soil pH gradient. The first 4 columns correspond to the Venezuelan Amazon region of San Carlos (SC) and La Esmeralda (LE). Forests in these regions were wet forest tall caatinga and low bana forests (Medina and Cuevas 2023). Soil pH was from García Montero (2023) and nutrient concentrations from nearby shrubby meadows (Zinck and García Montero 2023). The 2 volcanic columns correspond to secondary forest stands in the Barranquitas (Lugo et al. 1999, Popper et al. 1999) and Utuado (Lugo et al. 2011, Popper et al. 1999) municipalities of Puerto Rico. Moist alluvial and moist karst data correspond to *Spathodea campanulata* forests in this study. Dry karst data are from the Guánica Biosphere Reserve (Lugo and Murphy 1986). Mangrove forest data correspond to a forest in the Jobos Bay National Estuarine Research Reserve (Lugo et al. 2007). “-” indicates data not available.

Parameter	Location/forest type									
	SC		LE		Puerto Rico					
	Tall	Low	Tall	Low	Moist volcanic	Moist alluvial	Moist karst	Dry karst	Fringe mangroves	
Litterfall (Mg/ha•yr)										
Leaf Fall	4.0	2.1	4.3	4.2	5.5	4.4	8.4	7.1	4.3	10.1
Total Litterfall	5.4	2.4	6.7	5.2	7.2	6.0	15.4	13.4	4.8	16.9
Nutrient concentration in leaf litterfall (mg/g)										
Nitrogen	7	6	8	7	20	17	18	17	-	-
Phosphorus	0.5	0.2	0.2	0.2	0.5	0.6	1.8	1.4	-	-
Potassium	2.1	4.7	2.0	2.3	5.0	6.4	6.8	5.7	-	-
Calcium	8	7	6	16	7	16	38	46	-	-
Magnesium	3.1	2.5	1.7	2.0	2.3	3.2	3.5	3.7	-	-
Nutrient flux in leaf litterfall (kg/ha•yr)										
Nitrogen	28	12	33	29	105	82	141	119	44	63
Phosphorus	2.0	0.4	0.8	1.0	3.0	3.0	15.0	9.0	0.7	2.0
Potassium	8	10	9	10	29	28	49	33	35	57
Calcium	31	15	28	69	38	75	394	339	-	204
Magnesium	13	5	7	8.3	13	15	30	25	-	63
Nutrient flux in total litterfall (kg/ha•yr)										
Nitrogen	-	-	-	-	133	108	228	203	49	108
Phosphorus	-	-	-	-	4	4	31	19	1	8
Potassium	-	-	-	-	35	39	124	79	36	91
Calcium	-	-	-	-	46	93	480	470	-	274
Magnesium	-	-	-	-	15	19	47	32	-	80
Nutrient concentration in loose litter (mg/g)										
Nitrogen	-	-	-	-	-	18	16	17	13	-
Phosphorus	-	-	-	-	-	0.8	1.9	1.3	0.3	-
Potassium	-	-	-	-	-	3.1	4.0	3.3	1.4	-
Calcium	-	-	-	-	-	15	41	55	-	-
Magnesium	-	-	-	-	-	4.6	3.4	4.0	-	-
Nutrient concentration in topsoil (mg/g) – (SC and LE sites combined)										
Nitrogen	3–7				3	5	30	40	11	-
Phosphorus	0.0–1.0 mg/kg				0.03	0.001	0.80	1.20	0.60	-
Potassium	1.00–9.00 mg/kg				0.11	0.01	0.90	0.70	0.40	-
Calcium	1.0–10.0 mg/kg				0.1	0.4	12.0	39.0	5.0	-
Magnesium	0.30–2.00 mg/kg				0.07	0.11	8.40	2.20	0.90	-
pH	3.6–5.1				4.0	5.1	6.2	6.7	7.8	-

overall absence of nutrient limitation to forest functioning. *Spathodea* stands on karst, however, do appear more phosphorous-limited than at alluvial sites, with ecosystem-level consequences that can include a higher limit to primary productivity and hence lower LAI, litterfall mass, and biomass on stands on karst compared to alluvial substrates.

