

133

Genetic variation in silvicultural traits and carbon stock content in a provenance-progeny test of *Genipa americana* L. (Rubiaceae)

A. L. Coleto¹, W. Santos¹, M. A. Moraes², J. Cambuim¹, S. S. Nascimento³, J. Ferracini¹, E. L. Longui⁴, M. L. M. Freitas^{4*}, M. L. T. Moraes¹

¹ Faculdade de Engenharia de Ilha Solteira/UNESP, Av. Brasil Centro, 56, CP 31, CEP 15385-000, Ilha Solteira (SP), Brazil. ² Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto/USP, Av. Bandeirantes, 3900, CEP 14040-901, Ribeirão Preto (SP), Brazil.

³ Faculdade de Ciências Agronômicas/UNESP, Rua José Barbosa de Barros, 1780, CEP 18610-307, Botucatu (SP), Brazil.

⁴Instituto Florestal do Estado de São Paulo, CP 1322, CEP 01059-970, São Paulo (SP), Brazil.

*Corresponding author: Miguel Luiz Menezes Freitas. E-mail: miguellmfreitas@yahoo.com.br

Abstract

The aim of this study was to determine the genetic variation of growth traits, wood basic density, dry mass of crown, leaf, and stem, and carbon stock within and between two Genipa americana L. provenances. The provenance and progeny test was installed in the Teaching, Research and Extension Farm, located in Selvíria, Mato Grosso do Sul, Brazil. The test was established using a randomized block design with two provenances and 36 progenies, a spacing of 3 x 2 m, four replicates, and six plants per plot. At 11 years of age, height and diameter at breast height (DBH) were measured. To estimate wood basic density, biomass, and carbon stock, 45 plants were thinned. Growth traits for crown, leaf, and stem, as well as wood basic specific gravity showed significant differences. Both provenances present high carbon storage, demonstrating the potential of this species to be included in carbon credit programs that help to minimize the effects of global warming. In general, heritability values were low, suggesting limited genetic control of the evaluated traits. However, the traits presented a high coefficient of genetic variation, indicating adequate sampling among populations; these results are promising for ex situ conservation and for future breeding programs.

Keywords: : breeding programs; ex situ conservation; global warming; natural populations.

Introduction

Consumerism in contemporary society has direct consequences on the environment. While agrarian development must meet the demands for food production and improved technologies, such development requires large areas of land to grow food and raise livestock, inevitably leading to forest fragmentation. These actions result in the loss of biodiversity, which hinders the maintenance of ecosystems and associated impacts including abiotic factors, such as climate change, biotic factors, such as species distribution and abundance, and biological factors, such as organism interactions in the environment (Murcia, 1995). Forest fragmentation reduces the size of tree populations, which suffer further consequences from external factors owing to edge effect, thus increasing tree mortality (Trindade et al., 2004). The problems related to fragmentation are compounded by the existence of multiple endemic or rare species which may experience genetic decline or become extinct.

Forest conservation is essential to protect the structure and functioning of the landscape. However, conservation can also help minimize the effects of climate change resulting from the release of greenhouse gases, particularly carbon dioxide as it is the main component of photosynthesis. More specifically, forests absorb carbon in the form of $CO_{2^{\prime}}$ especially during the growth phase, with the accumulation of carbon decreasing over time. Through photosynthesis, forest tree species incorporate this carbon into plant biomass, but the ability to sequester carbon for years or decades and store it in the form of wood differentiates trees from other plant species (Litton et al., 2007).

Genipa americana L. (Rubiaceae), popularly known as jenipapo, is a native, but not endemic, species of Brazil (Zappi, 2015). G. americana is distributed across all regions and states of the country, except Rio Grande do Sul, and occurs naturally in the Amazon, Caatinga, Cerrado, Atlantic Forest, and Pantanal biomes. Beyond Brazil, the species occurs in southern Mexico, Central America (Echenique-Manrique et al., 1975), and throughout northern South America, into Paraguay and Argentina (López et al., 1987). The species is dioecious, with height ranging from 8 to 14 m and trunk diameter at breast height (DBH) from 40 to 60 cm (Lorenzi, 2002). As the species is flood-tolerant, it has been recommended for planting in degraded and swampy areas (Durigan and Nogueira, 1990). In addition to its ecological contribution maintaining ecosystem equilibrium, G. americana has countless uses, including food, timber, medicinal, cosmetic, or industrial, and all of its components from root to seed can be used.

Studies to better understand G. americana are necessary as intense degradation of its natural habitat caused by agricultural expansion in Brazil has led to the species being considered threatened. Little is known about the species' genetic structure and ability to store carbon. Current literature on this topic is scarce, and most genetic studies involve biochemical traits in seeds (Oliveira et al., 2009), genetic diversity with the use of molecular markers (Silva et al., 2015; Silva et al., 2014; Rabbani et al., 2012; Sebbenn et al., 1998), and gene flow and mating system (Manoel et al., 2017). As such, the goal of this study was to better understand the development and genetic variability of G. americana through assessment of growth traits, biomass production, and carbon sequestration at eleven years of age. The results aim to support ex situ conservation, the formation of a seed orchard for future breeding programs, and inform carbon credit programs focused on mitigating the effects of global warming.

