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

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ABSTRACT

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

1. Introduction

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

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

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

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

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

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

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

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

2. Materials and methods

2.1. Study sites

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

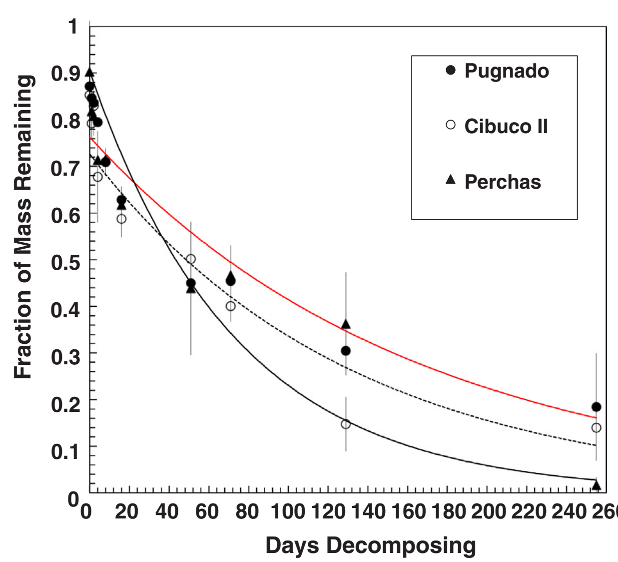

Fig. 1. Decomposition rate of *Spathodea campanulata* leaves in three locations with different geologic substrates: Perchas (volcanic), Pugnado (karst), and Cibuco II (alluvial). All sites are located in the subtropical moist forest life zone. Lines represent an exponential fit, Section 3.1 contains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