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Productivity, aboveground biomass, nutrient uptake and carbon content in fast-growing tree plantations of native and introduced species in the Southern Region of Costa Rica

D. Arias^a, J. Calvo-Alvarado^{a,*}, D. deB. Richter^b, A. Dohrenbusch^c

^a Escuela de Ingeniería Forestal, Instituto Tecnológico de Costa Rica (ITCR), Apdo. 159-7050 Cartago, Costa Rica

^b Nicholas School of the Environment, Duke University, Durham, NC, USA

^c Department Silviculture and Forest Ecology, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Germany

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ABSTRACT

Early growth performance of four native and two introduced tree species was studied during six years at 13 sites in the southern region of Costa Rica. Selected study sites represent a wide environmental gradient. The selected species were: *Pinus caribaea* Morelet var *hondurensis* (Barret y Golfari) and *Gmelina arborea* Roxb as the introduced species, and *Terminalia amazonia* (J.F. Gmelin) Exell, *Vochysia ferruginea* Mart., *Vochysia guatemalensis* Donn. Sm. and *Hieronyma alchorneoides* Fr. Allemao. A study about the distribution of aboveground biomass, nutrients and total carbon content of these young plantations by compartments (branches, stem, bark and leaves) was also conducted. Biomass equations for tree compartments were fitted simultaneously using the data corresponding to 24 trees felled. Total export quantities of nutrient from stem and bark biomass were estimated in order to conduct an evaluation of the potential effect of harvesting these species on soil nutrient reserves. The data presented in this study related to plantation growth, aboveground biomass and nutrient concentration and C content by tree compartment, aboveground biomass equations by tree compartment, soil nutrient reserves, stability indices can be used as a reference for: a) selection of tree species vs site characteristics, b) estimation of nutrient export by stem + bark harvesting, c) planning for a second rotation, c) maintenance of site productivity and d) generate better carbon sequestration estimations.

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1. Introduction

Global forest plantation was 187 million ha in 2005, about 1.4% of the total world available land area. Of this planted area 36% was located in the tropics and 64% in the non-tropical regions. The tropical forest plantation area more than doubled from 1995 to 2005, and on average, the growth rate of tropical forest

plantations was 8.6% per year [18]. The two principal commercial objectives of these tropical and non-tropical forest plantations are the production of wood for saw timber and pulp for paper [17,27]. Many industrial plantations are into their second and third rotations and managers are increasingly concerned about their production sustainability, since, repeated harvesting in short rotation cycles could remove

* Corresponding author. Tel.: +506 2550 2440/2279; fax: +506 2591 4182.

E-mail address: jucalvo@itcr.ac.cr (J. Calvo-Alvarado).

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considerable amounts of nutrients from the site decreasing tree productivity by depleting soil nutrients [32,36,42]. The amount of this nutrient depletion depends on species characteristics, growth rate, tissue nutrient content, harvesting rotation period, harvesting methods used and nutrient reserves in the soil [21].

With respect to soil nutrients reserves, it has been demonstrated that in tropical soils it can be modified through the export of biomass (trunk and bark), confirming the need to study the impact of different tree species harvesting on soil nutrient depletion. Well reported examples for tropical species include: *Pinus patula* and *Cupressus lusitanica* [31]; *Gmelina arborea* and *Pinus caribaea* [16]; *Agathis damara* [7]; *Tectona grandis* [24]; *Pinus radiata* [5]; *Pinus caribaea* [44], *Eucalyptus urograndis* [37], *Eucalyptus* hybrid PFI -Clone 1.41 [29], *Eucalyptus camadulensis*, *Eucalyptus grandis* and *Dalbergia sissoo* [26], *Accacia mangium*, *Eucalyptus globulus*, and *E. grandis* [42] and *Gmelina arborea* [39]. The conclusions of these studies are that a number of soil nutrients, particularly potassium (K) and phosphorus (P), are susceptible to depletion by the extraction of whole bole (stems + bark).

In practice, timber productivity has been well addressed by researchers and foresters in Costa Rica, but little is known about the quantity of nutrients (kg ha^{-1}) extracted from the soil by harvesting [13,38]. Most specifically the concern of nutrient depletion arises nowadays when fast-growing species are planted (i.e. *Gmelina arborea*, *Tectona grandis*) on acid low fertility soils (i.e. Ultisols, Inceptisols) in short rotations systems [12,34,35].

On the other hand, data on carbon content of tree tissues, and in particular stem wood, are essential for accurate assessments of forest carbon sequestration. The figure of 50% carbon content of woody tissues on a mass/mass basis has been used almost universally in the literature, and has been promulgated by the governmental and scientific bodies such as the IPCC [25]. This figure is also assumed in essentially all ecosystem models concerned with carbon fluxes and pools [8]. Some argue that a 50% generic value could be an oversimplification and that currently there is better information available to improve the carbon content estimations for the concept of 'carbon credits'. For example several authors found that conifers tend to have appreciably higher wood C content than do hardwoods (angiosperms): 51.5% conifers vs 48.4% hardwoods in USA [30], 52.6% conifers vs 49.7% hardwoods in USA [4], 50.9% conifers vs 49.6% hardwoods in China [40], 50.5% for eucalyptus species and 54.1% for *Pinus radiata* in Australia [22].