Materials and Methods

Provenances, planting area, and experimental design

In 2003, seeds of open-pollinated plants were collected from two natural provenances of *G. americana*: 21 trees from Mogi Guaçu, São Paulo, Brazil (MG; 22°20' S, 47°10' W; elevation 600 m); and 15 trees from Selvíria, Mato Grosso do Sul (SE; 20°22' S, 51°25' W; elevation 345 m). The provenance and progeny test was established in 2004 at the Teaching, Research and Extension Farm of the Faculdade de Engenharia de Ilha Solteira (UNESP) in Selvíria (20°19' S, 51°26' W; elevation 327 m). The spacing used between trees was 3 x 2 m, with six trees per plot, four randomized blocks, and one external border row of the same species. In the study area, the relief is moderately flat and undulating. The soil is classified as dystrophic Red Latosol (Oxisol) with a clayey texture (Embrapa, 2013). The average annual temperature of the warmest months is 23.7° C (December to February), and the coldest months is 20.5° C (June and July). The average annual rainfall is 1300 mm, with a climate of Aw according to the Köppen classification (Hernandez et al., 1995).

Growth traits data

The following silvicultural traits were evaluated at eleven years of age: height (H) in meters, using Vertex; diameter at breast height (DBH, 1.3 m from the ground surface) in centimeters; Survival (S) in percentage (a score of 1 was attributed to plant presence and 0 for absence). In total, 864 trees were evaluated, 504 from MG and 360 from SE.

Biomass, basic specific gravity, and carbon stock

To determine the variables of biomass, basic specific gravity, and carbon stock, 45 trees were harvested (15 from MG and 30 from SE). Trees were selected based on low DBH and less bifurcated or crooked stems. To determine biomass, fresh samples from the crown, leaves, and stem were weighed in the field using an analytical balance. Samples were then labeled, transported to the laboratory, and air-dried for five days. Subsequently, samples were oven-dried at 65° C until reaching a constant weight, and then weighed again using an analytical balance. Basic specific gravity (G_b) was determined based on the ratio of the oven-dried mass to green volume of DBH disc samples (Glass and Zelinka, 2010).

Estimation of variance components

The analyses were performed within and between provenances. For within provenance analysis, we used mixed linear models from REML/BLUP (Resende, 2016), and the following statistical model:

where *y*, *r*, *a*, *p*, and *e* refer to effects of data vector, repetition (fixed), genetic (random), plot (random), and error (random), respectively, and **X**, **Z**, and **W** are the incidence matrices of these effects (Resende, 2002; Resende, 2007a). Genetic parameters were estimated using the statistical software Selegen Reml/Blup, Model 93 (Resende, 2007b).

For between provenance analysis, we use the following statistical model:

$$\mathbf{y} = \mathbf{X}r + \mathbf{Z}a + \mathbf{W}\mathbf{p} + \mathbf{T}\mathbf{s} + e$$

where *y*, *r*, *a*, *p*, *s*, and *e* refer to the effects of data vector, repetition (fixed), genetic (random), plot (random), provenance (random), and error (random), respectively, and **X**, **Z**, and **W** are the incidence matrices of these effects. We used the software Selegen–Reml/Blup, Model 5 (Resende, 2007b).

The components of the variance and genetic parameters were estimated according to the following:

a) Individual phenotypic variance ($\hat{\sigma}_{f}^{i}$):

$$\hat{\sigma}_f^2 = \hat{\sigma}_a^2 + \hat{\sigma}_c^2 + \hat{\sigma}_e^2$$

b) Individual heritability in the strict sense, or the mean of additive effects:

$$\hat{h}_a^2 = \frac{\hat{\sigma}_a^2}{\hat{\sigma}_f^2}$$

c) Additive heritability within plot:

$$\hat{h}_{ad}^2 = \frac{0.75.\hat{\sigma}_a^2}{0.75.\hat{\sigma}_a^2 + \hat{\sigma}_e^2}$$

