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Allometry, biomass, and chemical content of Novel African Tulip Tree (*Spathodea campanulata*) Forests in Puerto Rico

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Abstract The African tulip tree, *Spathodea campanulata*, the most common tree in Puerto Rico, forms novel forest types with mixtures of native and other introduced tree species. Novel forests increase in area in response to human activity and there is no information about their biomass accumulation and nutrient cycling. We established allometric relationships and chemically analyzed plant parts of African tulip trees to determine the concentration and standing stock of chemical elements (C, N, P, K, Ca, Mg, S, Mn, Al, Fe, Na), and ash. Trees ranged in diameter at breast height from 8 to 85 cm and in height from 8.8 to 28 m. The concentrations of N, P, K, and Ca in leaves of the African tulip tree were similar to those of the native pioneer *Cecropia schreberiana* and higher than those of mature forest tree species in Puerto Rico. The over bark wood volume of African tulip trees in nine forest stands where it was dominant ranged from 163 to 849 m^3/ha. Aboveground biomass ranged from 60 to 296 Mg/ha, and N and P stocks ranged from 190 to 988 and 32 to 137 kg/ha, respectively. Novel forests on abandoned agricultural lands can store more biomass and elements than native and plantation forest stands of similar age.

Keywords Nutrient concentration · Nutrient cycling · Stemwood volume · Biomass · Carbon · Introduced species · Puerto Rico · Secondary forests · Novel forests

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Introduction

Accurate estimation of forest biomass and chemical stocks is required to improve the ecosystem models used to estimate the carbon balance and study nutrient cycling of tropical forests. Such information helps us understand the influence of forests on atmospheric carbon concentrations, global warming processes, and ecological services. In spite of the need to understand carbon and chemical fluxes of tropical forests, information about these fluxes is limited and more so for novel forest ecosystems that emerge as a result of anthropogenic activities (Hobbs et al. 2006). This is now a critical data need given that secondary and novel forests cover the largest areas of tropical forests (Lugo 2009).

In Puerto Rico, novel forests are emerging following the deforestation, use, degradation, and abandonment of agricultural lands (Lugo and Helmer 2004). *Spathodea campanulata* Beauv., the African tulip tree, is an introduced species that forms novel forests in alluvial, karst, and volcanic substrates throughout the subtropical moist and wet forest life zones of Puerto Rico (Abelleira Martínez and Lugo 2008, Abelleira Martínez et al. 2010). This tree has been the most abundant tree species in the island since 1982 (Birdsey and Weaver 1982, Brandeis et al. 2007). In Puerto Rico, the African tulip tree forms and maintains monodominant stands for about 50 years (Aide et al. 2000, Abelleira Martínez and Lugo 2008). Afterwards, native species invade the canopy of these stands and share dominance with the African tulip tree (Abelleira Martínez 2009). Stands dominated by the African tulip tree develop large basal areas and height, as well as a species-rich understory (Abelleira Martínez et al. 2010). In general, however, ecologists have limited information about the functional parameters and silviculture of novel forests including those dominated by the African tulip tree (Francis 2000). Nevertheless, documenting the chemical and carbon cycle of these new forests is important to the overall understanding of tropical forest dynamics because secondary forests now occupy more land area than primary forests, and secondary forests are even less studied than primary forests (Brown and Lugo 1990).

Our objective for this study was to develop allometric regressions to estimate wood volume, biomass, and chemical elements and ash stocks of African tulip trees in Puerto Rico. We also apply these regressions to stands dominated by the African tulip tree to see if the numerical dominance of this species translates to high accumulation of biomass and chemical elements, and to compare the biomass and chemical stocks to other tree species and forest types in Puerto Rico.

Methods

The study took place on the first week of July 2007 in an abandoned farm near the Caguas Botanical Gardens in central Puerto Rico. The forest was growing on a volcanic substrate in the subtropical moist forest life zone. At the time of the study African tulip trees were not in full leaf, flowering, or fruiting (Photo 1). Thus, the biomass data underestimates leaf, flower, and fruit biomass. Our systematic observations of these parameters show that they change constantly (Abelleira Martínez 2009) but not so the woody component. Therefore, we took advantage of the opportunity to develop biomass regressions for trees that had to be harvested in July. Also, trees had survived Hurricane Georges, which passed over the site in 1998. The hurricane affected tree architecture of snapped trees that survived by developing large branches (Photo 2). Therefore, these data are relevant to hurricane-impacted trees.