The aim of the present study was to characterize the productivity, distribution of aboveground biomass, carbon and nutrients content in bark, stem, branches and leaves of native and introduced species planted in the southern region of Costa Rica at 6 years of age. This assessment is made to illustrate and provide information for: a) future site management strategies and species selection aimed to conserve site productivity or replenish soil fertility, and b) improve the accuracy in the estimation of aboveground biomass and total carbon content for assessing the contribution of these species to the increasingly important ecosystem service of carbon fixation and storage [34,35,45].

2. Materials and methods

2.1. Study site

Species productivity statistics was generated from data bases of 13 trees experimental blocks of introduced and native species, established in four ecological regions in 1994 in the Southern Region of Costa Rica. Priority in site selection was given to farms located within the mosaic of abandoned pasturelands within the Rio Terraba Watershed along four eco-regions.

In this study an Eco-region combined climate (Holdridge Life Zones System - [6] and soil (USDA soil taxonomic classification, [33,43] and as the two main biophysical factors that hypothetically define four environments for growth. Eco-region 1 (Tropical Moist Forest) and 2 (Tropical Wet Forest) represent the most challenging environmental conditions with their ustic soil moisture regimes and lengthy dry season each year; soils of very low fertility, very acid, clayey texture, compacted, and after the last few decades of land use, a loss of aggregation [28]. Eco-region 3 (Premontane Rain Forest) is dominated by volcanic soils, Andisols with loamy texture and medium to high fertility. Because these sites are at higher elevation, the dry season exerts much less water stress on plants. Eco-region 4 (Tropical Wet Forest) has only one experimental plot, which is located on a young alluvial Inceptisol, with loamy texture, high fertility and perudic moisture regime [13].

A simultaneous analysis on the distribution of aboveground biomass, nutrients uptake and C content of the selected tree species was conducted in year 2000 in four experimental blocks located in Eco-region 2, around the Canton of Buenos Aires, in the Puntarenas Province of Costa Rica at approximately 500 m a.s.l. These blocks are located within the Holdridge Tropical Wet Forest Life Zone, with a mean annual temperature of 24.3 °C, annual precipitation of about 3300 mm with a dry season of <3 months from January to April. The experimental blocks were established on deep residual soils, which are clayed, very acid and leached that are mapped as Haplustults and locally described to be Oxisols [28]. Soil most relevant chemical properties for the upper 15 cm layer have the following averages and standard deviation: pH in H_2O 5.10 ± 0.07 , effective cation exchange capacity 3.52 ± 2.2 in cmol kg^{-1} and aluminum saturation 68 ± 16 in percentage. A complete description of specific site locations and physical characteristics is found in [13].

2.2. Plant material

Tree species selection was based on elimination trials results of 41 native species, preference by farmers, economic value, seedling availability and previous forestry trials results obtained in other comparable regions of Costa Rica [3,9–11,14,15,23]. The selected native species for this study were: *Terminalia amazonia* (J.F. Gmelin) Exell, *Vochysia ferruginea* Mart., *Vochysia guatemalensis* Donn. Sm. and *Hieronyma alchorneoides* Allemao. Two introduced species were also selected for their economic value, proven adaptability and often excellent growth: *Gmelina arborea* Roxb. and *Pinus caribaea* Morelet var *hondurensis* (Barret y Golfari).

2.3. Experimental design and measurements

2.3.1. Experimental design

The trial tested six native against two introduced species in a complete randomized block design with thirteen replicates within 4 Eco-regions. Trees were planted in monoculture plots, in rows of 11 by 11 trees at a spacing of 3 × 3 m, for a total area of 1089 square meters. A buffer zone was determined and consisted of two rows of trees. Therefore, the sampling plot consisted of 7 × 7 trees, for a total of 49 trees evaluated [13] for details). Observations on growth and stand characteristics were recorded annually since establishment. Diameter was measured at 1.3 m (DBH) and total tree height by a calibrated pole. The experimental blocks were established on degraded pastureland and understory was cleared manually in all plots three times per year during the first three years and thereafter only once a year.

2.3.2. Species productivity and aboveground biomass

To provide a general view of growth variation basic average productivity indices at 6 year of age were obtained for each species across the four eco-regions. The considered productivity indices for this study were: DBH (cm), tree height (m), basal area ($\text{m}^2 \text{ha}^{-1}$), total volume ($\text{m}^3 \text{ha}^{-1}$) and mean annual increment (MAI) for DBH, tree height and volume. Total volume and the MAI indices were expressed in per ha basis assuming a tree planting density of 1111 trees per ha. Total commercial volume was estimated using the allometric equations presented in [13]. Data for this analysis were obtained from previous publications or from the original data base [1,13].

To make the aboveground biomass evaluation, we harvested four representative trees per species based on the diameter versus height curve which considered the total number of trees in all of the experimental blocks. These trees were felled and the total biomass analyzed by compartment (leaves, branches, stem and bark). For each tree, the fresh weight by compartment was obtained at the site using a spring balance. Portions of wood and bark from stems (lower, middle and top parts) and branches (tip, medium and bottom parts of branches) as well as foliage (tip, medium and lower portions of the crown), were collected and pooled to obtain one composite sample per tissue per tree. All tissue-types were oven-dried at 70 °C to constant weight and then ground to pass a 0.2 mm sieve for laboratory analysis at the University of Göttingen, Germany [2]. Dry/wet weight ratios from each tree compartment were used to correct the fresh field weight determinations to obtain biomass per compartment.