The low efficiency of nutrient-use has implications to stand productivity. The coincidence of high rate of litter productivity and low nutrient-use efficiency was also found in the response of a wet volcanic forest to hurricane Hugo in the Bisley sector of the Luquillo Mountains of Puerto Rico (Scatena et al. 1996). They assessed nutrient-use efficiency in several ways (efficiency of net aboveground biomass productivity:nutrient uptake, aboveground productivity:nutrient return by litterfall, and litterfall productivity:nutrient return) and found that when the forest was least efficient in nutrient-use, it exhibited the highest net primary productivity ever measured in that forest. Sterner and Elser (2002) suggested that stoichiometrically balanced ecosystems have high productivity, and based on some of the criteria that they used, our study sites appear to be stoichiometrically balanced. For example, the adult leaf C:N:P (612:26:1) of *Spathodea*, relative to adult leaves of *Dacryodes excelsa* Vahl (Tabonuco; see below) is closer to the Redfield ratio (106:16:1) and nutrient-use efficiency is low. In comparison, adult-leaf C:N:P of a *D. excelsa* forest in the Luquillo Mountains is 2326:56:1, and nutrient-use efficiency is high, which makes that forest stoichiometrically unbalanced according to Sterner and Elser (2002). Rapid decomposition rate in the *Spathodea* forest (Lugo

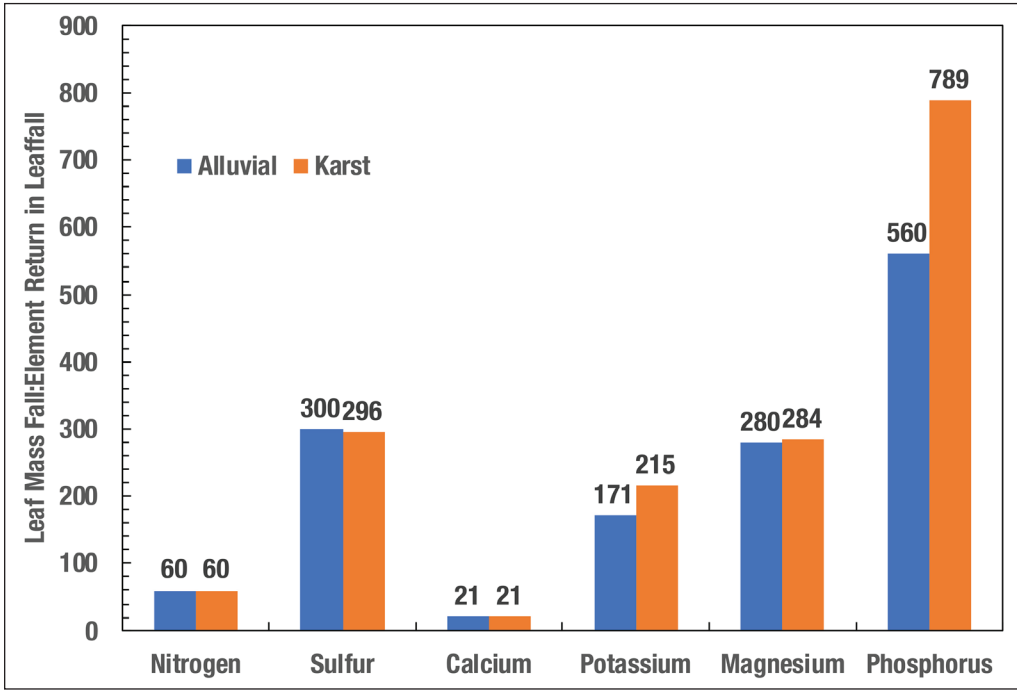


Figure 16. Within-stand nutrient-use efficiency of 6 elements for leaffall in *Spathodea campanulata* forest stands in north-central Puerto Rico growing on alluvial and karst substrates.

and Abelleira Martínez 2018) further supports the conclusion that these forests are stoichiometrically balanced.