We selected eight trees that ranged in diameter at breast height (dbh, D) between 8 and 85 cm. These trees were felled individually and dissected into leaves, flowers and fruits,

Photo 1 One of the *Spathodea campanulata* trees harvested for this study. Notice the bifurcation of large and medium sized branches and the low density of foliage at the time of the study

Photo 2 Proliferation of large branches on a *Spathodea campanulata* tree that had snapped during the passage of Hurricane Georges ten years prior to our study

Table 1 Wet to dry weight conversion factor and wood density (g/cm^3) of *Spathodea campanulata* plant parts

Component	Dry/Wet	CL	g/cm^3	Adjusted r^2
Bark (10)	0.24	0.02	0.24	0.69
Main Stem or Bole (26)	0.42	0.02	0.27	0.98
Large Branches (31)	0.48	0.02	0.27	0.91
Medium Branches (29)	0.50	0.02	0.39	0.94
Small Branches (39)	0.45	0.03	0.44	0.98
Dead Branches (33)	0.73	0.05	0.23	0.69
Roots (5)	0.34	0.03	N/A	N/A
Leaves[a] (4)	0.29	0.05	N/A	N/A
Flowers (4)	0.21	0.04	N/A	N/A
Fruits (5)	0.59	0.23	N/A	N/A
Sawdust (1)	0.39	N/A	N/A	N/A

The number of samples is in parenthesis. The 95% confidence level is CL. Estimates of wood density were based on the regression of dry weight and green volume of samples. The p at 0.05 α was < 0.000 for all estimates

[a] Includes the rachis

dead branches, small branches, medium branches, large branches, and main stem. One tree had the root stump exposed and we took the opportunity to dig it out for weighing and chemical analysis. The branch size class was based on the position of the branch relative to the main stem, with large branches representing the first bifurcation, followed by medium and small branches (Photo 1). Each of these tree parts was measured and weighed fresh in the field. These allometric measurements of diameter, length, and weight constituted a data set with 773 data points including 257 of main stem, 223 of large branches, 201 of other branch sizes, 69 leaf samples, plus other plant part samples such as fruits, flowers, root stump, etc. From the parts measured and weighed fresh in the field, 223 sub-samples were transported to the laboratory for dry weight determination and chemical analysis. Samples were oven-dried to constant weight at 60°C. We used the fresh to dry weight ratio in sub-samples (Table 1), to convert all field fresh weight data to dry weight.

We used a variety of field balances to maintain accuracy to the nearest kg regardless the size of the sample, and to the nearest mg for individual leaf blades. We dissected the compound leaves into leaf blades and rachis to obtain their weight independently. Leaflet petioles were small and included with the rachis. Before felling the tree, its dbh, height (H), and crown diameter were measured with a dbh tape at 1.37 m height, a clinometer, and with a linear tape, respectively. We also took the following precautions in the field: we collected sawdust generated by the chainsaws while cutting the main stem (Photo 3) and large branches. The fresh weight of sawdust was also converted to dry weight and used to correct the weight of large branches and main stems. The length of the tree (main stem plus large branches) was measured after the tree was felled, as was the diameter every meter for the whole length of the tree. The diameter, and sometimes three diameters if there was significant taper, and length of each main stem and large branch section used for a biomass determination were measured. With these data, we estimated the over bark volume of the main stem and large branches.

We also measured bark thickness in main stems and large branches along the main axis of the tree. We averaged the bark thickness measurements for main stems (n = 151) and

Photo 3 Processing the main stem of *Spathodea campanulata*. Notice that fluted shape of this cross section, which had to be considered in the estimation of volume

Photo 4 A downed *Spathodea campanulata* tree with prominent fluting of the main stem

large branches (n = 105) by tree and report it as the mean for harvested trees. These data were used to develop a correction factor to convert over bark volume to wood or under bark volume. Bark samples were also collected for fresh to dry weight conversion. Because large trees had fluted main stems (Photos 3, 4), we traced on paper 13 cross sections of these stems and large branches and determined their area using a LICOR Area Meter. We then established the ratio of actual to estimated area to correct all estimated volume determinations of large branches and main stems.

Oven-dried sub samples of all plant parts except flowers and fruits were ground through an 18-mesh sieve, and sent to the laboratory of the International Institute of Tropical

Forestry (IITF) for chemical analysis. Ground material was analyzed for P, K, Ca, Mg, Al, Mn, Fe, and Na utilizing a Spectro Plasma Emission Spectrometer (Spectro Ciros CCD-ICP). We used a modification of the digestion method recommended by Luh-Huang and Schulte (1985). Samples were digested with concentrated HNO_3 and 30 percent H_2O_2 and concentrated HCl. Total N, total C, and total S were analyzed using the dry combustion method by means of a LECO TruSpec CN and TruSpec S (add-on module) Analyzers (LECO-Corp 2005). In the dry combustion method a small weighed sample is combusted at 950°C for total C and N or 1,450°C for total S inside a resistance furnace and in a stream of purified oxygen. A sub sample of each plant part was oven dried at 105°C for 24 h and a moisture factor was calculated and applied to each analysis (Wilde et al. 1979). Precision for most analyses was assured by running samples of known chemical composition every forty determinations. For total C, total N, and total S, we analyzed using certified reference materials of similar matrix and known concentration, every twenty determinations. These analyses were used to assure consistency in the chemical analysis of samples. The following reference materials, obtained from the National Institute of Standards and Technology, USA, were used as control samples throughout the analysis procedure: tomato leaves (NIST-1573a), peach leaves (NIST-1547), apple leaves (NIST-1515) and pine needles (NIST-1575a). The reference materials used as calibration and control samples in the total C, N, and S analyses were: corn gluten, tobacco leaves, alfalfa, and orchard leaves, purchased from LECO Corporation (St. Joseph, MI).