The coefficient of genetic variation within progenies (CV_{pg}) , individual variation (CV_{gi}) , experimental variation (CV_{a}) ,

and effects of parcels (\hat{C}_p^2) were estimated as follows:

d) Coefficient of individual additive genetic variation:

$$CV_{gi}$$
 (%) = $\frac{\sqrt{\hat{\sigma}_a^2}}{\hat{m}}$.100 (\hat{m} = general character average);

e) Coefficient of genotypic variation within progenies:

$$CV_{gp}(\%) = \frac{\sqrt{0.25.\hat{\sigma}_a^2}}{\hat{m}}.100;$$

f) Coefficient of experimental variation:

$$CV_{e}(\%) = \frac{\sqrt{[(0,75.\hat{\sigma}_{a}^{2} + \hat{\sigma}_{e}^{2})/n] + \hat{\sigma}_{c}^{2}}}{\hat{m}}.100;$$

g) Coefficient of relative variation:

$$CV_r = \frac{CV_{gp}}{CV_e};$$

h) Coefficient of determination effects of parcels (\hat{C}_p^2):

$$\hat{C}_p^2 = \frac{\hat{\sigma}_c^2}{\hat{\sigma}_f^2}$$

Results

Biomass, basic specific gravity, and carbon stock In the analysis between provenances (Table 1) biomass varied for all traits, but not for the analysis between progenies. The average values of the crown, stem, and leaf were 3.74, 3.36, and 2.18 kg, respectively. Wood basic specific gravity (G_b) presented an average of 0.45 g.cm⁻³. The coefficient of individual genetic variation ranged from 0.7 % (basic specific gravity) to 56.2 % (crown). The coefficient of genotypic variation of progenies ranged from 0.3 % (Gb) to 28.1 % (crown). The individual heritability ranged from 0.6×10^{-3} for G_b to 0.1×10^{1} for crown and leaf.

Table 1

Estimates of statistical and genetic parameters of the joint analysis for traits related to dry mass: crown, leaf, stem and basic specific gravity (G_b) in a test of progenies and origins of 11-year-old *Genipa americana* in Selvíria - MS.

Estimates	Crown (kg)	Leaf (kg)	Stem (kg)	G _b (g.cm ⁻³)	
\hat{h}_a^2	0.1.10 ⁻¹ ±0.9.10 ⁻²	0.1.10 ⁻¹ ±0.9.10 ⁻²	0.1.10 ⁻¹ ±0.9.10 ⁻¹	0.6.10 ⁻³ ±0.1.10 ⁻²	
\hat{C}_{p}^{2}	0.9.10 ⁻²	0.1.10 ⁻¹	0.1.10 ⁻¹	0.1.10 ⁻¹	
(%)	56.2	14.7	14.4	0.7	
CV _{gp} (%)	28.1	7.3	7.2	0.3	
CV _e (%)	61.8	17.9	17.7	4.8	
ŵ	3.74	2.18	3.36	0.45	
LRT (χ ²) prog	3.81	1.87	1.85	0.01	
LRT (χ ²) prov	16.17**	15.2**	15.06**	7.62**	

Heritability at individual level (\hat{h}_{k}^{2}); Determination coefficients: The effects of parcels (\hat{C}_{p}^{2}); Variation coefficients: Individual additive genetics (T_{p}^{r}); Genotypic between progenies (T_{p}^{r}); Experimental (T_{e}^{r}); General average (\hat{m}); P<5% at 1 degree of freedom, T < 1% at 1 degree of T < 1%

For the Mogi Guaçu (MG) provenance, the crown and stem traits varied among progeny, whereas for Selvíria (SE), no differences were found (Table 2). The average values of the dried mass of the MG provenance ranged from 0.45 g.cm⁻³ (G_b) to 4.57 g.cm⁻³ (crown), while the SE provenance varied from 0.44 g.cm⁻³ (Gb) to 3.19 g.cm⁻³ (stem). MG presented a higher average than SE. The G_b of MG was 0.45 g.cm-³, while that of SE was 0.44 g.cm⁻³. The estimated heritability at individual level (h_a^2) was high for leaf and stem (0.4x10⁻¹) in the MG provenance, but of low magnitude compared to G_b (0.1x10⁻¹). The SE provenance presented values from 0.7x10⁻³ for crown, leaf, and stem to 0.4x10⁻² for G_b. The determination coefficient effects of parcels (\hat{C}_n^2) for MG ranged from 0.1x10⁻¹ for crown, leaf, and stem to $0.2x10^{-1}$ for G_b, while for SE it varied from $0.1x10^{-1}$ for crown to 0.09 for G_b. The coefficients of individual genetic variation (CV_{a}) of MG presented values from 3.7 % (G_b) to 77.4 % (crown), and SE presented values from 0.6 % (G_b) to 2.8 % (leaf). The coefficient of experimental variation (CV) for MG ranged from 5.13 % (G_k) to 70.3 % (crown), and for SE it varied from 4.3 % (G_{h}) to 17.0 % (leaf). The higher values for the coefficient of relative variation (CV,) were presented by leaf and stem of MG (0.63) and for crown, leaf, and stem of SE (0.08). G_b showed values with least magnitude at 0.1 % and 0.4 % for MG and SE, respectively. The accuracy of MG presented values from 0.05 (G_k) to 0.78 (leaf) and for SE from 0.13 (G_k) to 0.16 (leaf) and 0.16 (stem).

