Aboveground biomass, wood volume, nutrient stocks and leaf litter in novel forests compared to native forests and tree plantations in Puerto Rico

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Novel forest stands of *Castilla elastica* growing in the northern karst region of Puerto Rico.
This is a view of the forest canopy.
Photograph J. Fonseca Da Silva.

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RÉSUMÉ

BIOMASSE AÉRIENNE, VOLUME DE BOIS, STOCKS DE NUTRIMENTS ET LITIÈRE DE FEUILLES AU SEIN DE NOUVELLES FORÊTS, MIS EN COMPARAISON AVEC DES FORÊTS NATURELLES ET DES PLANTATIONS À PUERTO RICO

L'article présente une étude comparative de données de biomasse aérienne, de volume de bois, de stocks de nutriments (N, P, K) et de litière dans différents types de forêts à Puerto Rico. L'objectif de l'étude a été de procéder à une évaluation comparative de nouvelles forêts à *Castilla elastica*, arbre à caoutchouc, et *Spathodea campanulata*, tulipier du Gabon, avec des plantations et des forêts naturelles (aussi bien secondaires que matures). Il s'avère que ces deux types de nouvelles forêts peuvent rapidement accumuler en hauteur de grandes quantités de nutriments et de biomasse, produisant ainsi d'importantes chutes de feuillage. Elles peuvent égaler voire dépasser les plantations et les forêts naturelles pour tous les paramètres à l'exception de l'accumulation d'azote au niveau aérien. Ces résultats confirment bien le fait que ces nouvelles forêts peuvent contribuer à la restauration de la biomasse et des nutriments dans les sites déboisés. Cependant, à l'échelle de l'île dans son ensemble, les valeurs obtenues pour la biomasse dans plusieurs types de nouvelles forêts sont inférieures par rapport à celles observées dans cette étude pour les forêts à *Spathodea* et à *Castilla*. L'âge des peuplements et les conditions de site seraient ainsi des déterminants critiques du niveau d'accumulation d'éléments nutritifs et de biomasse dans ces forêts.

Mots-clés : nouvelles forêts, plantations, litière de feuilles, biomasse aérienne, nutriments, forêts caribéennes.

ABSTRACT

ABOVEGROUND BIOMASS, WOOD VOLUME, NUTRIENT STOCKS AND LEAF LITTER IN NOVEL FORESTS, COMPARED TO NATIVE FORESTS AND TREE PLANTATIONS IN PUERTO RICO

The article presents comparative data for aboveground biomass, wood volume, nutrient stocks (N, P, K) and leaf litter in different types of forests in Puerto Rico. The aim of the study is to assess how novel forests of *Castilla elastic,* Panama Rubber Tree, and *Spathodea campanulata*, African Tulip Tree, compare with tree plantations and native historical forests (both secondary and mature). It found that novel forests of these two species can accumulate large quantities of biomass and nutrients above ground that they do so at a rapid rate and that they exhibit high rates of leaf fall. They can match or exceed tree plantations and native forests in all parameters except the accumulation of nitrogen above ground. These results support the notion that novel forests can contribute to the restoration of biomass and nutrient stocks in previously deforested sites. However, across the island as a whole, the values for biomass in many types of novel forest are lower than those observed for *Spathodea* and *Castilla* in this study. The age of stands and site conditions appear to be critical to the level of nutrient and biomass accumulation in these forests.

Keywords: novel forest, plantings, leaf litter, aboveground biomass, nutrients, Caribbean forests.

RESUMEN

BIOMASA AÉREA, VOLUMEN DE MADERA, ESTOCS DE NUTRIENTES Y LECHO DE HOJAS EN BOSQUES NUEVOS, EN COMPARACIÓN CON BOSQUES NATIVOS Y PLANTACIONES EN PUERTO RICO

Este artículo presenta un estudio comparativo de datos de biomasa aérea, volumen maderable, estocs de hojarasca y nutrientes (N, P, K) en distintos tipos de bosques en Puerto Rico. El objetivo del estudio ha consistido en establecer una evaluación de bosques nuevos a base de *Castilla elástica,* Palo hule, y *Spathodea campanulata,* Tulipanero africano, comparados con plantaciones y bosques nativos (tanto secundarios como maduros). Los resultados muestran que ambos tipos de bosques nuevos pueden rápidamente acumular, en la parte alta, grandes cantidades de nutrientes y de biomasa, produciendo así importantes caídas de hojarasca. Sus resultados pueden igualar o superar a los de plantaciones y de bosques naturales en todos los parámetros, exceptuando la acumulación de nitrógeno en la parte aérea. Estos resultados respaldan la idea de que los bosques noveles pueden contribuir a la restauración de la biomasa y de los nutrientes en sitios deforestados. Sin embargo, a escala del conjunto de la isla, los valores de biomasa en otros tipos de bosques nuevos son inferiores a los observados en bosques de *Spathodea* y *Castilla* en este estudio. La edad de los rodales y las condiciones de sitio parecen ser determinantes críticos del nivel de acumulación de nutrientes y de biomasa en dichos bosques.

Palabras clave: bosque nuevo, plantaciones, lecho de hojas, biomasa aérea, nutrientes, bosques caribeños.