We estimated over bark dry wood density by converting all diameter and length measurements of main stem and large branch sections to green volume, and regressing those individual measurements to their dry weight (Y axis). The slope of that regression is the wood density in g/cm^3. We ran regressions for bark, main stem, and large, medium, small, and dead branches used in the determination of fresh to dry weight conversion ($n = 168$). For main stems and large branches, we corrected the volume estimates for the irregular shape of their cross sections. The correction averaged 20%.

We used JMP 7 software (SAS Institute Inc. 2007) to graphically and statistically explore linear and non-linear allometric relationships. We found the linear regression to be more suitable than the nonlinear ones. The exceptions were some volume regressions, where we used a natural log relationship. This was necessary given the formation of large branches by the selected trees, which we attribute to the response to hurricane passage (Photo 2). In one case, the tree formed two massive large branches that doubled the wood volume in the main stem. While the tree fitted the allometric relations with its main stem volume and biomass, it was an outlier in the regression of large branch volume. Thus, we omitted this tree in the large branch volume regressions.

We analyzed relationships for total tree and by tree component between tree biomass and over bark volume, versus tree D, H, D^2H, and crown diameter (CD). All data were tested for normality (Shapiro–Wilk W test) and homogeneity of variance with the JMP 7 software. Differences among means of normal data were tested with ANOVA, and if significant differences were detected, we ran a Tukey–Kramer HSD to identify differences between pairs of means. We used a Kruskal–Wallis test for non-normal and/or unequal variance data. Regression equations were developed and tested for significance using the JMP 7 software. Significance for all statistical tests was set at $p < 0.05$.

To estimate chemical stocks we multiplied chemical concentration data by the corresponding biomass of each plant part harvested in the field. We also estimated the mass-weighted concentration of all branches, all wood, and whole tree to facilitate the conversion of biomass data derived from regressions to chemical and ash stocks. Regression equations were used to convert stem diameter data for populations of African tulip trees to

over bark volume, biomass, and chemical element and ash stocks. We used structural data from nine African tulip-dominated stands, three each in karst, alluvial, and volcanic substrates in north central Puerto Rico (Abelleira Martínez et al. 2010). We entered individual African tulip tree stem dbh data for each stand for trees ≥15 cm dbh and converted the sum of tree stocks to an area basis dividing by the area sampled. Our estimates do not include African tulip trees <15 cm dbh or trees of other species of any size in the stands. Therefore, to help with data interpretation, we estimated and report the fraction of total stand tree density (for trees ≥10 cm dbh) represented in the African tulip tree population selected for the analysis of stocks.

Results

Main stem biomass averaged 56 percent of the aboveground biomass of the eight trees that we harvested (Fig. 1). Large and other branches averaged 23 and 20 percent of the aboveground biomass, respectively, while leaves averaged one percent. The compound leaves averaged 3.5 ± 0.5 g (n = 35) and there was a significant ($p < 0.001$) difference in the ratio of leaf to rachis dry weight, which was larger for upper canopy leaves (7.0) than for lower canopy leaves (5.2). Compound leaves averaged 9.2 ± 0.3 (n = 35) leaflets per leaf with a range from 6 to 13 (although we counted 15 leaflets in saplings). The leaflet area at our site ranged from 20 to 35 cm^2.

With the exception of C, the highest concentrations of elements and ash were found in either leaves or rachis (Tables 2, 3). Carbon concentrations were highest in main stems, dead branches, large branches, and roots. The lowest C concentrations were in rachis, medium branches, and main stem bark. The rachis had a higher K concentration than leaves. All other tree components had much lower K concentrations than leaves and rachis. A similar pattern was found in the P concentration, except that the rachis and small branches had similar P concentrations but different from leaves (lower) and other plant components (higher). Main stem bark was high in Ca and Ash. Wood components tended to be low in N, Ca, and Mg concentrations, particularly the main stem.

Sodium concentration was significantly higher in the rachis compared to leaves (Table 2), and was generally higher in main stems, main stem bark, dead branches, roots,

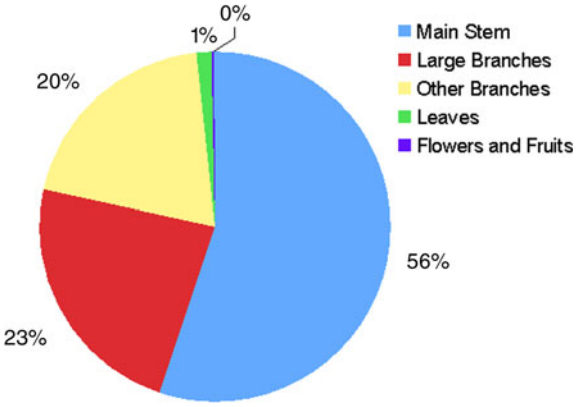

Fig. 1 Distribution of aboveground biomass on eight trees of *Spathodea campanulata*