Table 2

Estimates of genetic parameters for dry mass: crown, leaf, stem and basic specific gravity (G_b) of the DBH disc in a test of progenies and provenances for 11-year-old *Genipa americana* in Selvíria – MS.

Mogi Guaçu			Selvíria					
Estimates	crown (kg)	leaf (kg)	stem (kg)	G _b (g.cm ⁻³)	crown (kg)	leaf (kg)	stem (kg)	G _b (g.cm ⁻³)
\hat{h}_a^2	0.3.10 ⁻¹ ±0.1.10 ⁻¹	0.4.10 ⁻¹ ±0.2.10 ⁻¹	0.4.10 ⁻¹ ±0.2.10 ⁻¹	0.1.10 ⁻¹ ±0.1.10 ⁻¹	0.7.10 ⁻³ ±0.2.10 ⁻²	0.7.10 ⁻³ ±0.2.10 ⁻²	0.7.10 ⁻³ ±0.2.10 ⁻²	0.4.10 ⁻² ±0.2.10 ⁻¹
\hat{C}_{p}^{2}	0.1.10 ⁻¹	0.1.10 ⁻¹	0.1.10 ⁻¹	0.2.10 ⁻¹	0.1.10 ⁻¹	0.1.10 ⁻¹	0.1.10 ⁻¹	0.09
\hat{h}_m^2	0.5.10 ⁻¹	0.6.10 ⁻¹	0.6.10 ⁻¹	0.3.10 ⁻¹	0.2.10 ⁻²	0.2.10 ⁻²	0.2.10 ⁻²	0.1.10 ⁻¹
r _{âa}	0.74	0.78	0.78	0.5.10 ⁻¹	0.16	0.16	0.16	0.13
CV _{gi} (%)	77.4	21.6	21.3	3.7	2.7	2.8	2.7	0.6
CV ₅₇ (%)	38.7	10.8	10.7	1.9	1.3	1.4	1.4	0.3
CV _e (%)	70.4	17.0	17.0	5.1	16.4	17.0	16.5	4.3
CV,	0.55	0.63	0.63	0.36	0.08	0.08	0.08	0.07
ŵ	4.57	2.29	3.53	0.45	2.98	2.06	3.19	0.44
LRT (χ ²) prog	1184.5**	2.92	23.62**	0.86	0.01	0.01	0.01	0

Heritability at individual level $\{k_i^2\}$; Determination coefficients. The effects of parcels (C_{ρ}^2) ; Mean heritability (k_{na}^2) ; Accuracy (T_{de}) ; Variation coefficients: Individual Additive genetics (C_{ρ}') ; General average (\tilde{m}) ; $P \sim 5\%$ at 1 degree of freedom, ** P< 1% at 1 degree of freedom, termination coefficients; Likelihood Ratio Test.

Carbon Stock

The carbon stock values were higher in SE in all compartments compared to MG (Table 3).

Table 3

Carbon stock in a test of progenies and provenances of 11-year-old *Genipa americana* in Selvíria – MS.

Carbon storage	Mogi Guaçu SP (kg)	Selvíria MS (kg)
Crown	49.59	61.7
Leaf	6.65	7.13
Stem	103.51	157.26

Variation within provenances for growth traits The likelihood ratio test (LRT) showed significant differences at 5 % probability at 11 years of age between the MG and SE progeny for DBH and H (Table 4). Average survival was lower for MG (76 %) than SE (82 %), and average values obtained for H (8.59 m and 9.39 m) and DBH (6.53 and 7.23 cm) were lower in SE than MG.

Table 4

Estimates of genetic parameters for height (H), diameter at breast height (DBH) and survival (S) of 11-year-old *Genipa* americana in Selvíria – MS.

	Mogi Guaçı	1		Selviria		
Estimates	H (m)	DBH (cm)	S (%)	H (m)	DBH (cm)	S (%)
\hat{h}_{a}^{2}	0.51±0.23	0.47± 0.22	0.24± 0.13	0.01± 0.03	0.01± 0.03	0.0± 0.01
\hat{C}_{μ}^{2}	0.30	0.18	0.19	0.28	0.12	0.19
\hat{h}_{m}^{2}	0.56	0.61	0.42	0.02	0.02	0.01
r _{àa}	0.74	0.78	0.65	0.16	0.16	0.11
CV _{si} (%)	16.4	19.0	27.7	2.3	2.4	2.9
CV # (%)	8.22	9.5	13.9	1.1	1.2	1.5
CV _c (%)	14.5	15.0	32.0	14.2	14.8	26.4
CV,	0.6	0.6	0.4	0.08	0.08	0.05
ŵ	7.23	9.39	0.76	6.53	8.59	0.82
I PT (w ²) prog	3.16	4 32*	1 97	0.01	0	0

Individual heritability in the narrow sense (\hat{h}_{x}^{i}) ; Determination coefficients: The effects of parcels (\hat{C}_{p}^{i}) ; Mean heritability (\hat{h}_{m}^{i}) ; Accuracy (T_{ax}) ; Variation coefficients: Individual Additive genetics (CT_{p}) , Genotypic between progenies (CT_{p}) , experimental (CT_{e}) and relative (CT_{e}) ; Ceneral average (\hat{m}) , *P<5% at 1 degree of freedom, *' P<1% at 1 degree of freedom, RT: Likelihood Ratio Test.