2.3.3. Aboveground biomass nutrient and carbon content

To obtain total concentration of Al, Mn, Fe, K, Na, Ca and Mg for the different tree compartments, tissue samples were digested with concentrated HNO_3 and measured by inductively coupled plasma atomic emission spectrometry. P was measured using the Low Injection Analyzer and total N and C was determined with gas chromatographically after dry combustion (Carlo Erba Analyser 1500).

2.3.4. Soil nutrient reserves

A composite soil sample from the four plots was taken during the rainy season of year 2000 at three depths (0–15, 15–30 and

30–45 cm), air-dried and passed through a 2 mm sieve for laboratory analysis at the University of Göttingen, Germany [2]. For total N and C, an aliquot was ground and analyzed gas chromatographically after combustion (Carlo Erba Analyser 1500); and pH was determined in distilled water and 1 N KCl. Exchangeable Ca, Mg, K and P were extracted according to [41]. Bulk soil density was obtained for each of the three sampled depths with stainless steel rings of 10 cm long and 5 cm wide. Three sub-samples were taken at each depth, which were then deposited in separate paper bags identified with the cylinder used and the depth sampled. The analysis was done in the laboratories of the Instituto Tecnológico de Costa Rica and the oven dry weight was obtained at 80 °C after 24 h. The bulk density (g cm^{-3}) was obtained by relating dry weight in grams to the volume of the cylinder in cm^3 . Based on soil layer thickness, bulk density and nutrient concentration, we estimated the average soil nutrient reserves.

2.3.5. Balance of soil nutrient reserves and aboveground nutrient export

Total export quantities of nutrient from stem and bark biomass were estimated by obtaining the product of total biomass (Mg ha^{-1}) from each compartment by the average of estimated nutrient concentrations (mg kg^{-1}) of that compartment. In order to conduct a comparable evaluation of the potential effect of each species on soil nutrient reserves, it was decided to fix a standard harvestable volume (bark + stems) of 100 Mg ha^{-1} for all the selected species. The relationship between estimated exported nutrients (bark + stem) and the nutrient reserves in the soil up to 45 cm depth, known as the Stability Index was estimated [20]. This relationship can be used as an indicator for ecological stability for the management of production systems, hence, values of Stability Index < 0.6% will be considered as very stable and values >100% as extremely unstable [20].

2.4. Statistical analysis

One-way analyses of variance (ANOVA) were used to determine the statistical significance differences between species for growth indices (DBH and tree height), aboveground biomass (all compartments), nutrients and carbon content. Multiple comparisons of means were conducted using LSD or Duncan tests with a statistical significance of ≤ 0.05 probability level. A set of equations to estimate aboveground biomass by tree compartment and whole tree, based on DBH (tree diameter at breast height in cm) as the independent variable, was developed for each of the studied species using simple linear regression analysis. We tested the equation best goodness of fit by judging the resulting MSE (mean squared error) and the adjusted r^2 .

3. Results

3.1. Species growth

Table 1 summarizes the most important growth indices for the selected species after six years of growth. As discussed by [13] the species with the best adaptation and growing pattern

Table 1 – General mean growth and productivity indices for six native and introduced tree species in pure plantations with a density of 1111 trees/ha at 6 years across along 4 Eco-regions of Southern Region Costa Rica.

Species	Diameter at breast height (DBH, cm) ¹	Total Height (m) ¹	Basal area (m ² /ha)	Total Volume (m ³ /ha)	MAI ³ DBH (cm/year)	MAI ³ Total Height (m/year)	MAI ³ Volume (m ³ /ha/year)
Eco-Region 1							
<i>G. arborea</i>	13,1 ± 2,1 b	10,59 ± 3,70 a	14,97	102,12	2,18	1,77	17,02
<i>P. caribabaea</i>	15,4 ± 2,3 a	8,57 ± 2,55 b	20,69	72,56	2,57	1,43	12,09
<i>V. guatemalensis</i>	6,6 ± 1,3 b	4,86 ± 1,36 c	3,80	13,04	1,10	0,81	2,17
<i>V. ferruginea</i>	7,4 ± 1,3 b	4,36 ± 1,09 c	4,78	12,47	1,23	0,73	2,08
<i>H. alchorneoides</i>	3,7 ± 1,5 c	3,46 ± 0,69 c	1,19	2,27	0,62	0,58	0,38
<i>T. amazonia</i>	3,9 ± 1,5 c	3,30 ± 0,72 c	1,33	3,17	0,65	0,55	0,53
Eco-Region 2							
<i>G. arborea</i>	14,2 ± 2,7 a	12,6 ± 3,97 a	17,59	127,15	2,37	2,10	21,19
<i>P. caribabaea</i>	15,1 ± 2,6 a	8,44 ± 2,08 b	19,90	79,88	2,52	1,41	13,31
<i>V. guatemalensis</i>	12,5 ± 3,8 a	8,73 ± 2,94 b	13,63	59,00	2,08	1,46	9,83
<i>V. ferruginea</i>	11,4 ± 2,7 b	7,99 ± 2,43 b	11,34	54,69	1,90	1,33	9,12
<i>H. alchorneoides</i>	6,3 ± 2,3 d	6,60 ± 2,57 b	3,46	14,51	1,05	1,10	2,42
<i>T. amazonia</i>	7,4 ± 2,1 c	7,36 ± 3,32 b	4,78	28,12	1,23	1,23	4,69
Eco-Region 3							
<i>G. arborea</i>	14,9 ± 3,6 b	12,17 ± 4,21 a	19,37	129,25	2,48	2,03	21,54
<i>P. caribabaea</i>	17,1 ± 1,6 a	10,43 ± 0,97 b	25,52	106,80	2,85	1,74	17,80
<i>V. guatemalensis</i>	13,1 ± 5,0 c	9,46 ± 3,42 b	14,97	67,94	2,18	1,58	11,32
<i>V. ferruginea</i>	8,7 ± 2,5 f	8,68 ± 0,88 c	6,60	72,00	1,45	1,45	12,00
<i>H. alchorneoides</i>	11,6 ± 1,5 d	10,72 ± 1,15 b	11,74	49,57	1,93	1,79	8,26
<i>T. amazonia</i>	9,9 ± 3,7 e	10,19 ± 4,17 b	8,55	56,16	1,65	1,70	9,36
Eco-Region 4²							
<i>G. arborea</i>	15,82	14,00	21,84	150,00	2,64	2,33	25,00
<i>P. caribabaea</i>	15,20	9,00	20,16	72,00	2,53	1,50	12,00
<i>V. guatemalensis</i>	19,95	13,67	34,73	129,93	3,33	2,28	21,66
<i>V. ferruginea</i>	13,00	11,00	14,75	69,00	2,17	1,83	11,50
<i>H. alchorneoides</i>	16,09	12,68	22,59	88,44	2,68	2,11	14,74
<i>T. amazonia</i>	14,23	13,25	17,67	97,51	2,37	2,21	16,25