Table 2 Mean chemical element concentration (mg/g) in plant parts of *Spathodea campanulata*

Plant part	P	CL	K	CL	Ca	Mg	CL	Mn	CL	Na	CL	Al	Fe	CL
Leaves	1.82^{a}	0.13	15.72^{b}	1.20	20.0^{a}	3.77^{a}	0.23	0.032	0.002	0.181	0.030	0.200^{a}	0.138	0.015
Rachis	1.14^{b}	0.10	18.25^{a}	1.77	15.5^{bc}	2.30^{b}	0.14	0.011	0.001	0.289	0.035	0.148^{bc}	0.060	0.005
Branches														
Small	0.65	0.09	3.22	0.52	6.8^{d}	1.26	0.15	0.010	0.002	0.082	0.039	0.066^{d}	0.029	0.005
Medium	0.46	0.20	3.98	5.02	5.6^{d}	1.07	0.30	0.005	0.001	0.078	0.068	0.049^{d}	0.015	0.001
Large	0.35	0.38	3.54	4.09	4.8^{d}	0.92	0.30	0.004	0.002	0.084	0.123	0.046^{d}	0.017	0.013
Dead	0.23	0.07	1.31	0.92	10.1 ^{cd}	2.24	1.02	0.010	0.001	0.219	0.252	0.096^{d}	0.047	0.011
Stem	0.30	0.11	3.99	0.97	4.4^{d}	1.11	0.28	0.002	0.000	0.157	0.059	0.039^{d}	0.012	0.008
Bark	0.50	0.21	6.23	8.57	26.9^{ab}	1.93	3.19	0.014	0.010	0.114	0.195	0.237^{ab}	0.115	0.217
Roots	0.43	0.10	5.22	4.08	6.7 ^{cd}	1.41	0.56	0.014	0.008	0.241	0.111	0.260^{a}	0.393	0.322

The 95% confidence level is CL. The CL is not given for columns with the results of a Tukey–Kramer HSD test. Stem refers to the main stem or bole, bark refers to main stem bark, and leaves refer to the leaf blades of the compound leaves. Data in columns with the same letter are not significantly different at $p < 0.05$. Kruskal–Wallis tests indicated significant differences in all columns ($p < 0.000$)

Table 3 Mean N, C, S, and ash concentration in plant parts of *Spathodea campanulata*

Plant part	N	CL	C	S	CL	Ash	CL
Leaves	2.75[a]	0.12	51.5[b]	0.35[a]	0.02	9.2	0.4
Rachis	0.86[b]	0.04	49.9[c]	0.13[b]	0.01	7.8	0.5
Branches							
Small	0.55	0.04	52.1[b]	0.05	0.01	2.6	0.4
Medium	0.45	0.07	51.7[bc]	0.05	0.02	2.4	1.1
Large	0.38	0.15	53.2[ab]	0.03	0.02	2.0	1.0
Dead	0.43	0.07	55.4[a]	0.06	0.03	3.2	2.1
Stem	0.25	0.03	54.8[a]	0.04	0.01	2.0	0.3
Bark	0.79	0.65	50.9[bc]	0.06	0.06	8.1	1.9
Roots	0.34	0.15	53.0[ab]	0.06	0.02	3.6	1.6

All data are in percent. The 95% confidence level is CL. The CL is not given for columns with the results of a Tukey–Kramer HSD test. Stem refers to the main stem or bole, bark refers to main stem bark, and leaves refer to the leaf blades of the compound leaves. Data in columns with the same letter are not significantly different at $p < 0.05$. Kruskal–Wallis tests indicated significant differences in all columns ($p < 0.000$)

and rachis than in the other tree components. Leaves had the highest Mn concentration and shared with main stem bark and roots, the highest Al concentrations. Roots had the highest Fe concentration.

The wood density was higher in medium and small branches, and lowest in dead branches and bark (Table 1). Large branches and main stem had similar wood density.

The mean bark thickness of the harvested trees averaged 0.64 cm (SE = 0.11, n = 8) for main stems and 0.36 cm (SE = 0.04, n = 5) for large branches. For those wood samples for which we had a volume and bark thickness measurement (142 for main stems and 105 for large branches) we developed a correction to estimate under bark volume and report it here by harvested tree. For main stems the correction is 0.931 (SE = 0.006, n = 7) and for large branches it is 0.904 (SE = 0.017, n = 5). We found a positive relation between D (in cm) and bark thickness (cm) for main stems (bark thickness = 0.237 + 0.009 * D; adjusted $r^2 = 0.57$, $p < 0.02$).