The relationship of N:P and C:P for our study sites further separate *Spathodea* forests from historic mature and successional forests in Puerto Rico (compare our Figure 17 with figure 5 in Lugo et al. [2022]). The slopes of the relationships are similar, but the values for our study sites are at the extreme lower values for both element ratios. Within our study, alluvial sites had lower values than karst sites (Fig. 17). The displacement of the karst sites to higher N:P and C:P element ratios relative to alluvial sites are related to the differences in phosphorous concentration among soils at alluvial and karst sites, which affects N:P and C:P, and to the availability of nitrogen and phosphorous in the soil, which in turn is mediated by pH. All components of foliage, litterfall, and standing litter have higher values of N:P and C:P in *Spathodea* stands at karst compared to alluvial sites despite similar values for those ratios in the soils of both substrate types. These results suggest that *Spathodea* stands on karst modify tissues to reabsorb and retain phosphorous, further illustrating phosphorous limitations in the soil of karst sites.

Lugo (1992) found that the storage of nitrogen and phosphorus in soil to a depth of 1 m at plantations and secondary forests of similar age were correlated with the

Table 13. Nutrient-use efficiency of leaffall (except when noted) of several tropical forests in Puerto Rico, Venezuela, and Hawaii, arranged from the least phosphorus efficient to the most phosphorus efficient. Venezuelan forests are from San Carlos (SC) and Hawaiian forests represent a transect along geological age of substrates. Puerto Rico sites are from this study, the Luquillo Experimental Forest (LEF), Barranquitas (B), Utuado (U), and Guánica (G). *Hernandia sonora* is a plantation with the lowest nutrient-use efficiency among 10 plantations that were studied. “-” indicates data not available.

Tropical forest type	Nutrients					Source
	N	P	K	Ca	Mg	
Moist alluvial <i>Spathodea</i>	60	560	171	21	280	This study
Moist karst <i>Spathodea</i>	60	789	215	21	284	This study
Wet <i>Hernandia sonora</i> 26 yr (LEF)*	62	1200	200	128	217	Cuevas and Lugo 1998
Wet volcanic 18 yr (LEF)	66	1329	434	-	-	Lugo 1992
Moist volcanic 60 yr (B)	56	1472	167	68	315	Lugo et al. 1999
Moist volcanic 50 yr (U)	52	1833	190	145	423	Lugo et al. 2011
Wet volcanic, post hurricane (0 to 60 mo., LEF)	112	2300	148	-	-	Scatena et al. 1996
Wet tall caatinga (SC)	143	1965	499	127	319	Cuevas and Medina 1986, Medina and Cuevas 2000
Wet volcanic 18 yr (LEF)	118	2366	447	-	-	Lugo 1992
Wet volcanic 50 yr (LEF)	91	3222	527	-	-	Lugo 1992
Wet mixed forest (SC)	63	3570	492	582	1455	Cuevas and Medina 1986, Medina and Cuevas 2000
Hawaii geologic age series	190– 400	3900– 7000	-	-	-	Vitousek 2004
Wet bana (SC)	171	4813	207	209	406	Cuevas and Medina 1986, Medina and Cuevas 2000
Dry karst (G)*	98	6057	134	-	-	Lugo and Murphy 1986

* Total litterfall

mass-weighted concentration of nitrogen and phosphorus, respectively, of leaf fall, vegetation, and understory vegetation. The negative correlations observed in this study (Fig. 13) differed from the positive ones reported by Lugo (1992). Given the low nutrient-use efficiency in these *Spathodea* forests, it is possible that they are at the high end of the soil-fertility gradient beyond the range of nutrient limitation and beyond the optimal nutritional conditions. In support of this hypothesis, the negative relationship of soil nitrogen to total litterfall would turn positive if the outlier site, JN, which is the only nitrogen-limited site, is included in the relationship (Fig. 13). Positive correlation with nutrient richness such as that reported by Lugo (1992) would be expected when there are nutrient limitations, and negative ones such as ours, when nutrients are not limiting. When nutrients are not limiting, some other environmental factor, such as flooding or other disturbance regimes, may be driving ecological functioning.