Notes 1: Mean ± standard deviations, statistical significance in letters (Duncan $p < 0.05$), 2: Eco-region 4 had only one experimental block, contrary to the other three eco-regions that have 4 blocks which allows the performance of statistical multiple comparisons, 3: MAI = Mean annual increment.

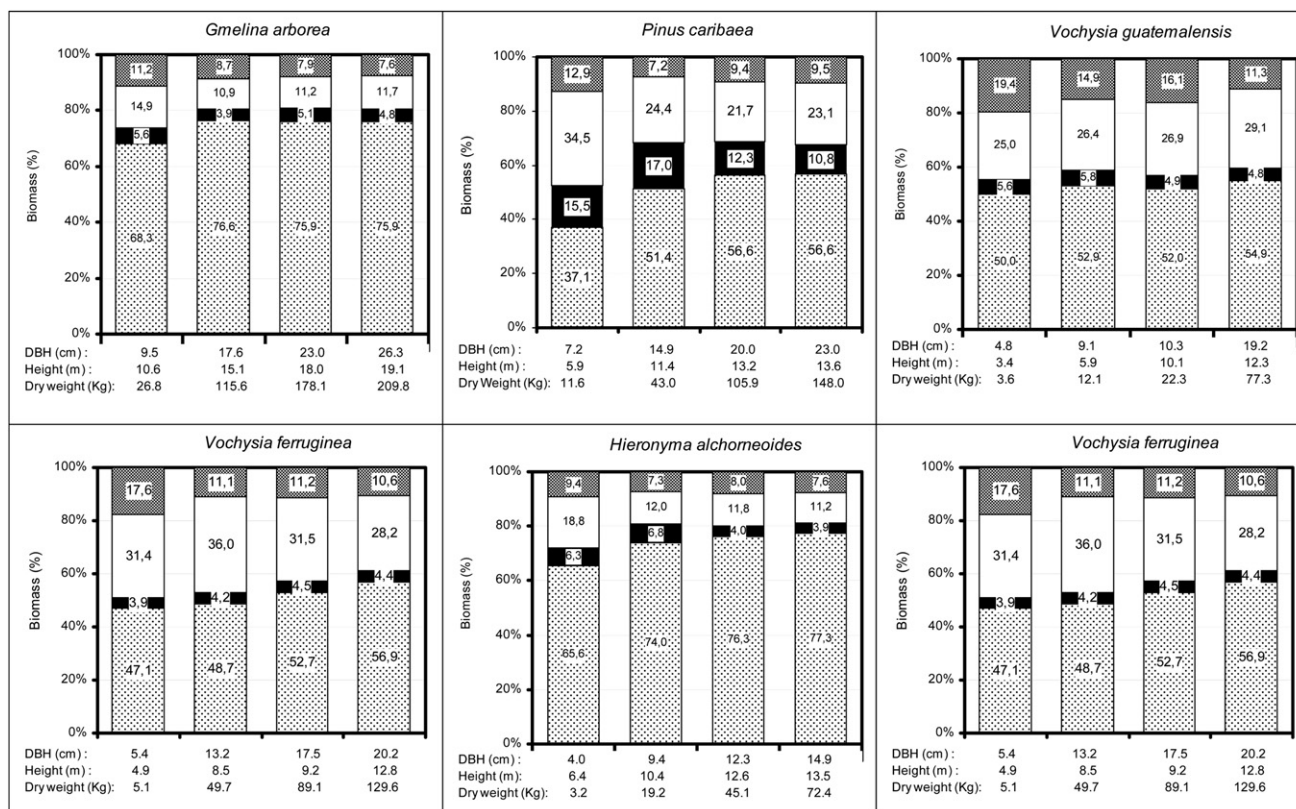


Fig. 1 – Distribution of aboveground biomass by tree compartments (■ Stem, ■ Bark, □ Branches and ■ Foliage) according to species and tree dimension (DBH=Diameter at breast height in cm, Height of tree in m, Dry weight—biomass in Kg) at six year of age on pure tree plantations. Southern Region, Costa Rica.

for southern region of Costa Rica on acid soils (Eco-region 1 and 2) were the two introduced species *Gmelina arborea* and *Pinus caribaea* followed by the two native *Vochysias*. In volcanic soils (Eco-region 3) and alluvial soils (Eco-region 4) the *Hieronyma alchorneoides* and *Terminalia amazonia* resulted in comparable adaptability and productivity indices as the two *Vochysia* species, a clear indication that these two native species prefer more fertile soils (Andisols and alluvial Inceptisols) with a shorter dry season.