Introduction

As the Anthropocene, the era of human dominance over the Earth, unfolds, changes in species composition of forests will become more prevalent and obvious to observers. Thus, LUGO (2009) suggested that the World is entering the era of novel forests and HOBBS *et al*. (2012) systematized the study and management of novel ecosystems with worldwide examples. Species composition and species combinations not seen before in the geographic location where they occur characterize novel forests or novel ecosystems. These novel systems are replacing historic native systems, usually with a dominant component of introduced species.

In Puerto Rico, most of the island was deforested and farmed for centuries before agricultural activity ceased and lands were abandoned during the second half of the 20th century. This led to the establishment of novel forests described by LUGO & HELMER (2004). These novel forests have species composition different from that of native forests, whose species composition is all native species. Novel forests contain both native and introduced tree species, and in many instances are dominated by introduced species as is the case with the *Spathodea campanulata* and *Castilla elastica* forests highlighted in this paper. The study sites had been deforested, farmed for many decades, and abandoned before reverting to forest cover. These two types of forest stands did not occur in the island in the first half of the 20th century, but today occupy large land areas.

Novel forest stands of *Castilla elastica* growing in the northern karst region of Puerto Rico. This is a close view of the forest canopy. Photograph J. Fonseca Da Silva.

Critical questions, whose answers require new research, are: What is the level of function of these novel systems? How do they compare with historic native ecosystems? The importance of these questions resides in the need to understand whether or not familiar ecological services performed by historic ecosystems will prevail when novel ecosystems become prevalent. The objective is to review available information on aboveground biomass and nutrient stocks, wood volume, and litter fall of novel forests in Puerto Rico and compare the results with the corresponding results from historical native forests and tree plantations.

Methods

Literature from Puerto Rico was reviewed for the following parameters of forests: aboveground wood volume, aboveground biomass, aboveground nutrient stocks (N, P, K), and rates of leaf fall. The resulting gathered information was compared with similar information obtained from studies of novel forests of *Spathodea* and *Castilla*. Where possible, the results were compared with those reported for historic native forests and with those of an independent Island-wide biomass assessment of forests, including many types of novel forests (BRANDEIS, SUÁREZ ROZO, 2005). The comparisons are visual rather than statistical because available data are few, but they provide a first approximation of the comparative levels of selected ecosystem attributes.

The available data for novel forests of *Castilla* and *Spathodea* are from recent studies in Puerto Rico, which contain description of the forests and methods used (ABELLEIRA MARTÍNEZ *et al*., 2010; ABELLEIRA MARTÍNEZ, 2011, FONSECA DA SILVA, 2011; LUGO *et al*., 2011a). For the comparison of aboveground volume, biomass, and nutrient stocks the search was limited to forests in Puerto Rico, all studied with the same methods (table I). Also data on leaf fall were sought from Puerto Rico and elsewhere in the tropics where the stands could be classified by geologic substrate. The objective was to compare parameters in three different geologic substrates: alluvial, karst, and volcanic. The comparison of aboveground biomass in *Spathodea* and *Castilla* novel forests with an independent Island-wide biomass assessment of BRANDEIS & SUÁREZ ROZO (2005) had the objective of finding out how the individual site studies compared with a large-scale analysis of biomass. Specifically, as discussed below, the analysis compared the nutrient-rich study sites with Island-wide average sites that possibly reflect a greater degree of site degradation.

Table I.
Field methods used to estimate the forest parameters that are compared in this manuscript. Detailed methodologies are found in ABELLEIRA MARTÍNEZ *et al.* (2010), ABELLEIRA MARTÍNEZ (2011), FONSECA DA SILVA (2011), and LUGO *et al.* (2011a).

Parameter	Method	Analysis
Aboveground biomass	For ***Spathodea campanulata*** forests aboveground biomass (stems, branches, and leaves) was estimated by tree harvest regressed against tree diameter (dbh ≥ 15 cm) and height. Leaf biomass was negligible. For ***Castilla elastica*** forests aboveground biomass was based on tree density multiplied by the product of stem wood density, basal area, and height. All trees ≥ 4 cm dbh were included.	The diameter of each ***Spathodea*** tree with a dbh ≥ 15 cm was entered in regressions to estimate the biomass of all trees in a stand. Results were expressed per unit ground area. Native species were not included in the estimate. For *Castilla* forests, the biomass of trees of all species, (native and introduced), was estimated by its stem wood density, basal area, tree height and tree density and added to obtain the stand biomass per unit area.
Stem volume	The volume of each harvested ***Spathodea*** tree was measured and regressed to tree diameter and height.	The diameter and height of each ***Spathodea*** tree with a dbh ≥ 15 cm was entered in regressions to estimate the over bark volume of only ***Spathodea*** trees in a stand, results were expressed per unit ground area.
Nutrient stocks (N, P, K)	All aboveground tree parts of ***Spathodea*** were chemically analyzed for N, P, and K and the resulting concentration per unit dry weight was multiplied by the mass of the part per unit area.	Aboveground nutrient stocks was estimated by the sum of nutrients in leaves, branches, and stems, expressed per unit area.
Leaf fall	Ten baskets of known area were suspended aboveground and emptied every two weeks for at least a year in forests of ***Spathodea* and *Castilla***. When emptied, the contents of the baskets were sorted by plant part, and dried to constant weight.	Rate of leaf fall was estimated bi-weekly by dividing the dry weight of leaves by the time interval of collection and the area of the baskets. A mean leaf fall value was estimated for each collection date per site and integrated over a year to estimate annual leaf fall.
Rates of nutrient and mass accumulation	These rates were estimated using the aboveground stocks and age of the stand. We used the age of the oldest stand to assure a conservative result.	Aboveground stocks of biomass and of each nutrient were divided by the age of the stand to estimate an annual accumulation rate.