In a study of the stoichiometry of forests on acid soils, Lugo et al. (2022) found that acidity could drive forest productivity positively and negatively through its effects on the availability of phosphorus and aluminum, respectively. The pH values found at our study sites are higher than those measured by Lugo et al. (2022) in volcanic substrates and wetter conditions. But our forests were not exposed to the higher pH that typically selects for calcitrophic species adapted to conditions

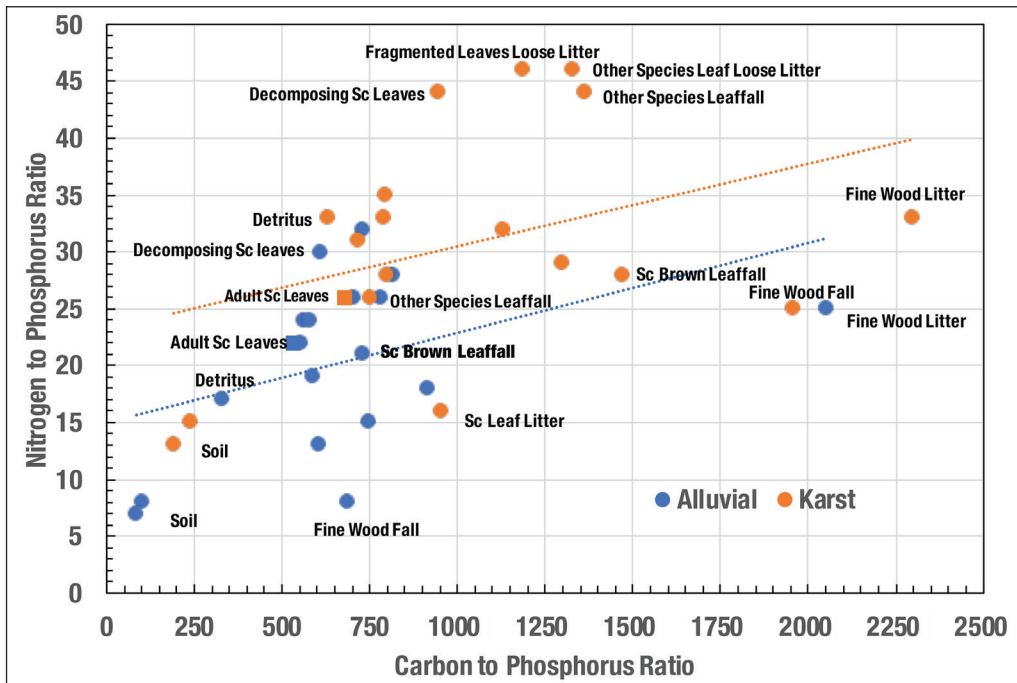


Figure 17. Relationship between the N:P molar ratio to the C:P molar ratio in plant compartments and soils of *Spathodea campanulata* (Sc) forests growing on alluvial and karst substrates. The square points represent the ratios for adult leaves of Sc. The respective trend lines have the same slope. Not all points are labeled but all data are available in Supplemental Table S5 in Supplemental File 1.

that limit ecological processes due to phosphorus limitation (Medina 2015). Our sites were functioning between the extreme acid volcanic soils and extreme basic karst soils under optimal moisture conditions and fertile soils. Still, soil pH, within the small range in our sites, appeared to have a definitive influence in their stoichiometry of vegetation and soils. Soil pH has a great influence on soil nutrient concentrations and fertility (Brady and Weil 2002, Thompson and Troeh 2005). In the case of *Spathodea* forest stands, the influence of soil pH on the element ratios is an indication of the coupling of soil properties to processes involved in nutrient uptake by roots. Our study illustrates that soil pH affects the stoichiometry of forest canopy and litterfall components of *Spathodea* stands, and of ecosystem processes, such as microbial decomposition, that depend on the elemental ratios of biomass of these components (Table 11).

Comparison with other tropical forests

Spathodea campanulata forests in Puerto Rico, whether growing on alluvial or karst substrates, exhibit faster rates of leaf and total litterfall than 5 of the 6 other forest types listed in Table 12. Only fringe mangroves exhibited faster rates of leaf and total litterfall. Those other forest types, arranged along a gradient of increasing soil pH, represent the tall and short caatinga forests on white sands in the Venezuelan and Colombian Amazon, secondary forests of similar age to our study sites on volcanic substrates in the Luquillo Mountains of Puerto Rico, and a dry karst forest at Guánica on the south coast of Puerto Rico. Notably, the return of the macronutrients by leaf and total litterfall in *Spathodea* forests was much higher than measured in all other forests, including mangroves. These data suggest a lower nutrient-use efficiency in *Spathodea* litterfall fluxes, which is also reflected in the high concentration of nutrients in leaf litterfall, particularly phosphorus, calcium, and magnesium. Calcium concentration remains high in leaf loose litter on the forest floor.