Table 4 contains all the significant allometric volume and biomass equations that we derived from the eight study trees. Data are presented by plant part or combination of parts (main stem, all branches, all woody parts, leaves, and total tree, respectively). The best regressions were those based on D and D^2H. A significant regression between large branch volume and D^2H was not attained. Crown diameter regressions had lower significance and adjusted r^2, while H resulted in regressions with the least significance and lowest adjusted r^2. For leaves, we could not find significant relations using CD and H. Those significant regressions that estimated leaf biomass had the lowest significance and adjusted r^2 among all reported in Table 4. This was because trees were not in full canopy development, thus underestimating leaf biomass. To estimate chemical stocks we recommend using the mass-weighted chemical concentration data in Table 5 and the biomass obtained from regressions in Table 4.

Discussion

The nutrient concentrations of African tulip tree plant parts tend to be high in comparison to other tree species, particularly the leaf and rachis N and P concentrations, which are

Table 4 Over bark volume and/or biomass regression equations for main stems, all branches, all wood, leaves, and total tree mass of *Spathodea campanulata*

Regression parameter	Diameter at breast height (D in cm)	Height (H in m)	D^2H (m^2m)	Crown diameter (CD in m)
Main stem volume (Y)				
Equation: Y in m^3 =	$-0.89 + 0.05 * D$	$-5.44 + 0.24 * H$	$0.10 + 0.22 * D^2H$	$-1.03 + 0.33 * CD$
r^2 adjusted ($p <$)	0.92 (.000)	0.91 (.000)	0.94 (.000)	0.79 (.005)
Main stem biomass (Y)				
Equation: Y in kg =	$-146 + 10.6 * D$	$-342 + 33 * H$	$49 + 41 * D^2H$	$-192 + 65 * CD$
r^2 adjusted ($p <$)	0.89 (.000)	0.59 (.016)	0.88 (.000)	0.80 (.004)
Large branch volume (Y)				
Equation: Y in m^3 =	$-4.05 + 0.05 * D$	$-5.85 + 0.20 * H$	NS	$-0.52 + 0.13 * CD$
r^2 adjusted ($p <$)	0.66 (.032)	0.59 (.046)	NS	0.63 (.036)
All branch biomass (Y)				
Equation: Y in kg =	$-135 + 8.8 * D$	$-308 + 27 * H$	$30.7 + 34 * D^2H$	$-208 + 60 * CD$
r^2 adjusted ($p <$)	0.73 (.004)	0.50 (.031)	0.69 (.007)	0.88 (.001)
Wood volume (Y)				
Equation: Y in m^3 =	$-1.94 + 0.06 * D$	$-4.93 + 0.23 * H$	$0.24 + 0.25 * D^2H$	$-1.71 + 0.49 * CD$
r^2 adjusted ($p <$)	0.88 (.001)	0.83 (.003)	0.85 (.002)	0.84 (.006)
Wood biomass (Y)				
Equation: Y in kg =	$-285 + 19.6 * D$	$-658 + 61 * H$	$81 + 76 * D^2H$	$-405 + 126 * CD$
r^2 adjusted ($p <$)	0.87 (.000)	0.58 (.017)	0.84 (.001)	0.89 (.001)
Leaf biomass (Y)				
Equation: Y in kg =	$-5.9 + 0.29 * D$	NS	$-1.0 + 1.23 * D^2H$	NS
r^2 adjusted ($p <$)	0.44 (.044)		0.51 (.027)	
Total tree biomass (Y)				
Equation: Y in kg =	$-292 + 19.9 * D$	$-669 + 62 * H$	$81 + 77 * D^2H$	$-409 + 128 * CD$
r^2 adjusted ($p <$)	0.87 (.000)	0.58 (.017)	0.84 (.001)	0.89 (.001)

The volume equation with H results in Log Y, as does the volume regression with D for large branches. If the regression was not significant at $p < 0.05$, it is reported as NS. Leaf biomass is underestimated in relation to wet periods with full canopy development

Table 5 Mass-weighted concentrations of elements and ash for use with biomass regressions

Constituent	All branches	All wood	Whole tree
N	0.43	0.33	0.36
P	0.52	0.42	0.44
K	2.92	3.48	3.62
Ca	5.52	4.90	5.07
Mg	1.08	1.09	1.12
Mn	0.006	0.004	0.004
Na	0.09	0.13	0.13
Al	0.05	0.04	0.05
Fe	0.022	0.016	0.017
C	52.8	53.3	53.1
S	0.04	0.04	0.04
Ash	2.3	2.1	2.2

Nitrogen, C, S, and ash in percent, all others in mg/g

among the highest measured in Puerto Rico (Lugo 2004). To verify this report, we summarized plant part concentration data in the files of the Chemistry Laboratory of the IITF (data available from the senior author). This data set contains 4,126 chemical analyses for plant parts of 285 tree species growing in all climatic life zones and most soil orders in Puerto Rico. The data set provides a wide range of conditions under which trees grow in the island. For the analysis of leaf chemistry data we analyzed the chemistry of introduced species separate from that of native tree species. For the analysis of stems, we combined all species. Figure 2 shows that leaves of the African tulip tree have higher N, P, K, and Ca concentration and lower Mn, and Fe concentration than the mean for either introduced or native tree species in the data set. The C/N was also low in the African tulip tree. In contrast, the main stem of the African tulip tree has lower N, K, Ca, Mg, Mn, Fe, Al, and ash concentration than the mean for all species stems in the data set (Fig. 3).