The Basis for the Comparisons

The comparisons presented in this paper are based on studies conducted with consistent methodology for all the parameters reported (table I). Also, the comparisons, with the exception of leaf fall, are based on forest stands within Puerto Rico across gradients of rainfall, substrate geology, and age of forests. The moisture gradient consists of dry, moist, and wet stands with respective annual rainfall ranges of 500 to 1,000, ›1,000 to 2,000, and ›2,000 to 4,000 mm. The substrate geology consisted of stands growing on volcanic, karst, and alluvial substrates, which result in different types of soils and drainage conditions. The alluvial soils were the most nutrient-rich followed by karst stands growing on valleys with high pH soils. Both alluvial and karst stands periodically flooded. Volcanic sites tended to be at higher elevation and slopes than both alluvial and karst sites. The ages compared included mature native forests whose ages exceeded 60 years, mature novel forests with ages exceeding 30 years, successional native and novel forests with less then 30 years of age, and forests that were in the processes of invading abandoned agricultural land (termed reversion forests by BRANDEIS & SUÁREZ ROZO (2005)). Also, data from timber plantations of known ages were included.

For leaf fall comparisons, a global data set was assembled and the sites were classified by substrate geology to constrain the comparisons. Table I summarize the parameters reported and the methods used and refer the reader to the original publications where details of the studies are found. The biomass and volume values for *Spathodea* forests were conservative because they only included *Spathodea* trees with dbh ≥ 15 cm and excluded native trees.

Results

The range of biomass stocks in novel forests of *Castilla* and *Spathodea* spans the range found in all other forest types in figure 1. Mature wet forests on ridges had the highest reported aboveground biomass and that high value was approached by novel forest stands of *Castilla* (Tallonal 1) on karst and *Spathodea* on alluvial substrate. Most novel stands matched or exceeded the aboveground biomass values measured in plantations, and secondary and mature native forests. The same is true for the comparison between novel forests and plantations in terms of aboveground stem volume data (figure 2).

The aboveground nitrogen stocks in novel forests of *Spathodea* were generally larger than in native secondary, dry, wet, and riparian forests, and the younger mahogany plantation (figure 3). The alluvial novel forest sites were among sites with the highest nitrogen stocks, but the pine plantation and native palm forest had disproportional nitrogen stocks relative to their biomass, and they exceeded the novel forest values. Aboveground phosphorus stocks in most novel forest stands in figure 4 were disproportionally higher than any other forest type. Only the pine plantation, native palm forest, and mature native wet forest on a ridge, exceeded the novel forest stands with the lowest phosphorus standing stocks. The aboveground potassium stocks in novel forests were high relative to plantations, native mature and secondary forests (figure 5). However, plantations and paired native secondary forests exceeded the three novel stands with the lowest potassium stocks, and native palm and wet mature forest on ridges exceeded the potassium stocks of two other novel forest stands.

The rate of leaf fall in novel forests is high when compared to a pantropical data set, using geologic substrate as the basis for the comparison (figure 6). In alluvial and volcanic substrates the rates for novel forests (in red) were among the highest while in karst substrates they were intermediate.