The Variation coefficients: Individual Additive genetics (CV_{gl}) was higher in MG than SE. It also exceeded the values for the coefficient of genotypic variation between progeny (CV_{gp}) , revealing greater genetic variation within progeny. Values for coefficients of determining effects of parcels were high for most traits, indicating environmental influence between parcels within blocks. Another parameter that must be considered is the coefficient of experimental variation (CVe). This should be maintained at appropriate levels for each species and evaluated trait. Of all traits, accuracy was greatest for DBH (0.78) in MG, and the lowest value for this parameter was found in the SE provenance for survival (0.11). Mean heritability (\hat{h}_a^2) in MG for H was 0.51, for DBH was 0.47, and for S was 0.24; for SE, heritability was 0.01 for all traits.

Variation between provenances for growth traits

Genipa americana showed significant differences at 1 % probability between provenances for H and DBH and at the parcels level for all estimated traits (Table 5). At the progeny level, no significant differences were found. Average values for the 11-year-old progeny indicate that G. americana presented rapid growth for the evaluated traits (DBH of 9.00 cm and H of 6.88 m). The coefficient of experimental variation (CV) presented high values for H and DBH, suggesting limited environmental control. This was confirmed by the results for the coefficient of determination effects of parcels, which were above 10% for the studied traits, demonstrating the presence of environmental heterogeneity within plots. However, even with possible environmental interference in the estimates of genetic parameters for these traits, extensive genetic variation was detected between progenies with values of 12.9 % for H and 12.4 % for DBH.

Table 5

Estimates of genetic parameters for height (H), diameter at breast height (DBH) and survival (S) of 11-year-old *Genipa americana* progenies in a joint analysis between populations of Mogi Guaçu and Selvíria.

Estimates H (m) DBH (cm) S (⁴	%)
\hat{h}_a^2 0.25 ± 0.11 0.17 ± 0.09 0.0	9 ± 0.06
\hat{C}_{p}^{2} 0.25 0.15 0.2	2
^{CV} _{gi} (%) 12.9 12.4 15.	4
CV _{gp} (%) 4.1 4.2 5.3	
<i>CV_e</i> (%) 15.0 15.8 30.	8
<i>m</i> 6.88 9.00 0.7	9
LRT (χ ²) Prov 21.85** 12.85** 1.2	1
LRT (χ ²) Prog 2.31 1.61 0.5	4
LRT (χ^2) Parc 67.5** 25.01** 53.	6"

Individual heritability in the narrow sense (\hat{h}_a^2) ; Determination coefficients: The effects of parcels (\hat{C}_a^2) ; Variation coefficients: Individual Additive genetics

 (CV_{gi}) , Genotypic between progenies (CV_{gp}) , experimental (CV_e) ; General average (\hat{m}); *P< 5% at 1 degree of freedom, ** P< 1% at 1 degree of freedom; LRT: Likelihood Ratio Test.

For survival, the significance was only detected at the plot level; thus, the trunk shape of the trees (architecture) may not have been the result of genotypic expression, but rather due to behavior and competition of plants within plots. In other words, the experimental design contributed to trees with straighter trunks and less bifurcation. Meanwhile, individual heritability within the two provenances was low for all traits, indicating limited genetic control of the traits.

Discussion

We detected genetic variation in growth traits, biomass production, and carbon sequestration for 11-year-old G. americana trees analyzed individually and together. The likelihood ratio test demonstrated the existence of genetic variation in these traits within and between provenances, with the possibility of genetic improvement during the implementation of conservation strategies. Based on the scale defined by Resende (2002), heritability is considered low magnitude when \hat{h}_a^2 < 0.15, average magnitude between 0.15 < \hat{h}_a^2 < 0.50, and high with \hat{h}_a^2 > 0.50. Therefore, the heritability for growth traits, biomass production, and carbon sequestration found herein were moderate to high. Estimates of the coefficient of individual heritability in the restricted sense allows us to evaluate if the traits are heritable (Bueno et al., 2001). Studies on individual heritability within provenances for native trees in Brazil have reported low values for these growth traits (Kubota et al., 2015; Sant'ana et al., 2013; Senna et al., 2012; Guerra et al., 2009; Rocha et al., 2009; Souza et al., 2003).