At the outset (Table 1), we pointed out that the soils in our study sites, mostly Mollisols, are considered fertile soils, which is a factor that contrasts with the white sands of the Amazon caatinga, the karst soils of Guánica, and the volcanic soils in the mountain region of Puerto Rico (Table 12). The fertility of soils at our study sites is also reflected in the chemistry of adult leaves of *Spathodea*. The concentrations of ash and elements of adult *Spathodea* leaves (see Supplemental Tables S1 and S3 in Supplemental File 1), when compared to those of 143 tree species in Puerto Rico (Medina 2015), provides insight about the species, whether in alluvial or karst substrates, and about each of our study sites. In general, the concentrations of ash and elements in *Spathodea* leaves was higher than the median of the tree species reported by Medina (2015). For example, *Spathodea* adult leaves were in the high-concentration group for calcium with 830 and 940 mmol/kg for alluvial and karst sites, respectively, vs a median of 245 mmol/kg for the 143 tree species studied. Potassium and carbon, which is not a nutrient, were the exception, with lower concentrations in *Spathodea* leaves. Carbon concentration in *Spathodea* leaves was notably lower than reported for other tree species (36 vs 42.6 mol/kg). This result

suggests that a mol of carbon in *Spathodea* leaves is associated with a higher proportion of other elements than most leaves of trees so far reported. Of particular significance is the concentration of phosphorus in adults *Spathodea* leaves (see Supplemental Table S1 in Supplemental File 1). Phosphorus was significantly different between adult leaves on alluvial and those in karst substrates (75 vs 62 mmol/kg), but in both instances, the values are among the highest phosphorus concentrations reported (the median for the 143 tree species was 23 mmol/kg, Medina 2015).

The element ratios of adult leaves of *Spathodea* contrasted with those of *Metrosideros polymorpha* Gaudich. ('Ōhi'a lehua) and *D. excelsa*, each a dominant species in their respective volcanic and acidic soils of Hawaii and Puerto Rico, respectively (Table 14). Element ratios of potassium, nitrogen, and carbon to other elements were lower in *Spathodea*, which in turn had higher element ratios of calcium to other elements. Differences in soil acidity (lower in the volcanic sites) explain the differences in calcium element ratios. High calcium and phosphorus concentrations in *Spathodea* leaves help explain their lower nitrogen element ratios. Both *D. excelsa* and *M. polymorpha* are mature forest species with longer life spans compared to *Spathodea*, which is a pioneer with short life span, and this difference explains their higher carbon element ratios.

The high nutrient concentrations in *Spathodea* leaves are reflected in the element-composition signature (Fig. 18; sensu Medina 2015). The element-composition signature is a chemical profile of a species using the concentration of 6 major nutrients. *Spathodea campanulata* adult leaves at all 6 study sites are richer than 20 of the 21 species analyzed by Medina (2015:figure 7). Only *Guarea guidonia* (L.) Sleumer (Muskwood), a native successional species, had an element profile similar to those of *Spathodea*, with the difference that most of the profile of *G. guidonia* was nitrogen, while *Spathodea* had lower concentration of nitrogen but higher

Table 14. Comparison of adult leaf molar element ratios of tropical tree species dominant in forest stands on Hawaii and Puerto Rico. *Metrosideros polymorpha* from Vitousek (2004), *Dacryodes excelsa* from Medina (2015), and *Spathodea campanulata* from this study. “-” indicate no data are available.

Element ratios	<i>Metrosideros</i>	<i>Dacryodes</i>	<i>Spathodea</i>	
			Alluvial	Karst
Ca:Mg	1.5	2.6	5.0	6.0
Ca:P	4.0	6.7	12.0	17.0
Ca:Al	-	4	124	133
K:Ca	1.30	1.00	0.30	0.32
K:P	5.1	6.9	4.6	5.7
Mg:P	2.6	2.6	2.7	3.0
N:Ca	7.2	8.4	1.8	1.5
N:K	5.6	8.1	5.1	4.8
N:Mg	10.8	21.8	8.6	8.7
N:P	29	56	21	26
C:N	-	42	24	26
C:P	-	2326	536	688
C:S	-	501	336	370

concentrations of the other elements, particularly phosphorus and calcium. Figure 18 illustrates the dramatic reduction in the element composition of adult leaves when exposed to nutrient limitation such those of the acid soils of *D. excelsa* or the serpentine conditions in Susua and Maricao. Climate does not appear to influence the elemental composition of adult leaves. The high nutritional quality of *Spathodea* leaves is conducive to high rates of primary productivity, particularly given that the nitrogen concentration exceeded the valued considered “sufficient for adequate growth” sensu Epstein (1965). *Spathodea* leaves are also highly labile to decomposers (Lugo and Abelleira Martínez 2018).