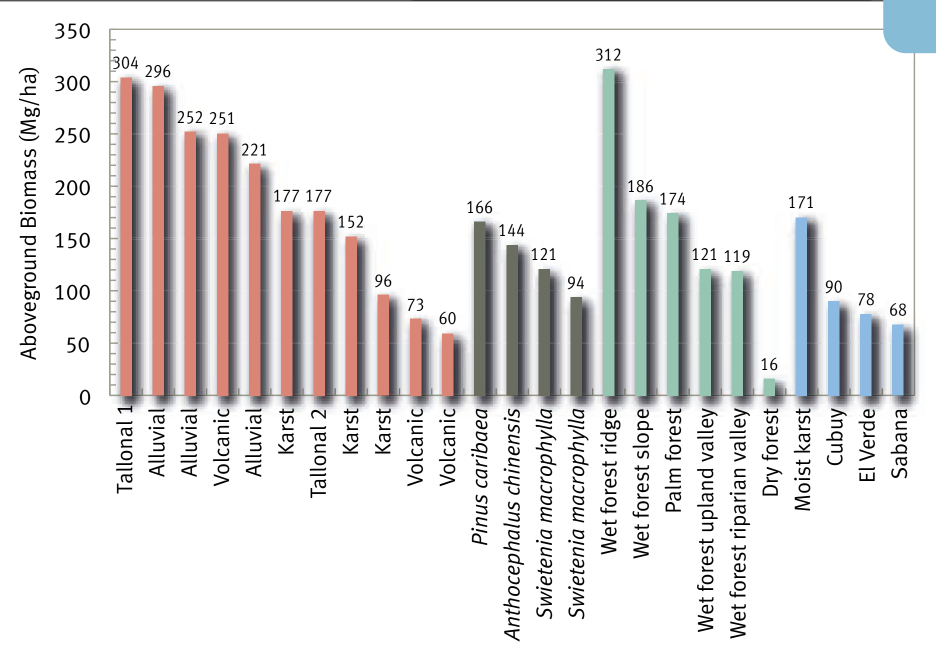

Figure 1.
Aboveground biomass in subtropical moist novel forests (red), subtropical wet forest tree plantations (black), mature native forests (green), and native secondary forests (blue) in Puerto Rico. Tallonal 1 and 2 were in karst substrate and dominated by *Castilla elastica* (FONSECA DA SILVA, 2011). All other novel forests were dominated by *Spathodea campanulata* (LUGO *et al.*, 2011a). Plantations of pine (*Pinus caribaea* - 18.5 yr) and mahogany (*Swietenia macrophylla* - 17 and 49 yr) were paired with subtropical wet forest secondary forests (Cubuy, Sabana, and El Verde) (LUGO, 1992). The *Anthocephalus chinensis* plantation (12.5 yr) data are from subtropical wet forest life zone (LUGO & FIGUEROA, 1985), and those for secondary moist karst are from BRANDEIS & SUÁREZ ROZO (2005). Mature natural forest data are from SCATENA & LUGO (1995) for ridge, slope, and valley wet forests, FRANGI & LUGO (1985) for subtropical lower montane wet palm forest, and LUGO & MURPHY (1986) for subtropical dry forest.

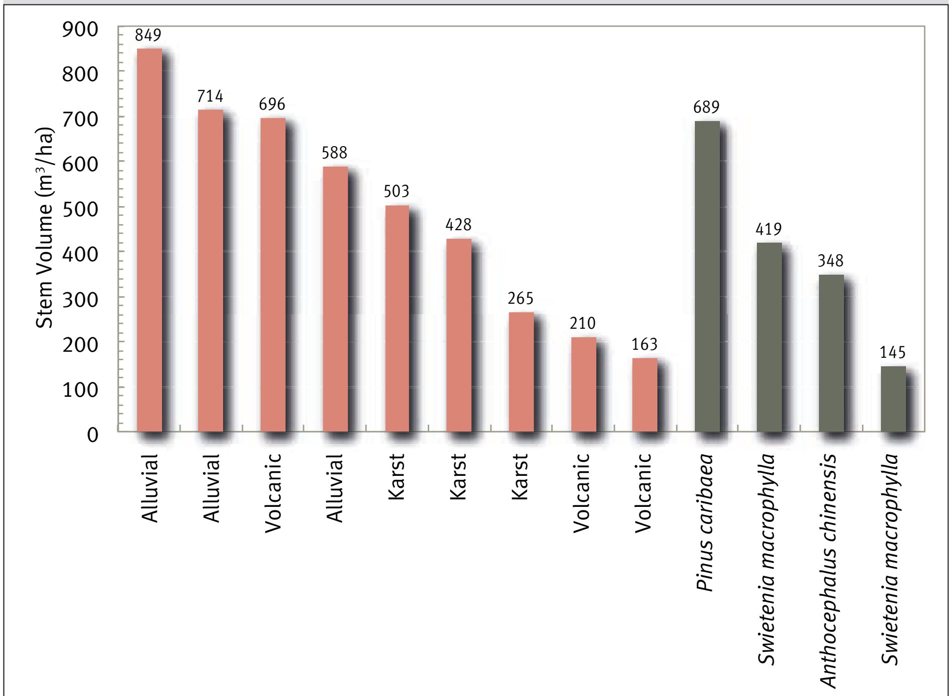

Figure 2.
Stem volume in subtropical moist novel forests (red) and subtropical wet tree plantations (black) in Puerto Rico. Novel forests were dominated by *Spathodea campanulata* (LUGO *et al.*, 2011). Plantation data for pine (*Pinus caribaea* - 18.5 yr) and mahogany (*Swietenia macrophylla* - 17 and 49 yr) are from LUGO (1992). The *Anthocephalus chinensis* plantation (12.5 yr) data are from subtropical wet forest life zone (LUGO & FIGUEROA, 1985).