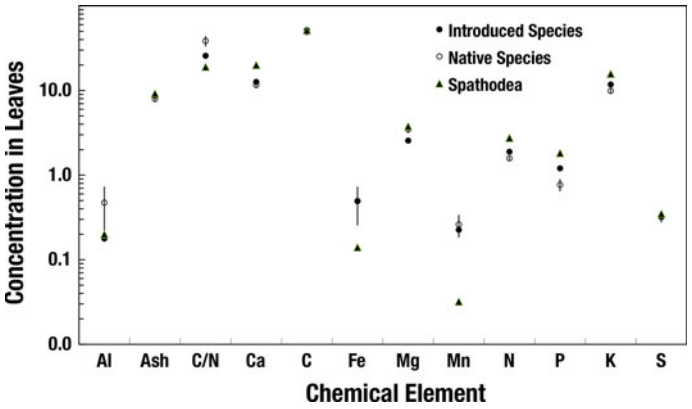

Fig. 2 Chemical element concentration data for leaves of *Spathodea campanulata* and leaves of introduced and native tree species (about 285 tree species total) growing in Puerto Rico. Each point is a mean and includes a 95% confidence level. The units of concentration are in percent for N, C, and Ash, and mg/g for all the other elements. Note the logarithmic concentration scale

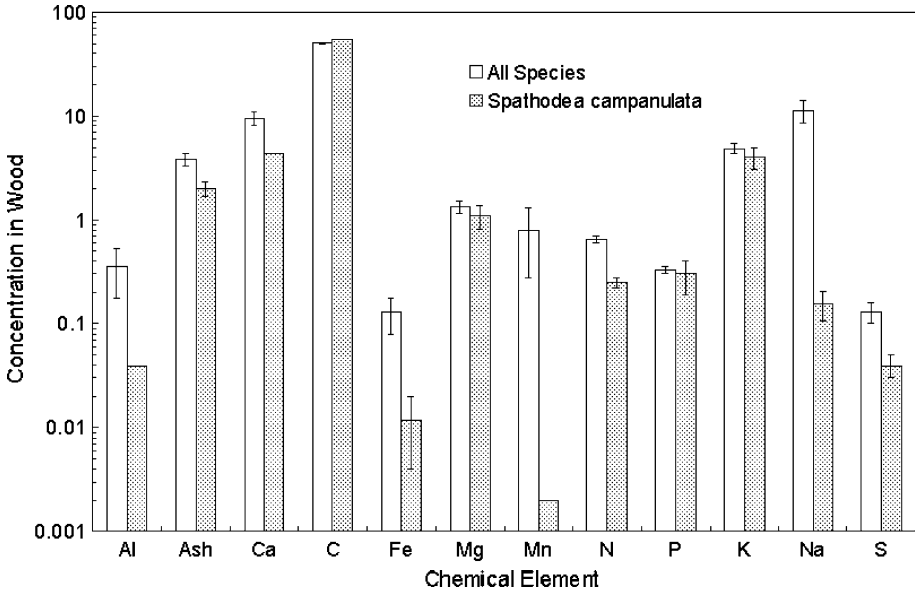

Fig. 3 Chemical element concentration data for main stems of *Spathodea campanulata* and woody material of 104 tree species growing in Puerto Rico (all species). Each point is a mean and includes a 95% confidence. Units of concentration are in percent for N, C, and Ash, and mg/g for all the other elements. Note the logarithmic concentration scale

African tulip trees have leaf N and P concentrations similar to those of *Cecropia schreberiana*, a native pioneer tree, but higher than *Tabebuia heterophylla,* a secondary forest tree in the Bignoniaceae that has a similar phenology, dispersal, and seed, and the two primary forest species *Dacryodes excelsa* and *Manilkara bidentata* (Table 6). The concentrations of K followed a similar trend but were higher in *C. schreberiana*. On the other hand, Ca concentrations also followed a similar trend but were higher in African tulip trees. The C/N of African tulip trees and *C. schreberiana* were similar and higher than primary forest species. No noticeable chemical patterns arising from tree growth strategies were found in the branches and trunks of these species (Table 6). The African tulip tree data reflect a higher than normal nutrient concentration in leaves and lower than normal microelements in leaves and most elements in wood.

Francis (2000) reports wood density data for the African tulip tree that ranges from 0.30 to 0.45 g/cm^3 in Gabon, 0.24 to 0.27 g/cm^3 in the Philippines, and 0.26 g/cm^3 in Puerto Rico. We believe that our result of 0.27 g/cm^3 for main stems (Table 1) represent an accurate estimate for the species, particularly when growing under favorable conditions as the African tulip tree finds in Puerto Rico. In branches we observed an increasing progression in wood density from large to small branches (Table 1). Small branches had the highest wood densities, perhaps because the woody tissue is yet to expand into the lighter wood characteristic of large branches and main stems. Alternatively, small branches are more horizontal and therefore have a greater percentage of reaction wood to counteract gravitational pull.

