Original Article

Whole-plant and leaf determinants of growth rates in progenies of *Genipa americana* L. (Rubiaceae)

Determinantes da taxa de crescimento de planta inteira e folha em progênies de *Genipa americana* L. (Rubiaceae)

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Abstract

Genipa americana (Rubiaceae) is a fruit tree with broad phytogeographic domain and suitable for different silvicultural systems in the tropics. The knowledge associated with the relative growth rate of species such as *G. americana*, provides important guidelines for the effective establishment and survival of seedlings after planting in the field. In this study we investigated differences in growth, biomass allocation and photosynthesis of seedlings originating from different mother plants of *G. americana* in southern Bahia, Brazil. For this, we evaluated fifteen variables associated with carbon balance at the whole plant and leaf scales of twelve *G. americana* progenies. All seedlings grew over a period of 198 days under similar microclimatic conditions with approximately 65% full sun. Our results showed significant differences in the relative growth rates (RGR), with the highest and lowest mean values being 29.0 and 38.0 mg g^{-1} day^{-1}, respectively. Differences in RGR between *G. americana* progenies were highly related to differences in biomass allocation at both whole plant and leaf scales. From a practical point of view, we demonstrate that the selection of mother plants to produce seedlings with higher growth rates, and consequently greater establishment capacity in field plantings, can be made from evaluations of growth and biomass allocation variables at the whole plant scale.

Keywords: tropical trees, biomass allocation, relative growth rate, carbon balance.

Resumo

Genipa americana (Rubiaceae) é uma árvore frutífera com amplo domínio fitogeográfico e adequada para diferentes sistemas silviculturais nos trópicos. O conhecimento associado à taxa de crescimento relativo de espécies como *G. americana* fornece diretrizes importantes para o estabelecimento e sobrevivência de mudas após o plantio no campo. Neste estudo investigamos diferenças no crescimento, alocação de biomassa e fotossíntese de mudas originárias de diferentes plantas-mãe de *G. americana* no sul da Bahia, Brasil. Para isso, foram avaliadas quinze variáveis associadas ao balanço de carbono em escala de planta inteira e escala foliar de doze progênies de *G. americana*. Todas as mudas cresceram durante um período de 198 dias sob condições microclimáticas semelhantes com aproximadamente 65% de pleno sol. Nossos resultados mostraram diferenças significativas nas taxas de crescimento relativo (RGR), sendo os valores médios mais altos e mais baixos 29.0 e 38.0 mg g^{-1} dia^{-1}, respectivamente. As diferenças na RGR entre as progênies de *G. americana* foram altamente relacionadas às diferenças na alocação de biomassa tanto na planta inteira quanto em escala foliar. Do ponto de vista prático, demonstramos que a seleção de plantas matrizes para produção de mudas com maiores taxas de crescimento, e consequentemente maior capacidade de estabelecimento em plantios em campo, pode ser feita a partir da avaliação de variáveis de crescimento e alocação de biomassa em escala de planta inteira.

Palavras-chave: árvores tropicais, alocação de biomassa, taxa de crescimento relativo, balanço de carbono.

1. Introduction

The Jenipap tree (*Genipa americana* L.) is a tropical fruit tree that belongs to the Rubiaceae family (Souza et al., 1999; Sousa-Santos et al., 2024), widely distributed in the tropical forests of Central and South America (Sousa-Santos et al., 2024). In Brazil, *G. americana* is found in almost all biomes (Pires et al., 2018; Santos et al., 2021, 2022). The fruit is