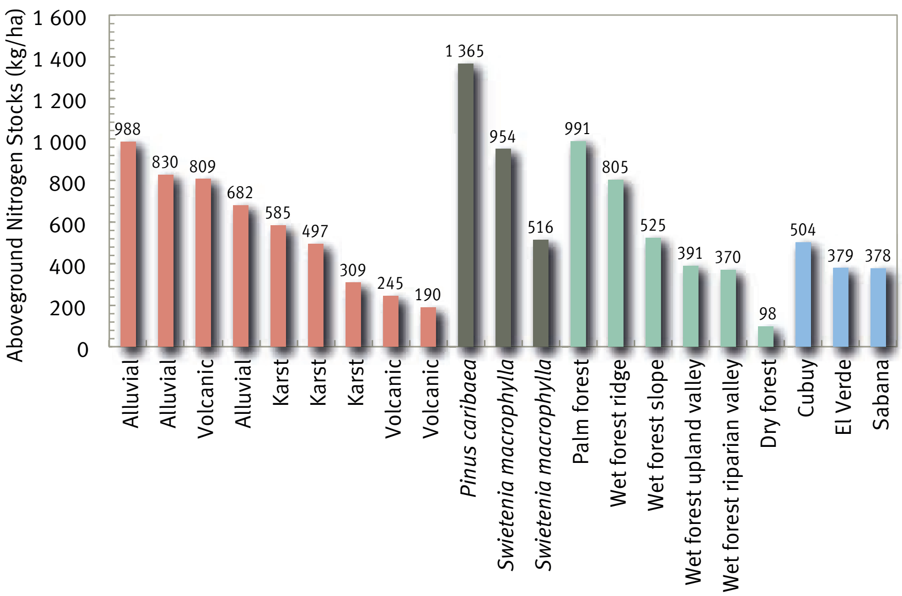

Figure 3.
Aboveground nitrogen stocks in subtropical moist novel forests (red), subtropical wet forest tree plantations (black), mature native forests (green), and secondary forests (blue) in Puerto Rico. Novel forests were dominated by *Spathodea campanulata* (LUGO *et al.,* 2011a). Plantations of pine (*Pinus caribaea* - 18.5 yr) and mahogany (*Swietenia macrophylla* - 17 and 49 yr) were paired with subtropical wet forest secondary forests (Cubuy, Sabana, and El Verde) (LUGO, 1992). Mature natural forest data are from SILVER *et al.* (1994) for ridge, slope, and valley subtropical wet forests, FRANGI & LUGO (1998) for subtropical lower montane wet palm forest, and LUGO & MURPHY (1986) for subtropical dry forest.

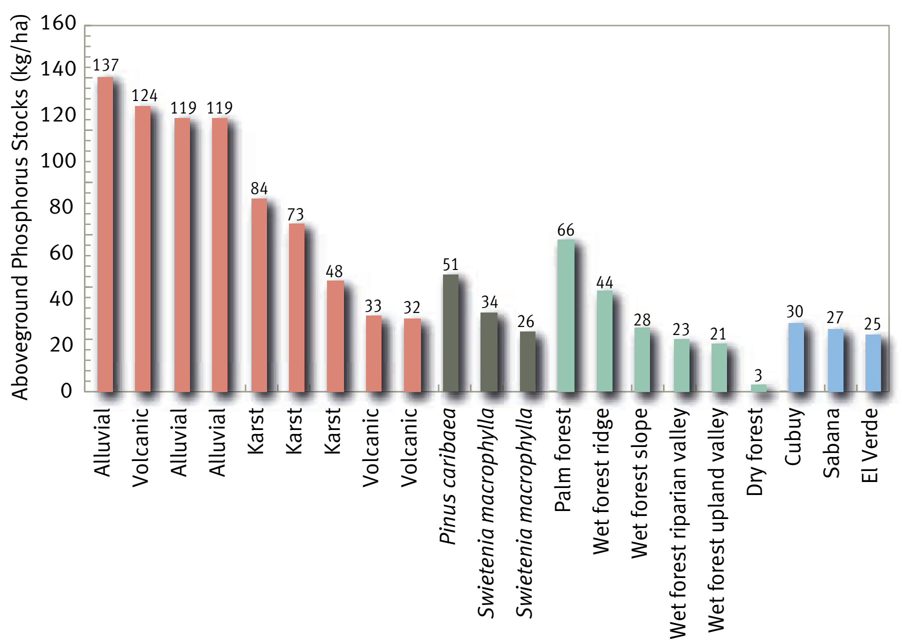

Figure 4.
Aboveground phosphorus stocks in subtropical moist novel forests (red), subtropical wet forest tree plantations (black), mature native forests (green), and secondary forests (blue) in Puerto Rico. Novel forests were dominated by *Spathodea campanulata* (LUGO *et al.*, 2011a). Plantations of pine (*Pinus caribaea* - 18.5 yr) and mahogany (*Swietenia macrophylla* - 17 and 49 yr) were paired with subtropical wet forest secondary forests (Cubuy, Sabana, and El Verde) (LUGO, 1992). Mature natural forest data are from SILVER *et al.* (1994) for ridge, slope, and valley subtropical wet forests, FRANGI & LUGO (1985) for subtropical lower montane wet palm forest, and LUGO & MURPHY (1986) for subtropical dry forest.