We applied the equations for total tree mass and over bark volume (Table 4) to the diameter distributions of African tulip trees in nine forest stands to estimate their standing volume and biomass (Table 7). Mass-weighted concentration data in Table 5 was multiplied by the corresponding standing biomass obtained from regressions to arrive at the

Table 6 Nitrogen, P, K, and Ca concentrations of leaves, branches, and stems, and C/N of leaves of *Spathodea campanulata* and native tree species on volcanic substrate in subtropical moist to subtropical wet life zones in Puerto Rico

	N (%)	P (mg/g)	K (mg/g)	Ca (mg/g)	C/N
Leaves					
Spathodea campanulata[a]	2.75	1.82	15.7	20.0	19
Cecropia schreberiana[a]	3.25	1.82	24.8	10.4	13
Tabebuia heterophylla[a]	1.40	1.06	10.4		
Dacryodes excelsa[b]	1.76	0.77	7.8	2.7	29
Manilkara bidentata[b]	1.15	0.47	6.8	5.9	43
Branches					
Spathodea campanulata	0.46	0.49	3.6	5.7	
Cecropia schreberiana	0.42	0.35	7.4	3.5	
Tabebuia heterophylla	0.67	0.86	10.8		
Dacryodes excelsa	0.41	0.27	3.9	5.2	
Manilkara bidentata					
Stem					
Spathodea campanulata	0.25	0.3	4.0	4.4	
Cecropia schreberiana	0.65	0.40	13.4	2.7	
Tabebuia heterophylla	0.65	0.37	7.7		
Manilkara bidentata		0.11	1.4	1.7	

Values for branches and stems include samples from the subtropical lower montane rain forest life zone. The sample size for *S. campanulata* parts is 43 for leaves, 6 for stems, and 10 for branches. Values for other species are from the files of the International Institute of Tropical Forestry Laboratory. They are available from the senior author. Empty cells mean there is no information

[a] Successional species

[b] Primary species

stock of chemical elements and ash in the eight African tulip tree stands (Table 7). African tulip tree populations have high biomass, over bark volume, and chemical element stocks, particularly those in alluvial conditions and the Perchas site in volcanic substrate. Low values were observed in two volcanic sites where the density of African tulip trees is low and the Juan Nieves site in karst substrate where the tree density was also low. In fact, the observed biomass stock is proportional to tree density (adjusted $r^2 = 0.60$, $p < 0.02$).

In spite of limiting the analysis to African tulip trees with dbh $\geq$ 15 cm, a comparison of these data with other native and plantation forests in Puerto Rico (Table 8) shows that African tulip tree biomass and chemical stocks can be as high or higher than reported for these other forests. For example, the over bark volume and biomass of African tulip tree populations in Table 7, with a few exceptions when the species was in low density, are clearly larger than the over bark volume and biomass of most forest stands in Table 8, even though the comparison includes only a fraction of the trees present in the African tulip tree forests versus all trees in the native forests and plantations. In addition, the data for plantation forests is usually for trees with dbh $\geq$ 2.5 or 4.0 cm. Moreover, most values in Table 7 for African tulip tree populations are higher than biomass values reported for single species in Table 8 (*Dacryodes excelsa*, *Prestoea montana*, pine (*Pinus caribaea*) and mahogany (*Swietenia macrophylla*). The pattern observed in the comparison of over bark volume and biomass applies as well to chemical elements and ash. A notable

Table 7 Aboveground over bark volume, biomass, and standing stocks of chemical elements and ash for *Spathodea campanulata* tree populations in nine locations in north central Puerto Rico

Site	Tree density (trees/ha)	Height (m)	Volume (m^3/ha)	Biomass (Mg/ha)	N (kg/ha)	P (kg/ha)	K (kg/ha)	Ca (kg/ha)	Mg (kg/ha)	S (kg/ha)	Mn (kg/ha)	Na (kg/ha)	Al (kg/ha)	Fe (kg/ha)	Ash (Mg/ha)
Karst (54 m^2/ha)															
Juan Nieves	414 (72)	24.4	265	96	309	48	338	480	101	93	0.34	12	4	2	2
Pugnado	580 (72)	29.7	503	177	585	84	632	895	190	192	0.65	23	8	3	4
Ollas y Calderas	536 (73)	24.1	428	152	497	73	539	764	162	156	0.55	20	7	2	3
Alluvial (84 m^2/ha)															
Cibuco I	814 (83)	22.3	714	252	830	119	899	1,272	269	266	0.92	32	12	4	6
Cibuco II	770 (77)	25.3	849	296	988	137	1061	1,497	318	343	1.10	38	14	5	6
Paso del Indio	1388 (83)	24.6	588	221	682	119	766	1,098	228	165	0.73	29	10	3	5
Volcanic (58 m^2/ha)															
Adjuntas	166 (28)	23.1	210	73	245	33	262	369	79	85	0.27	9	3	1	2
Perchas	1061 (68)	23.3	696	251	809	124	885	1,257	265	238	0.89	32	12	4	5
Pozas	344 (44)	16.9	163	60	190	32	209	299	63	57	0.21	8	3	1	1