3.2. Aboveground biomass

Fig. 1 shows the distribution of aboveground biomass by tree compartment and the variations according to tree dimensions (DBH, tree height and total dry weight) for each species ($n=4$). A common tendency for all the species is the increase in stem biomass as tree dimensions increase. This pattern is particularly evident in *Terminalia amazonia* whose trees of smaller dimensions the stem represents only 40% of the total aboveground biomass, while for trees of larger dimensions, the stem represents up to 80% of the total biomass. An inverse tendency in this same species is shown for foliage, branch and bark biomass, their percentages decrease as tree dimensions increase. Looking at the differences between species, the largest portion of aboveground biomass is concentrated in the stems of *Hieronyma alchorneoides* and *Gmelina arborea*. These two species distribute between 70% and 80% of their aboveground biomass in the stems regardless of tree dimensions.

The percentage of bark in *Pinus caribaea* is also notable, representing approximately 14% of the total biomass, while for the rest of the species it does not surpass 7%.

Table 2 shows the means multiple comparisons for aboveground biomass content according to tree compartments at 6 years of age. The species with the highest stem biomass is *G. arborea* which is an expected result due to the larger dimensions of sampled trees. *P. caribaea* by far has the highest bark biomass followed by *G. arborea*, while *T. amazonia* is the species with the least bark biomass. *V. ferruginea* has the highest branch biomass followed by the group of *V. guatemalensis*, *P. caribaea* and *G. arborea*. Foliage biomass is the highest for *G. arborea* followed by *P. caribaea* and *V. ferruginea*.

Table 3 includes a set of allometric equations used to estimated biomass by tree compartment and whole tree for each study species or group of species. These equations were developed using the 24 sampled trees for the biomass analysis. Fig. 1 provides extra information that provides the range of DBH values for which these equations should be applied.

3.3. Nutrient concentrations in aboveground tree compartments

Table 4 shows the means multiple comparisons for aboveground biomass nutrient concentrations according to tree compartments and species. On average, the distribution of nutrients contained in the aboveground biomass shows the following pattern for N, P, K and Mg: Foliage > Bark > Branches > Stem, and

Table 2 – Aboveground biomass (kilograms) by tree compartments of four native and two introduced tree species on per average tree dimension at six years of age. Mean, standard deviations (SD), statistical significance LSD with $P < 0.05$ (Sig) and % of total aboveground biomass.

Species	Above ground biomass (Mg ha^{-1})														
	Stems			Bark			Branches			Foliage			Total Tree		
	Mean	SD & Sig	%	Mean	SD & Sig	%	Mean	SD & Sig	%	Mean	SD & Sig	%	Mean	SD & Sig	
<i>T. amazonia</i>	22,7	23,98 b	71,5	1,2	0,91 d	3,9	5,6	3,9 c	17,7	2,3	1,2 c	7,2	31,8	29,6 c	
<i>V. guatemalensis</i>	17,3	20,37 b	53,9	1,6	1,73 c	4,3	9,1	10,9 b	28,3	4,1	3,9 c	12,8	32,0	36,9 c	
<i>V. ferruginea</i>	40,9	33,98 b	53,9	3,3	2,64 c	5,6	23,4	16,7 a	30,7	8,4	6,1 b	11,0	76,0	59,2 b	
<i>G. arborea</i>	111,4	68,95 a	75,7	6,9	4,41 b	7,7	17,0	9,9 b	11,5	11,9	6,3 a	8,1	147,3	89,6 a	
<i>H. alchorneoides</i>	29,6	26,28 b	76,3	1,7	1,20 c	5,0	4,5	3,6 c	11,7	3,0	2,6 c	7,7	38,9	33,7 c	
<i>P. caribaea</i>	47,2	39,97 b	55,1	10,6	6,98 a	15,5	19,9	14,9 b	23,2	7,9	6,5 b	9,3	85,7	68,2 b	

for Ca: Bark > Foliage > Branches > Stem. The concentrations of Mg in the different tree compartments show distinct tendencies between species: the bark of *Terminalia amazonia* has the highest concentrations of this nutrient, while in *Gmelina arborea*, the largest concentration of Mg is in the stem wood. Of all the species studied, only *Hieronyma alchorneoides* and *Pinus caribaea* show higher concentrations of Mg in the foliage. With the exception of *Pinus caribaea*, all of the species studied show high

concentrations of Ca in the bark that even surpass the concentrations of Ca in the foliage. The comparison of broadleaved species to the conifer reveals marked differences between the two. In general terms *Pinus caribaea* presents the lowest concentrations of nutrients in the biomass among all the species while *Hieronyma alchorneoides* and *Gmelina arborea* present the highest concentrations of N, P, K and Mg in the foliage. *Terminalia amazonia* and *Vochysia ferruginea* are characterized by maintaining higher concentrations of Ca in the bark. As observed in the table the two *Vochysia* trees concentrate the highest amounts of Al on their foliage, a result previously observed in other studies [19]. On the average *V. guatemalensis* and *V. ferruginea* concentrates 49 and 65 times more Al than the average of the remaining species.