Discussion

Aboveground biomass and wood volume of mature tropical forests are influenced by climate (BROWN & LUGO 1982), with peak biomass in tropical and subtropical moist and wet forests, and lower biomass towards dry and rain forests, i.e., the climatic extremes have low aboveground biomass. BRANDEIS & SUÁREZ ROZO (2005) confirmed this pattern for forests in Puerto Rico (figure 7). In figure 7 the lowest aboveground biomasses occur in dry and lower montane wet forests with higher values in moist and wet forests. However, when considering successional forests, aboveground biomass and wood volume is a function of age (BROWN & LUGO 1990), a pattern that is also reflected in the forests of Puerto Rico (figure 7). The figure 7 shows lower aboveground biomass values in reversion stands, followed by young secondary and mature forests. Therefore, the interpretation of the results in figures 1 and 2 requires knowledge of the age of the study stands. The novel forests used in figures 1 to 6 ranged in age from 24 to 50 years (table II). The *Spathodea* forests ranged in age from 24 to 39 and the *Castilla* forests from 40 to 50. The *Syzygium* forest in Fig. 6 was 26 yr-old (LUGO *et al.*, 2011b). These ages are in the range of Island-wide age of successional forests in figure 7, i.e., young forests with › 30 yr.

The results show that the *Spathodea* forests in alluvial and karst sites and *Castilla* forests in karst (all in moist climates) have a higher accumulation of aboveground biomass than that reported for the average Island-wide novel forests of similar age (compare figure 1 with figure 7). They also exceed native stands and plantations. What the two types of novel forests have in common is that they grow on nutrient-rich alluvial and karst valley soils (ABELLEIRA MARTÍNEZ & LUGO, 2008; VIERA MARTÍNEZ *et al.*, 2008). Results suggest that when soils are fertile, even after extensive agricultural use, introduced tree species can accumulate large aboveground stocks of wood volume, biomass and nutrients. The lower biomass values in figure 7 compared to that of novel forests in figure 1, reflect average conditions Island-wide, which are clearly not as favourable for biomass accumulation as those in the *Spathodea* and *Castilla* forest stands. Island-wide nutrient-rich conditions like those of alluvial and karst valley soils are not prevalent. Instead, one expects that the soil conditions of Island-wide novel forests reflect land degradation, particularly of volcanic and karst hills locations, where centuries of agricultural activity degraded soils and favoured the initial establishment of introduced trees rather than native ones. Thus, the high biomass production capacity of novel forests is modified by the conditions of sites at the time of abandonment of agricultural lands so that if the conditions are nutrient-rich, forests accumulate more mass and nutrients than if they are nutrient-poor, i.e., the contrasting results from figures 1 and 7. However, Island-wide results of aboveground biomass in figure 7, particularly for mature and young forests, are in the same order of magnitude as those for native mature and successional forests in figure 1.

Three of the study sites consistently reflected low aboveground biomass and nutrient stocks. These sites were *Spathodea* forests on volcanic (two sites) and karst (one site) substrates. These apparently low stocks are a result of the way the original study was conducted (LUGO *et al*., 2011a). The estimates were based on the biomass of introduced species at each site, thus all estimates are underestimated because the biomass and nutrient stocks of native species were not included. Table II shows that, in these three sites the proportion of stems of introduced species in the sites, was below 50 per cent, thus the low biomass and nutrient stock results for those three sites. All species, native and introduced, are included in the biomass estimates for *Castilla* forests at El Tallonal. But all *Spathodea* forest data are underestimated by some degree, making the comparisons conservative in relation to the potential of novel forests.

The high comparative biomass levels on fertile soil conditions where *Spathodea* grew did not translate to similar comparative levels of aboveground nitrogen stocks, although they stored relatively high levels of phosphorus and potassium in aboveground biomass (figures 3 to 5). In general, nitrogen is not a limiting factor to terrestrial forests in the tropics (VITOUSEK, 1982, 1984), but phosphorus and potassium can limit forests in Puerto Rico (SILVER *et al.*, 1994). It is thus notable that *Spathodea* stands contain high stocks of these two potentially limiting nutrients. Such high stocks of nutrients can be significant in contributing to the role of these introduced species in supporting the regeneration of native forests and in maintaining site fertility by sequestering and keeping