popularly known as "*Jenipapo*", in Tupi-Guarani it means "*fruit that is used to paint*" (Zappi, 2016). This coloring property occurs because in its initial stage of maturation the fruit is a natural source of genipin, an iridoid compound that imparts a blue color (Neri-Numa et al., 2018). The fruits of *G.americana* have a high iron content and can be consumed fresh or used for the production of sweets and drinks (Santos et al., 2021). The species has great socioeconomic and cultural importance in several parts of Northeast Brazil (Santos et al., 2021, 2022). In addition, *G. americana* is recognized as a multiple-use tree species for its valuable wood and ecological role in tropical forests (Santos et al., 2021; Sousa-Santos et al., 2022). This species has been indicated for the ecological restoration of tropical forests in South America, due to its high percentage of survival, high phenotypic plasticity of fruits and seeds (Santos et al., 2021; Sousa-Santos et al., 2022). In addition, *G. americana* is considered a priority tree species for the restoration of degraded areas in the Brazilian Atlantic Forest (Rolim et al., 2019). Therefore, these characteristics associated with the hardiness of *G. americana*, contribute to this fruit tree being considered an essential species for cultivation in agroecosystems (Mielke et al., 2003; Montagnini and Nair, 2004; Rolim et al., 2019), with numerous possibilities of use in tropical ecosystems.

The success of tree plantations depends, among other factors, on knowledge about the ecology and management related to the characteristics of the tree species that will be used (Piotto and Rolim, 2018), mainly to factors associated with growth and survival. Under these conditions, the initial growth and field establishment of young plants is one of the most important factors, because both survival and reproduction depend on plant size (Shipley, 2006). At the whole plant scale, the relative growth rate (*RGR*) corresponds to the increment in biomass from the initial biomass (Hunt, 2017). The *RGR* is considered a key ecological and silvicultural trait as it reflects adjustments between physiological (photosynthetic capacity - Net assimilation rate - *NAR*) and morphological characteristics (leaf efficiency in light interception - Leaf area ratio - *LAR*) (Hunt, 2017). Furthermore, in response to environmental heterogeneity, plants can change the pattern of biomass allocation to leaf, stems and roots, due to the availability of resources in the growing environment. Competition for resources below and above ground is an important factor that must be considered during plant establishment, as obtaining sufficient supplies of water, nutrients and light becomes essential to sustain an adequate growth rate (Poorter et al., 2012).

The ability of a plant genotype to modulate the expression of its physiological and morphological characteristics in response to environmental conditions is a determining factor for the success of plant acclimatization during its establishment (Grossnickle and MacDonald, 2018). Thus, studies related to the variability and genetic parameters of forest species are essential from an ecological point of view, mainly to define areas for collecting seeds (selection of mother trees), aiming to use the information in restoration programs and germplasm banks, in addition to uses in plantations for conservation and pre-improvement of tree species (Leites and Garzón, 2023). As being sessile

and photosynthetic organisms, plants have different adjustments related to changes in carbon balance at the whole plant and leaf scales. On a whole-plant scale, carbon balance is related to the ability of photosynthetic tissues to assimilate carbon and to the efficiency of biomass allocation and respiration of non-photosynthetic tissues. At leaf scale, carbon balance is dependent on the processes of carbon assimilation (photosynthesis) and loss (cellular respiration). For example, higher investment in the photosynthetic apparatus per unit of leaf area, expressed by higher values of leaf mass per unit area (*LMA*), contributes to greater carbon assimilation capacity (Riva et al., 2016). In addition, the environmental conditions experienced by the mother plant during its growth can influence the morphophysiological responses presented by the progenies, mainly related to the potential for growth and survival in the face of environmental changes (Vivas et al., 2019).

In this study we investigated the differences in growth, biomass allocation and photosynthesis between young plants originating from different mother plants of *G. americana*. We sought to answer two questions: (a) are there differences between the initial growth of *G. americana* progenies originating from different mother plants? (b) can growth rates of *G. americana* progenies be explained by differences in biomass allocation and carbon balance at whole plant or by differences in the at leaf scale?

2. Materials and methods

2.1. Areas of study

The experiment was carried out in the nursery of the State University of Santa Cruz (UESC), located in Ilhéus, south of Bahia, Brazil (14º45'15"S 39º13'59"W). The nursery has a structure 12 m long, 6 m wide and 3 m high, covered with a shading screen that allows the passage of approximately 65% of solar radiation in full sun. According to the classification established by Köppen, the southern region of the state of Bahia has an Af-type humid (or superhumid) tropical climate, with an average monthly temperature of 24 to 26°C, with annual precipitation exceeding 1.500 mm/year (Alvares et al., 2013).