Data apply to trees with a diameter at breast height $\geq$ 15.0 cm, which correspond to the tree density in the second column. Height refers to the canopy height and the basal area for the combined karst, alluvial, and volcanic sites is given in parenthesis after each subheading. The percent of the stand's total tree density (for trees $\geq$ 10 cm dbh) represented by the sampled population is in parenthesis in the second column. Volume is for main stem and large branches. Values were rounded to the nearest m^3, kg, or Mg

Table 8 Biomass, over bark volume, and standing stocks of nutrients and ash in trees of various forest types in Puerto Rico

Site (dbh in cm)	Height (m)	Basal area (m^2/ha)	Biomass (Mg/ha)	Volume (m^3/ha)	N (kg/ha)	P (kg/ha)	K (kg/ha)	Ca (kg/ha)	Mg (kg/ha)	Ash (kg/ha)	Source
Native forests											
Wet forest at Bisley (≥ 2.5)											
Ridge	20–30	54.2	312		805	44	702	655	153		Scatena et al. (1996)
Slope	20–30	33.4	186		525	28	446	398	100		Scatena et al. (1993)
Upland Valley	20–30	21.3	121		391	21	295	243	97		Scatena et al. (1993)
Riparian Valley	20–30	20.9	119		370	23	262	246	94		Scatena et al. (1993)
Dacryodes excelsa only	20–30	12.6	103		181	10	170	116	21		Scatena et al. (1993)
Wet forest at El Verde	20–30		284	238		112	917	1,235	335	1,784	Odum (1970)
Wet forest (≥ 4)	20–30		198	350							Weaver and Murphy (1990)
Palm forest (≥ 4)	17	30	174	210	991	66	792	625	187		Weaver and Murphy (1990), Frangi and Lugo (1991)
Prestoea montana only (≥ 4)	17	18.9	72		541	45	508	195	115		Frangi and Lugo (1991)
Colorado forest (≥ 4)	8–20	40.0	81–203	220							Weaver (1995), Weaver and Murphy (1990)
Cubuy secondary forest (≥ 4)	19	28.0	90		504	30	423			24	Lugo (1992)
Sabana secondary forest (≥ 4)	25	28.5	68		378	27	404			28	Lugo (1992)
El Verde secondary forest (≥ 4)	24	33.8	78		379	25	336			16	Lugo (1992)
Dry forest (≥ 5)			16		98	3	61			981	Murphy and Lugo (1986), Lugo and Murphy (1986)
Plantation forests											
Anthocephalus chinensis 12.5 years			144	348							Lugo and Figueroa (1985)
Pine 18.5 years (≥ 4)	33	55.6	166	689	1,365	51	443			90	Lugo (1992)
Mahogany 17 years (≥ 4)	25	29.5	94	145	516	26	337			13	Lugo (1992)
Mahogany 49 years (≥ 4)	27	31.9	121	419	954	34	388			6	Lugo (1992)

Values were rounded to the nearest m^3, kg, or Mg, except for some phosphorus stocks. Empty cells mean that there are no data reported. The value in parenthesis in column 1 corresponds to the minimum diameter at breast height (dbh) measured. All data except for the dry forest are for the Luquillo Experimental Forest. The dry forest is in Guánica. All forests are subtropical *sensu* Holdridge (1967)

exception is the stock of Na, which is ten times lower in African tulip tree populations relative to the subtropical wet forest (316 kg/ha) reported by Odum (1970).

Our results clearly show that African tulip tree accumulates high quantities of wood volume, biomass, and chemical elements in its aboveground structure. The chemical element concentration data for roots (Tables 2, 3) show high to moderate concentration of elements, but we don't have biomass data to estimate belowground accumulation of chemical elements in this species. We do know that for the tree for which we excavated the main root system, the belowground biomass was 28% of the aboveground biomass. Abelleira Martínez et al. (2010) showed that under alluvial soil conditions (nutrient-rich soils) African tulip tree develops basal areas and heights that are equal or exceed those of any standing native forest in Puerto Rico (compare data in Tables 7, 8). Our volume, biomass, and chemical stock data confirm the species ability to develop structure and sink high quantities of biomass and nutrients in its aboveground plant parts. A key ecological role played by this species is also the rapid turnover of mass and chemicals through rapid rates of growth, litterfall, and decomposition of dead wood and leaves (Francis 2000, Lugo 2004, Abelleira Martínez and Lugo 2008, and unpublished data of the two senior authors). Such high rates of growth, productivity, decomposition, and recycling require a source of nutrients, which the species probably derives by invading agricultural soils known for their high fertility.

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