Table 3 – Allometric models developed to estimate aboveground biomass in kilograms per tree compartments for six native and two introduced species growing in pure tree plantations. Southern Region of Costa Rica.

Bark biomass			
<i>P. caribaea</i>	$= 0,0425(\text{DBH})^{1,9014}$	$r^2 = 0,99$	$n = 4$
<i>T. amazonia</i>	$= 0,0093(\text{DBH})^{2,1121}$	$r^2 = 0,97$	$n = 20$
<i>G. arborea</i>			
<i>H. alchorneoides</i>			
<i>V. ferruginea</i>			
<i>V. guatemalensis</i>			
Stem biomass			
<i>G. arborea</i>	$= 0,075(\text{DBH})^{2,4167}$	$r^2 = 0,99$	$n = 12$
<i>T. amazonia</i>			
<i>H. alchorneoides</i>			
<i>P. caribaea</i>	$= 0,0321(\text{DBH})^{2,5048}$	$r^2 = 0,99$	$n = 12$
<i>V. ferruginea</i>			
<i>V. guatemalensis</i>			
Branches biomass			
<i>V. ferruginea</i>	$= 0,0265(\text{DBH})^{2,4432}$	$r^2 = 0,99$	$n = 4$
<i>G. arborea</i>	$= 0,1001(\text{DBH})^{1,662}$	$r^2 = 0,92$	$n = 12$
<i>T. amazonia</i>			
<i>H. alchorneoides</i>			
<i>P. caribaea</i>	$= 0,0348(\text{DBH})^{2,1756}$	$r^2 = 0,97$	$n = 8$
<i>V. guatemalensis</i>			
Foliage biomass			
All 6 species	$= 0,044(\text{DBH})^{1,7963}$	$r^2 = 0,91$	$n = 24$
Total Tree Biomass			
All 6 species	$= 0,1602(\text{DBH})^{2,1937}$	$r^2 = 0,97$	$n = 24$

Notes 1: Biomass in kilograms per tree compartment; DBH = diameter at the breast height (cm), r^2 measures the proportion of the variance of the biomass explained by the equation.

3.4. Balance of soil nutrient reserves and aboveground nutrient export

Table 5 presents the potential exports of nutrients contained in stems + bark based on a harvest yield of 100 Mg ha^{-1} , compared to the nutrient reserves in the soil (Mg ha^{-1}). Nutrient uptake by species show large differences among species, the following species are the ones that by far export more quantities of nutrients: *T. amazonia* (N and P), *V. guatemalensis* (K and Mg), *H. alchorneoides* and *G. arborea* (Ca). On the other hand the species that export less quantities of nutrients are: *P. caribaea* (N, K, Ca, Mg), *V. ferruginea* (P) and *T. amazonia* (Mg). Variation in the stability index shows a wide range of values, from <1.5 to >100% (extremely unstable).

3.5. Carbon content in aboveground tree compartments

Table 4 shows the means multiple comparisons for aboveground biomass C content according to tree compartments and species. On the average for all the species C content follows the pattern: Stems > Branches > Foliage > Bark. The conifer by far is the species with the highest values of C content in all compartments surpassing the 50% except for foliage (49.6%). All the broadleaf species have average C values minor than 50%. The smallest C values are *V. guatemalensis* for foliage (41%) and *T. amazonia* for bark (40.2%). On the average, C content for all the broadleaf species shows similar values for branches (47.9%) and stems (48.6%), although there are statistical significant differences among the species.

Table 4 – Nutrient concentrations in tissues of 6 natives and introduced tree species. Mean, standard deviation (SD) and statistical significance LSD with $P < 0.05$ (Sig).