The differences in element ratios observed when comparing adult leaves from mature forest species and *Spathodea* disappear, or are less pronounced, when the comparison is among leaves of the same species in loose litter (Table 15). *Spathodea* leaf litter maintains high calcium element ratios to other elements, but the difference is not as large when compared with *M. polymorpha* and *D. excelsa*. Of particular significance is the C:P ratio, which increases dramatically as the phosphorus is recycled in the litter layer. In contrast, the difference in the C:S ratio is

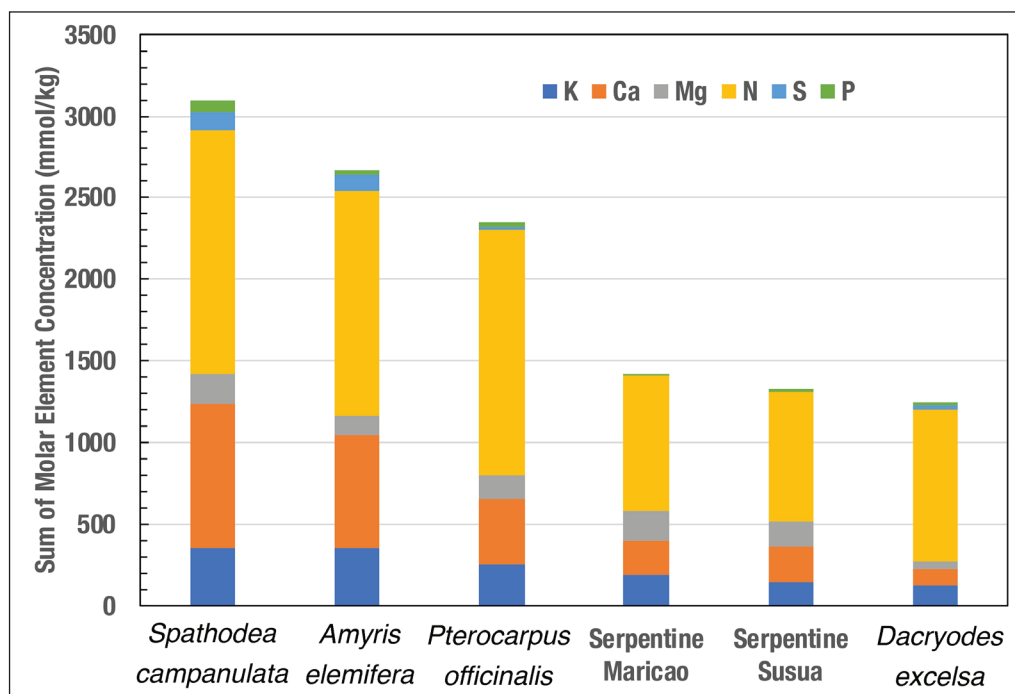


Figure 18. The molar element composition signature (sensu Medina 2015) of adult leaves from several locations in Puerto Rico. Data for *Amyris*, *Pterocarpus*, and *Dacryodes* are from Medina (2015). Data for the 2 serpentine sites are from Medina et al. (1994) and constitute the mean of several dominant species at those sites. Data for *Spathodea* are the mean of the 6 sites in this study. *Amyris* is a species from the karst, *Pterocarpus* is dominant on flooded alluvial sites, and *Dacryodes* is dominant on volcanic sites. All locations but 2 are in the subtropical moist forest life zone. Both *Dacryodes* and the Maricao serpentine are in the subtropical wet forest life zone.

maintained. These results reflect the rapid movement of elements in the loose litter of tropical forests as leaf litter approaches the element ratios of soil (discussed above). For carbon, *Spathodea* leaf litter maintains a lower C:P, reflecting the initial higher phosphorus concentration of falling leaves.