The MG provenance has greater genetic variability, while the SE provenance has a restricted genetic base. Genetic variation coefficients above 7% are considered high (Sebbenn et al., 1998). Low magnitude values for the coefficient of variation of plots indicate good precision in the method used to evaluate the traits analyzed and the experimental design (Kageyama et al., 1977). According to Vencovsky and Barriga (1992), traits with a higher relative coefficient of variation are indicated for selection. Therefore, selecting trees with greater carbon storage capacity would be the best strategy for individuals in the MG provenance based on leaf and stem traits. The estimate of accuracy showed intermediate values (25 < $V_{\hat{a}a}$ < 75%) (Resende, 2002), and represent the relationship between the true and estimated individual genetic value.

Values of carbon stock and plant biomass of the 45 trees harvested from the provenance and progeny test represent the phase at which resources are invested in fruit production. The carbon stock of *G. americana* presents values above those indicated in the literature. For example, Lacerda et al. (2009) observed greater concentration in the canopy than the other two compartments in plantations of native Atlantic Forest species in Brazil at 2, 4.5, 5.5, and 7 years of age. Further, Salomão et al. (2014), assessing agroforestry systems (AFS) at five years, reported 9.85 kg for seven trees (all parts); Vieira et al. (2009) found 1.14 kg in the leaves, 9.27 kg in the canopy, and 22.21 kg in the stem of *Nectandra grandiflora*; while Fernandes et al.

(2007) evaluated a *Hevea* sp. at 12 years of age and found 2.8 kg in the leaves, 17.4 kg in the canopy, and 26.6 kg in the stem. Schneider et al. (2005) also found higher average values in descending order of stem> crown> leaf in *Acacia mearnsii* at four years of age.

The distribution of carbon storage across plant compartments most often follows the decreasing order of stem> root> crown> leaves, as reported by Saidelles et al. (2009) for A. mearnsii at four years of age and Caldeira et al. (2015) for Araucaria angustifolia at 23 to 32 years. However, this arrangement does not always hold true. Urbano et al. (2008) noted that the average carbon content of Mimosa scabrella is highest in the leaves, followed by bark> branches> stem. This distribution can be explained by the initial stages of development of a forest plant during which most carbohydrates are directed to the production of crown and roots. With time, biomass production of the stem increases and then gradually decreases (Schumacher, 1996). According to D'Almeida (1988), the high concentration of carbon in tree compartments is a result of wood composition, which is 50 % cellulose, 25 % hemicellulose, and between 15 to 35 % lignin. On the other hand, leaves, branches, and roots have considerable carbon concentrations when compared to bark.

In general, secondary and young forests stock high levels of carbon, with primary forests and mature plantations achieving a balance of carbon sequestration by releasing an equal amount to that sequestered through the decomposition of dead wood and senescent trees. Thus, it is estimated that one hectare of planted trees can absorb around 10 t of carbon per hectare per year from the atmosphere (Arevalo et al., 2002).

Studies on experimental plantations similar to the present study (with native species and established age) are rare. Therefore, the information provided herein is novel as it: a) provides information on long-term silvicultural behavior of *G. americana*; b) suggests appropriate management measures; (c) assesses the survival rate and adaptation of these species for *ex situ* conservation purposes; d) informs assessments of genetic variability and control in the field in order to establish improved seed orchards to supply the reforestation market; e) provides information on biomass productivity and carbon stock, enabling the inclusion of this species in carbon credit programs aimed at minimizing the effects of global warming.

Acknowledgements

We are very grateful to the technicians at the Teaching, Research and Extension Farm of the Faculdade de Engenharia, Campus de Ilha Solteira (FEIS/UNESP) for technical assistance and support in data collection. This study was supported by FAPESP (State of São Paulo Research Foundation, Process: 2013/08655-6 – IC). We also thank CNPq (National Council for Scientific and Technological Development) for a grant to Miguel Luiz Menezes Freitas and Mario Luiz Teixeira de Moraes. We also thank Dr. Evelyn R. Nimmo for editing the English of the manuscript.

References

- Arevalo LA, Alegre JC, Vilcahuman LJM (2002) Metodologia para estimar o estoque de carbono em diferentes sistemas de uso da terra. Colombo, Brasil: Embrapa Florestas, 41 p, ISSN 1517536X
- Bueno LCS, Mendes ANG, Carvalho SP (2001) Melhoramento de plantas: princípios e procedimentos. Lavras, Brasil: UFLA, 282 p. ISBN 8587692054
- Caldeira MVW, Watzlawick LF, Vieira M, Balbinot R, Castro KC (2015) Biomassa e carbono orgânico em povoamentos de Araucaria angustifolia (Bertol.) Kuntze. Ciência Florestal 25(4):1027-1034.