Tissue/Species	Al			Mn			Fe			N			P			K			Ca			Mg			C		
	Mean	SD	Sig	Mean	SD	Sig	Mean	SD	Sig	Mean	SD	Sig	Mean	SD	Sig	Mean	SD	Sig	Mean	SD	Sig	Mean	SD	Sig	Mean	SD	Sig
	(mg/kg)			(mg/l)			(mg/l)			(%)			(mg/kg)			(mg/kg)			(mg/kg)			(mg/kg)			(%)		
Leaves																											
<i>V. ferruginea</i>	18886,4	3149,8	b	79,2	12,5	c	116,5	36,8	a	1,45	0,20	c	113,4	11,3	c	5170,0	260,1	d	6431,5	1453,6	c	1585,3	272,7	d	45,9	1,49	c
<i>V. guatemalensis</i>	24898,9	1915,3	a	125,7	47,3	c	147,2	35,2	a	1,53	0,21	c	122,0	11,7	c	7349,5	1276,4	c	12244,8	1639,9	a	3384,6	190,8	b	41,0	0,93	e
<i>H. alchorneoides</i>	220,3	63,0	c	55,4	19,8	c	112,5	29,1	b	2,21	0,06	b	1450,6	168,8	a	8537,8	964,6	b	5458,8	992,4	d	3038,2	1312,1	b	49,8	1,44	a
<i>T. amazonia</i>	345,5	78,3	c	253,4	134,3	a	59,5	33,3	d	1,41	0,27	c	817,3	266,0	b	6836,6	1431,4	d	8847,2	3117,8	b	2543,2	482,4	c	45,5	1,99	d
<i>G. arborea</i>	426,6	43,7	c	168,9	56,8	b	62,2	3,4	c	2,86	0,04	a	1644,6	169,3	a	9906,3	2861,5	a	7145,1	896,4	c	4806,2	634,2	a	48,1	0,63	b
<i>P. caribaea</i>	538,9	37,9	c	106,3	23,4	c	123,5	24,6	a	1,06	0,15	d	278,9	29,9	c	5431,1	666,5	d	3201,2	439,6	e	1090,1	389,1	e	49,6	0,84	a
Bark																											
<i>V. ferruginea</i>				288,9	138,9	b	76,1	15,0	b	0,37	0,02	e	52,3	9,5	e	4017,4	237,5	b	16261,8	2207,8	a	1196,1	55,6	c	46,6	0,41	c
<i>V. guatemalensis</i>				66,2	28,1	c	299,4	116,1	a	0,48	0,08	c	322,5	185,8	b	4235,0	530,1	b	7948,3	89,3	d	1018,1	151,6	c	44,6	1,37	e
<i>H. alchorneoides</i>				21,4	5,1	c	149,0	67,6	b	0,62	0,05	a	122,1	51,2	d	7290,2	1699,7	a	5927,5	1461,5	e	1526,4	591,2	b	48,1	0,15	b
<i>T. amazonia</i>				788,3	29,4	a	145,0	36,6	b	0,40	0,04	d	447,7	54,0	a	4399,7	218,7	b	18919,9	185,5	a	727,1	92,4	d	40,2	1,01	c
<i>G. arborea</i>				71,5	20,4	c	61,2	32,7	b	0,57	0,07	b	219,1	22,7	c	8657,5	796,5	a	9239,0	3394,2	b	2559,9	539,3	a	45,6	1,00	d
<i>P. caribaea</i>				17,5	6,3	c	59,2	11,2	b	0,18	0,04	f	66,2	24,8	e	811,1	347,8	c	1862,3	824,3	f	610,0	220,8	d	52,4	1,05	a
Branches																											
<i>V. ferruginea</i>				152,7	7,2	b	60,0	4,5	a	0,21	0,04	c	34,1	4,0	c	3218,2	208,5	c	2130,1	2,8	c	718,7	54,2	d	47,1	0,22	c
<i>V. guatemalensis</i>				295,9	55,9	a	53,2	2,2	b	0,28	0,05	b	32,8	3,0	c	4104,5	903,7	b	2770,3	372,5	b	1202,4	145,7	b	47,7	0,02	c
<i>H. alchorneoides</i>				50,4	24,7	c	50,1	1,2	b	0,31	0,01	a	396,8	80,0	a	3677,2	930,0	c	1480,5	314,0	d	778,9	129,5	c	47,5	0,85	b
<i>T. amazonia</i>				9,9	2,1	c	46,4	11,5	c	0,48	0,15	b	70,0	26,8	c	3495,6	916,9	c	2886,2	596,3	a	1525,0	229,1	a	48,6	0,23	c
<i>G. arborea</i>				39,5	17,1	c	23,0	8,3	d	0,29	0,03	b	135,8	21,0	b	5640,7	1628,7	a	2353,2	554,4	b	896,5	93,6	c	46,7	0,61	d
<i>P. caribaea</i>				23,2	5,1	c	53,9	8,0	b	0,14	0,04	d	50,1	19,3	c	830,7	320,0	d	1124,6	38,7	e	523,8	102,0	e	50,1	0,16	a
Stems																											
<i>V. ferruginea</i>				306,5	29,9	b	49,7	10,0	b	0,10	0,01	c	20,6	2,1	e	1933,0	271,0	b	818,1	38,2	b	423,4	77,2	a	48,2	0,38	c
<i>V. guatemalensis</i>				282,7	58,8	c	170,2	77,8	a	0,16	0,01	b	32,4	6,9	d	3964,6	127,0	a	1005,2	308,7	b	746,9	322,2	a	47,5	0,24	d
<i>H. alchorneoides</i>				6,0	1,2	d	54,1	6,8	b	0,14	0,01	b	50,7	20,5	c	2186,4	206,8	b	3217,6	706,1	a	394,3	144,9	a	49,0	0,36	b
<i>T. amazonia</i>				25,7	3,6	d	202,1	95,6	a	0,33	0,03	a	115,8	7,6	a	1390,2	72,0	c	1084,6	246,4	b	426,4	96,6	a	49,3	0,36	b
<i>G. arborea</i>				541,1	316,8	a	71,0	35,8	b	0,10	0,00	c	63,4	8,3	b	2087,6	114,8	b	3212,9	2749,4	a	541,1	316,8	a	47,0	0,52	d
<i>P. caribaea</i>				14,0	2,4	d	48,5	10,3	b	0,10	0,02	c	47,4	7,4	c	643,0	24,5	d	613,8	26,9	b	432,1	5,8	a	50,83	0,56	a

Table 5 – Comparison between the export of nutrient contained in stems + bark (Mg ha^{-1}), nutrient reserves in the soil and the Stability Index (nutrient contained in stems + bark/soil nutrient reserves $\times 100$) in 6 native and introduced tree species in acid unfertile soils in the southern region of Costa Rica.