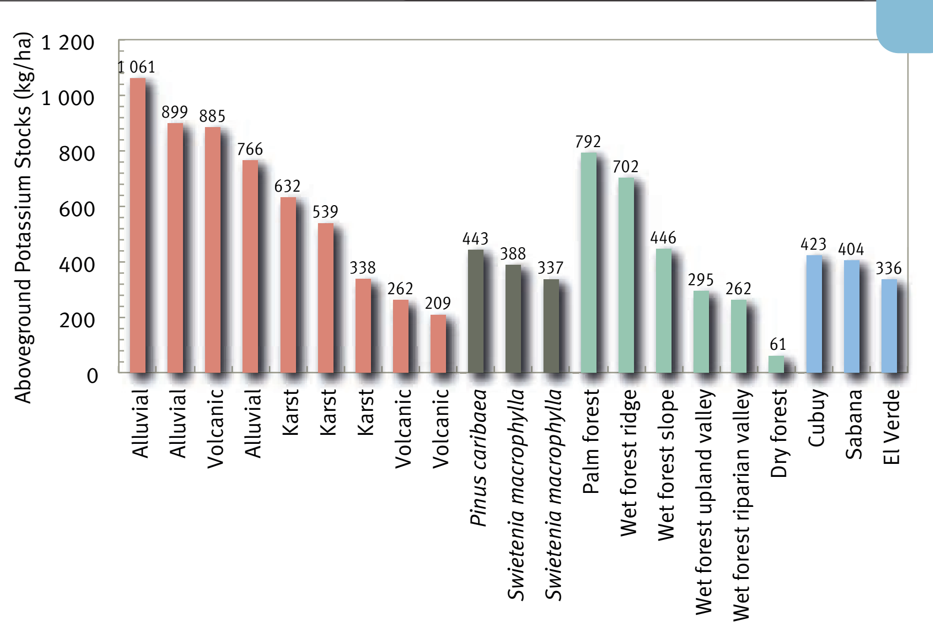

Figure 5.
Aboveground potassium stocks in subtropical moist novel forests (red), subtropical wet forest tree plantations (black), mature native forests (green), and secondary forests (blue) in Puerto Rico. Novel forests were dominated by *Spathodea campanulata* (LUGO *et al*., 2011a). Plantations of pine (*Pinus caribaea* - 18.5 yr) and mahogany (*Swietenia macrophylla* - 17 and 49 yr) were paired with subtropical wet forest secondary forests (Cubuy, Sabana, and El Verde) (LUGO, 1992). Mature natural forest data are from SILVER *et al*. (1994) for ridge, slope, and valley subtropical wet forests, FRANGI & LUGO (1985) for subtropical lower montane wet palm forest, and LUGO & MURPHY (1986) for subtropical dry forest.

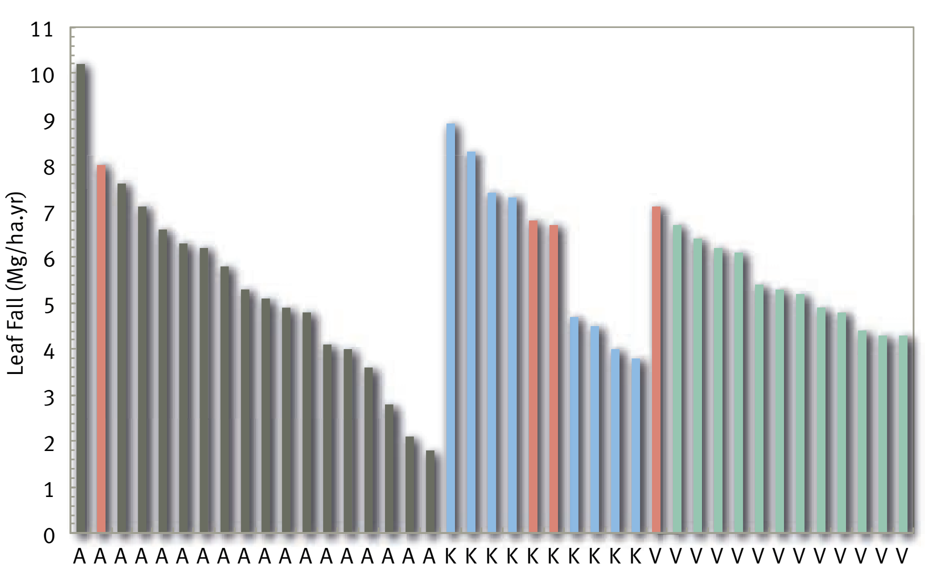

Figure 6.
Leaf litterfall in novel forests (red), mature and native tropical forests on alluvial (A, in black), karst (K in blue) and volcanic (V in green) substrates. Novel forest data are for *Spathodea campanulata* (alluvial and karst from ABELLEIRA MARTÍNEZ, 2011), *Castilla elastica* (karst from FONSECA DA SILVA, 2011), and *Syzygium jambos* (volcanic from LUGO *et al*., 2011b). The tropical forest data set is pantropical and the references can be obtained from the authors.

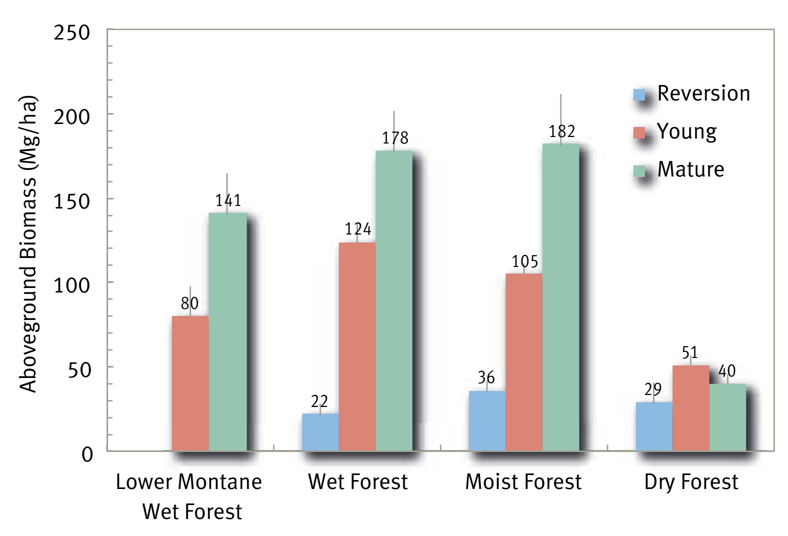

Figure 7.
Biomass of forests of different stages of succession and in different life zones of Puerto Rico. Data are based on Island-wide forest inventories for trees with diameter at breast height ≥ 2.5 cm in BRANDEIS & SUÁREZ ROZO (2005). Reversion, young, and mature correspond to secondary succession stands in the process of reverting to forests, up to about 30 years of age, and older than 30 years of age, respectively. Error bars are one standard error of the mean.