Conclusion

We found support for our initial expectations: we generally found higher C:N, C:P, and N:P on canopy foliage, litterfall, and standing litter on *Spathodea* stands at karst relative to alluvial sites. We also found that higher C:N,C:P, and N:P were associated to lower primary productivity in *Spathodea* stands at karst compared to alluvial sites, as we had expected. Additionally, we showed that these element ratios, as found in the soil, are modified by vegetation as nutrients are incorporated into biomass, and that decomposition processes return these element ratios in decomposing biomass tissues back to values found in the soil. Since plant parts of forest compartments in *Spathodea* stands at alluvial sites are more stoichiometrically balanced with soils when compared to stands on karst substrate, soils can support higher primary productivity rates in *Spathodea* stands at alluvial sites.

Our study underscores the importance of tracking the response of ecological systems to variation in substrate conditions and illustrates how the chemistry of the plant parts of a pioneer introduced tree species responds to variation in soil chemistry and stoichiometry. *Spathodea campanulata* forests growing under similar climatic conditions exhibited significant stoichiometric differences related to the soil properties on which stands functioned. This means that ecosystem function, specifically primary productivity and nutrient capture, of novel *Spathodea* forest stands is mediated by local soil conditions. Therefore, concomitant ecosystem services of carbon sequestration for climate-change mitigation, and nutrient storage

Table 15. Comparison of leaf-litter molar element ratios of tropical tree species from Hawaii and Puerto Rico. *Metrosideros polymorpha* from Vitousek (2004), *Dacryodes excelsa* and *Tabebuia heterophylla* from Lugo et al. (2022), and *Spathodea campanulata* from this study. Recently fallen leaf litter data were used for this table. “-” indicates no data are available.

Element ratios	<i>Metrosideros</i>	<i>Dacryodes</i>	<i>Tabebuia</i>	<i>Spathodea</i>	
				Alluvial	Karst
Ca:Mg	2.7–3.1	2.8	2.71	4	8
Ca:P	7.9–38.6	14.2	23.3	16	27
Ca:Al	-	30.3	22.3	15	9
K:Ca	0.1	0.1	0.2	0.7	0.2
K:P	0.5–2.6	2.0	4.1	5	5
Mg:P	2.9–12.5	5.1	8.6	4	3
N:Ca	0.9–1.0	4.20	2.72	5	1
N:K	13.3–16.7	31.1	15.7	6	9
N:Mg	2.7	11.8	7.2	8	9
N:P	7.8–34.4	59.2	60.8	28	32
C:N	-	28.6	45.9	37	35
C:P	-	1687	2746	1049	1132
C:S	-	612	722	283	299

and retention for soil rehabilitation, that are provided by these novel ecosystems also vary with these local conditions. This variation should be considered in quantification of ecosystem services and to inform regional land-use planning in Puerto Rico, where novel forest ecosystems dominate the landscape.

Acknowledgments

This work was done in collaboration with the University of Puerto Rico. O.J. Abelleira's participation in manuscript preparation was partially supported by the USDA National Institute of Food and Agriculture's McIntire–Stennis congressional funds program (project no. 7004374) and the Agricultural Facilities and Equipment-Resident Instruction Grants for Institutions of Higher Education in Insular Areas (RIIA-AGFEI) program (project no. 2024-70008-43392). Nataly Soto, Vanessa San Miguel, and Ivonne Rosado collaborated with the collection and processing of litter samples. Vicente El Indio (RIP), Carlos Marrero Otero, and Dixon Irizarry Negrón aided with litterfall and fresh-leaf collection. Lucy Gaspar (RIP) and Josefina Arce helped to organize and coordinate data collection with K–12 students. Institute chemists Mary Jean Sánchez, Maribelis Santiago, Edwin López, and Maysaa Ittayem conducted the chemical analyses, reviewed the manuscript and/or supported data archival. Ernesto Medina provided invaluable insight for the interpretation of results, and he and Kathleen McGinley reviewed the manuscript. Humfredo Marciano Vega made available unpublished data from after the impact of Hurricane María for *Spathodea campanulata*. Helen Nunci collaborated with the assembly of the literature cited section of the manuscript.

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