Species	Biomass (Mg ha^{-1})		Nutrient content (kg ha^{-1})				
	Stems	Bark	N	P	K	Ca	Mg
<i>V. ferruginea</i>	92,5	7,5	115,4	2,3	208,9	197,6	48,1
<i>V. guatemalensis</i>	91,6	8,4	190,1	5,7	398,7	158,8	77,0
<i>H. alchorneoides</i>	94,6	5,4	163,3	5,5	246,2	336,4	45,5
<i>T. amazonia</i>	95,1	4,9	333,4	13,2	153,8	195,9	44,1
<i>G. arborea</i>	94,1	5,9	127,7	7,3	247,5	356,8	66,0
<i>P. caribaea</i>	81,7	18,3	111,7	5,1	67,4	84,2	46,5
Soil nutrients content up to 45 cm			7609	2,63	114	519	121,7

Species	Nutrient Stability Index %				
	N	P	K	Ca	Mg
<i>V. ferruginea</i>	1,5	87,3	183,3	38,1	39,6
<i>V. guatemalensis</i>	2,5	215,9	349,8	30,6	63,2
<i>H. alchorneoides</i>	2,1	207,4	216,0	64,8	37,4
<i>T. amazonia</i>	4,4	502,2	134,9	37,7	36,2
<i>G. arborea</i>	1,7	275,9	217,1	68,8	54,2
<i>P. caribaea</i>	1,5	193,2	59,1	16,2	38,2

4. Discussion of results

4.1. Species growth

The results of the present study provide valuable information to support the establishment and management of plantations of four native and two introduced species in pure designs along an environmental gradient in the southern region of Costa Rica. Native species cannot compete in growth and adaptability against the two introduced in very unfertile acid soil with prolong dry season (Eco-region 1). As soil fertility and soil moisture improves the native species become more competitive but in most cases they hardly surpass the productivity indices of the two introduced species, except in very fertile and humid sites (Eco-region 4). The point to emphasize here is that in Costa Rica there is a strong tendency to establish forest plantation in unfertile or degraded sites [12] and hence the promotion of using native species instead of introduced species must be strongly reconsidered. Further discussions about this aspect are better treated in [13].

4.2. Aboveground biomass and C content

As expected the two introduced species had the highest aboveground biomass (and hence carbon sequestration) due to its high adaptability and growth on acid unfertile soils (Eco-region 2). But as discussed before these differences could be reduced as site fertility and soil moisture improve. The information about C content and the set of equations to estimate aboveground biomass by tree compartments and whole tree, for each of the species or group of species, are significant contributions for further studies of nutrient cycling, site nutrient management and carbon sequestration. Caution must be taken when using these equations; their application should be preferably along the sampled range of DBH of each

of the study species. As found in prior publications, this study confirm that steam C content was appreciably higher in conifers (*P. caribaea*) than the selected broadleaf species (50.8% vs. 48.2%, respectively). Our results indicate that the widely used 50% wood C content figure is a fair rule of thumb when there is lack of information. We recognized that our estimation method of C content did not include chemical forms of volatile C. As shown by [40] the volatile C fraction is non-negligible, averaging 2.2% with a high variation among species in China.

4.3. Balance of soil nutrient reserves and aboveground nutrient content

Nutrients with very unstable indices ($>100\%$) are P and K, except for P in *V. ferruginea* (87%) and K in *P. caribaea* (59%). Ca and Mg resulted in unstable stability indices that range from 16% to 68% depending on species, and N is the nutrient with the less unstable values ranging from 1.5 to 4. Hence, given that these sites are growing on Ultisols and Oxisols, with minimal to no weatherable minerals that can resupply bioavailable forms of soil nutrients; the soil nutrients reserves on these sites may not support many rotations of trees without nutrient amendments. In general terms *P. caribaea* resulted with the better nutrient stability indices in comparisons with broadleaf species. This species has the lowest concentrations of nutrients in the bark and stem, with the exception of P (*V. ferruginea* has the lowest value). At present, forest plantations in Costa Rica concentrates in two species *T. grandis* and *G. arborea* and are often planted on infertile and degraded soils that are notable for their low nutrients reserves to sustain a good tree growth under intensive management. Taking this into account, if managers are seeking productivity models that guarantee sustainability, plans should be considered that includes residues management and nutrient amendments to replenish soil nutrient reserves during

rotation cycle. If these plantations are taking place on medium to high fertility soils, nutrient losses by harvesting could be relatively small and probably be replaced by soil weathering and natural inputs such as rainfall.

5. Conclusions

The data presented in this study related to plantation productivity, aboveground biomass and nutrient concentration and C content by tree compartment, aboveground biomass equations by tree compartment, soil nutrient reserves stability indices, plus already published information (e.a [13] and [1]), can be used as a reference for: a) selection of tree species vs site characteristics, b) estimation of nutrient export by stem + bark harvesting, c) planning for a second rotation, c) maintenance of site productivity and d) generate better carbon sequestration estimations.

In light of the results of this study, the total lack of interest in Costa Rica to plant *Pinus caribae* and other *Pinus* species deserves future consideration for three main reasons: a) these species competes very well on degraded or unfertile soils with *T. grandis* and *G. arborea* with the advantage of having higher carbon fixing capacity and better soil nutrient stability indices, b) the silviculture and wood technological package for industrial use of this species is well known, c) the timber from this species is widely used and has a guaranteed market. Surprisingly this species has been neglected in commercial and small farmers' reforestations projects because of its ecological reputation. Further discussion on this issue must take place between ecologists and foresters to recognize that this species is a useful alternative for small landowners who are willing to plant small plots, live fences or wind breaks on degraded lands. These farmers will plant trees with the fair expectation of an economical return and with minimum management requirements to improve their livelihoods. We agree that *P. species* is not one of the best choices for biological conservation, but is an excellent choice for other ecological services such as soil and water conservation, restoration of degraded lands and carbon sequestrations, while undoughtly supporting rural economy and land use diversification.

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