Table II.
Age at the time of study, and tree density of introduced species in novel forests highlighted in this study. The value in parenthesis for tree density of introduced species corresponds to the percent of the total density. FONSECA DA SILVA (2011) and LUGO *et al.* (2011a) are the source for information on *Castilla* and *Spathodea*, respectively. Age data for *Spathodea* are from ABELLEIRA MARTÍNEZ (2010).

Substrate	Age (yr)	Tree Density of Introduced Species (stems/ha)
Castilla elastica		
Karst	50	299 (49)
Karst	40	344 (79)
Spathodea campanulata		
Karst	38	414 (72)
Karst	24	580 (72)
Karst	31	536 (73)
Alluvial	24	814 (83)
Alluvial	38	770 (77)
Alluvial	24	1 388 (83)
Volcanic	25	166 (28)
Volcanic	39	1 061 (68)
Volcanic	39	344 (44)

nutrients on site (LUGO, 2004; ABELLEIRA MARTÍNEZ *et al.*, 2010). This is more important for phosphorous and potassium because neither are fixed from the atmosphere as nitrogen, and when leached, they are lost to the system. Potassium in particular is highly mobile and phosphorus is in low concentrations.

The effectiveness of novel forests in restoring site conditions depends on the same factors as already discussed by BROWN & LUGO (1990) and LUGO *et al.* (2004) for native secondary forests, i.e., their productive capacity including the turnover of nutrients and mass. The analysis of nutrient and mass turnover rates for *Castilla* and *Spathodea* novel forests in this study are in progress, but leaf fall rates in figure 6 and estimates of annual mass accumulation rates provide an insight on nutrient and mass turnover. Compared pantropically and by geologic substrate, novel forests of *Castilla* and *Spathodea* rank high in the return of leaf mass to the forest floor (figure 6; ABELLEIRA MARTÍNEZ, 2011). To complement the measurements of high rates of leaf litter fall, the fluxes associated with the accumulation of biomass and nutrients in aboveground compartments of these novel forests were estimated. For this calculation the oldest age estimate of *Spathodea* sites was used in table II. The resulting flux rates are high (table III). The 18.5 yr pine plantation had higher nitrogen accumulation rate than any other site, as did the *Anthocephalus* plantation in terms of biomass accumulation rate. Novel forests were high in phosphorus and potassium accumulation. They also had high rates of aboveground biomass accumulation. For example, biomass accumulation in mature forests is usually less than 5 Mg/ha.yr, which are the rates estimated for the low performing sites as explained above. These flux estimated reinforce the potential of productive novel forests for restoring stocks of mass and nutrients after agricultural abandonment.

Table III.
Estimates of annual aboveground biomass and nutrient accumulation rates in novel forests of *Spathodea campanulata* and *Castilla elastica* (Tallonal 1 and 2, biomass only) by geologic substrate using age estimates in Table II. *Castilla elastica* forests at El Tallonal were in karst substrate. Values are in kg/ha.yr for nitrogen, phosphorus, and potassium and in Mg/ha.yr for biomass. Similar data for plantations on volcanic substrates are shown. Empty cells mean no data.

Substrate or Species and Age	N	P	K	Biomass
Alluvial	26	3	28	8
Alluvial	35	6	37	11
Alluvial	28	5	32	9
Karst	24	2	26	7
Karst	16	3	17	5
Karst	8	2	9	3
Volcanic	6	3	7	6
Volcanic	8	1	8	3
Volcanic	21	1	23	2
Tallonal 1				6
Tallonal 2				4
Pinus caribaea-18.5 yr	74	3	24	9
Swietenia macrophylla-17 yr	30	2	20	2
Swietenia macrophylla-49 yr	19	1	8	2
Anthocephalus chinensis-12.5 yr				12

Stem of *Castilla elastica* growing in the northern karst region of Puerto Rico. Photograph J. Fonseca Da Silva.

Conclusions

The visual comparison of aboveground wood volume, biomass, and nutrient stocks of novel forests of *Spathodea* and *Castilla* on nutrient-rich sites shows that these forests can match or exceed native and plantation forests. Like native forests, novel forest aboveground biomass increases with age and with moisture availability from dry to wet climatic conditions. These novel forests also show high rates of leaf fall and high rates mass and nutrient accumulation aboveground. However, the Island-wide mean aboveground biomass of novel forests is lower than the values observed in the nutrient-rich conditions of *Spathodea* and *Castilla* forests. This lower Island-wide average compared to nutrient-rich sites reflects the extensive areas of nutrient-poor degraded sites where these forests occur. Nevertheless, the lower average aboveground biomass for Island-wide novel forests is within the range of values observed for native secondary forests and plantations, which suggests their vigorous growth.

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Novel forest stands of *Castilla elastica* growing in the northern karst region of Puerto Rico. View includes inside the forest. Photograph J. Fonseca Da Silva.

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