https://doi.org/10.5902/1980509820664

- D'Almeida MLO (1988) Composição química dos materiais lignocelulósicos. São Paulo, Brasil: Instituto de Pesquisas Tecnológicas, 105 p.
- Durigan G, Nogueira JCB (1990) Recomposição de Matas Ciliares. Série Registros Instituto Florestal de São Paulo 4:1-14.
- EMPRESA BRASILEIRA DE PESQUISA AGROPECUÁRIA Embrapa. (2013) Sistema brasileiro de classificação dos solos. Brasília, Brasil: Embrapa, 353 p. ISBN 9788570351982
- Fernandes TJG, Soares CPB, Jacovine AG, Alvarenga AP (2007) Quantificação do carbono estocado na parte aérea e raízes de Hevea sp., aos 12 anos de idade, na zona da Mata Mineira. Revista Árvore 31(4):657-665. <u>https://doi.org/10.1590/s0100-67622007000400010</u>
- Glass S, Zelinka SL (2010) Moisture relations and physical properties of wood. In: Ross, R. (Ed) Wood handbook – wood as an engineering material. Madison, United States of America: U.S. Department of Agriculture, Forest Service, pp 4.1-4.19. <u>https://doi.org/10.2737/fpl-gtr-190</u>
- Guerra CRSB, Moraes MLT, Silva CLSP, Canuto DSO, Andrade JAC, Freitas MLM, Sebbenn AM (2009) Estratégias de seleção dentro de progênies em duas populações de Myracrodruon urundeuva Fr. All. Scientia Forestalis 37(81):79-87.
- Hernandez FBT, Lemos Filho MAF, Buzetti S (1995) Software HIDRISA e o balanço hídrico de Ilha Solteira. Ilha Solteira, Brasil: UNESP/FEIS Área de Hidráulica e Irrigação, 45 p.
- Kageyama PY, Spelts RM, Silva AP, Ferreira M (1977) Variação genética entre e dentro de progênies de Pinus patula Schiede e Deppe na região de Telêmaco Borba-PR. Boletim Informativo IPEF 15:21-39.
- Kubota TYK, Moraes MA, Silva ECB, Pupin S, Aguiar AV, Moraes MLT, Freitas MLM, Sato AS, Machado JAR, Sebbenn AM (2015) Variabilidade genética para caracteres silviculturais em progênies de polinização aberta de Balfourodendron riedelianum (Engler). Scientia Forestalis 43(106):407-415.
- Lacerda JS, Couto HTZ, Hirota MM, Pasishnyk N (2009) Estimativa da biomassa e carbono em áreas restauradas com plantio de essências nativas. METRVM 5:1-23.
- Litton C, Raich JW, Ryan MG (2007) Carbon allocation in forest ecosystems. Global Change Biology 13(10):2089-2109.

https://doi.org/10.1111/j.1365-2486.2007.01420.x

- López JA, Little Jr EL, Ritz GF (1987) Arboles communes del Paraguay. Washington, United States of America: Peace Corps, 425p.
- Lorenzi H (2002) Árvores brasileiras: manual de identificação e cultivo de plantas arbóreas nativas do Brasil. Nova Odessa, Brasil: Plantarum, (2)368p. ISBN 8586714070
- Manoel RO, Freitas MLM, Furlani Junior E, Alves PF, Moraes MLT, Sebbenn AM (2017) Low levels of pollen and seed flow in a riparian forest fragment of the dioecious tropical tree Genipa americana L. Forestry Research and Engineering: International Journal 1:2-12.

https://doi.org/10.15406/freij.2017.01.00003 Murcia C (1995) Edge effects in /fragmented forests: implications for conserva-

tion. Trends in Ecological and Evolution 10(1):58-62. https://doi.org/10.1016/s0169-5347(00)88977-6

- Oliveira AO, Bonjorno II, Alves PF, Moraes MA, Freitas MLM, Moraes MLT, Polizeli MLTM (2009) Variação genética para compostos bioquímicos em sementes de duas populações naturais de Genipa americana L.: 1- análises individuais e univariada. Scientia Forestalis 37:71-78.
- Rabbani ARC, Silva-Mann R, Ferreira RA (2012) Variabilidade genética de Genipa americana L. pertencente ao baixo curso do Rio São Francisco. Revista Árvore 36:401-409. <u>https://doi.org/10.1590/s0100-67622012000300002</u>

- Resende MDV (2016) Software Selegen-REML/BLUP: A Useful Tool for Plant Breeding. Crop Breeding and Applied Biotechnology 16:330-339. https://doi.org/10.1590/1984-70332016v16n4a49
- Resende MDV (2002) Genética biométrica e estatística no melhoramento de plantas perenes. Brasília, Brasil: Embrapa Informação Tecnológica, 975 p. ISBN 8573831618
- Resende MDV (2007a) Matemática e estatística na análise de experimentos e no melhoramento genético. Colombo, Brasil: Embrapa Florestas, 561 p. ISBN 9788589281157
- Resende MDV (2007b) SELEGEN-REML/BLUP: sistema estatístico e seleção genética computadorizada via modelos lineares mistos. Colombo, Brasil: Embrapa Florestas, 359 p. ISBN 9788589281164

Rocha BR, Rocha MGB, Santana RC, Vieira AH (2009) Estimação de parâmetros genéticos e seleção de procedências e famílias de Dipteryx alata Vogel (Baru) utilizando metodologia de Reml/Blup e E(QM). Cerne 15(3):331-338.

- Saidelles FLF, Caldeira MVW, Shumacher MV, Balbinot R (2009) Uso de equações para estimar carbono orgânico em plantações de Acacia mearnsii de Wild. no Rio Grande do Sul-Brasil. Revista Árvore 33(5):907-915. https://doi.org/10.1590/s0100-67622009000500013
- Salomão GB, Fernandes SSL, Pereira ZV, Nascimento JS, Moitinho MR, Padovan MP (2014) Estoque de carbono por espécies arbóreas em um sistema agroflorestal biodiverso em Dourados, Mato Grosso do Sul [online] Available at < <u>http://www.aba-agroecologia.org.br/revistas/index.php/cad/article/</u> view/16646/10423> [cited 12/15/2015].
- Sant'Ana VZ, Freitas MLM, Moraes MLT, Zanata M, Zanatto ACS, Moraes, MA, Sebbenn AM (2013) Parâmetros genéticos em progênies de polinização aberta de Enterolobium contortisiliquum (Vell.) Morong em Luiz Antonio, SP, Brasil. Hoehnea 40(3):515-520.

https://doi.org/10.1590/s2236-89062013000300011

- Schneider PR, Finger CAG, Sobrinho VG, Schneider PSP (2005) Determinação indireta do estoque de biomassa e carbono em povoamento de Acácia-Negra (Acacia mearnsii de Wild.). Ciência Florestal 15(4):391-402. https://doi.org/10.5902/198050981876
- Schumacher MV (1996) Ciclagem de nutrientes como base da produção sustentada em ecossistemas florestais. In: Simpósio sobre ecossistemas naturais do Mercosul: o ambiente da floresta, 1., 1996, Santa Maria. Anais... Santa Maria: UFSM/CEPEF, p.65-77.
- Sebbenn AM, Kageyama PY, Vencovsky R (1998) Variabilidade genética, sistema reprodutivo e estrutura genética especial em Genipa americana L. através de marcadores isoenzimáticos. Scientia Forestalis 53:15-30.
- Senna SN, Freitas MLM, Zanatto ACS, Morais E, Zanata M, Moraes MLT, Sebbenn AM (2012) Variação e parâmetros genético em teste de progênies de polinização livre de Peltophorum dubium (Sprengel) Taubert em Luiz Antonio-SP. Scientia Forestalis 40(95):345-352.
- Silva AVC, Muniz EN, Almeida CS, Vitoria MF, Ledo AS, Melo MFV, Rabbani ARC (2015) Genetic diversity and sex identification in Genipa americana L. Tropical and Subtropical Agroecosystems 18:81-86.
- Silva AVC, Freire KCS, Ledo AS, Rabbani ARC (2014) Diversity and genetic structure of jenipapo (Genipa americana L.) Brazilian accessions. Scientia Agricola 71:345-355.
- Souza CS, Aguiar AV, Silva AM, Moraes MLT (2003) Variação genética em progênies de Gonçalo-alves (Astronium fraxinifolium) em dois sistemas de plantio. Revista do Instituto Florestal 15(2): 137-145.
- Trindade MB, Figueira SB, Silva HP, Silva ACBL, Schessl MA (2004) fragmentação da Mata Atlântica no litoral norte de Pernambuco: Uma análise da estrutura da paisagem [online] Available at <<u>http://www.cprh.pe.gov.br/rbma/downloads/frag-mata-atl.pdf</u>> [cited 11/22/2017].
- Urbano E, Machado SA, Figueiredo Filho A, Koehler HS (2008) Equações para estimar o peso de carbonofixado em árvores de Mimosa scabrella Bentham (Bracatinga) em povoamentos nativos. Cerne 14: 194-203.
- Vencovsky R, Barriga P (1992) Genética biométrica no fitomelhoramento. Ribeirão Preto, Brasil: Sociedade Brasileira de Genética, 496 p.
- Vieira G, Sanquetta CR, Barbeiro LSS (2009) Estoque individual de biomassa e carbono em Nectandra grandiflora nees (canela-amarela). Revista Floresta 39(3): 547-554. https://doi.org/10.5380/rf.v39i3.15354
- Zappi D (2015) Genipa in Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro [online]. Available at <<u>http://floradobrasil.jbrj.gov.br/jabot/</u> <u>floradobrasil/FB14045</u>> [cited 06/08/2016].