2.2. Plant material and growth conditions

The seeds of *G.americana* for seedling production were obtained from fruits of 12 mother plants growing in the southern region of Bahia, Brazil (39º31'29"W; 15º11'47"S). The southern region of Bahia is made up of 26 municipalities, and a total area of 14.664.54 km² (Cerqueira and De Jesus, 2017). Fruit collection was carried out in 12 areas, within 6 municipalities, in a total area of 3.083 9 km² and an elevation gradient varying between 29-400 masl (see Table S1). During collection, only healthy (without pericarp deformation or other visible damage) and fully ripe fruits were collected. After collection, 10 fruits from each mother plant were packed separately in plastic boxes and transferred to the Plant Physiology Laboratory at UESC. To obtain the seeds, the fruits were pulped and washed under running water. Subsequently, the seeds were dried in the shade and germinated in beds containing washed

sand for 60 days, according to the methodology proposed by Santos et al. (2021). During the processing process, the fruits and seeds were separated taking into account the mother plant. After the germination period, 20 seedlings of each mother plant were separated, totaling 240 seedlings. Of these, 120 seedlings (10 seedlings from each mother plant) were destined to determine the initial biomass and 120 were transferred to plastic pots measuring 21.0 cm in height x 17 cm in diameter (volume of 5.0 L). After transference the plants remained in the UESC nursery for approximately 198 days. During the entire growth period, cultural treatments were carried out, such as weed control and direct irrigation on the roots daily, in order to maintain soil moisture close to field capacity. Subsequently, related characteristics were validated biomass allocation, initial growth and carbon balance, at whole plant and leaf scales, of young *G.americana* plants (Table 1).

The soil used in this study was collected in the southern region of the state of Bahia in a rustic agroforestry. The physicochemical characteristics were analyzed at the Laboratory of Soil, Plant Tissue and Fertilizer Analysis at the Federal University of Viçosa (UFV), Viçosa, MG, Brazil. The soil pH was 5.9, the cation exchange capacity (CEC) was 192.0 mmolc dm³, the base saturation index (BS) was 86%, the Nitrogen (N) content in the soil was 1.20 g kg $^{-1}$, the Phosphorus (P) content was 107.0 mg dm^{-3}, the Potassium (K) content was 90.0 mg dm^{-3}, the Magnesium (Mg) content was 33.0 mmolc dm^{-3} and the Matter Organic (OM) was 42.0 g kg^{-1}. Thus, according to the soil analysis methodology proposed by Teixeira et al.

(2017), the soil used in the experiment has good natural fertility, measured by the cation exchange capacity (CEC) and base saturation index (BS), pH and nutrient availability.

2.3. Growth and biomass allocation

At the beginning of the experiment, 120 seedlings (10 seedlings from each mother plant) were used to determine the leaf area (LA), leaf dry mass (LDM), stem dry mass (SDM), root dry mass (RDM) and total dry mass (TDM). The LA was calculated using digital images, using the ImageJ software according to the methodology described by Brito-Rocha et al. (2016). Digital images of the leaf were obtained through the OfficeLens application (Microsoft, Inc.), using a smartphone and a standard white background sheet. To determine the dry mass, the plants were separated into roots, stems and leaf, and the samples were dried in a forced ventilation oven at 50°C until a constant mass was obtained. At the end of the 198 days of the experiment, the number of leaf (LN) was counted, as well as the LA and the final biomass of all 120 plants. Subsequently, leaf area (LA) and leaf mass per area (LMA) were calculated. From the data of dry mass and LA (initial and final time), the following variables were calculated: root mass ratio (RMR), stem mass ratio (SMR), leaf mass ratio (LMR), ratio of leaf area (LAR), relative growth rate (RGR) and net assimilation rate (NAR), as described by Hunt (2017).

2.4. Leaf gas exchange

Measurements of the net photosynthetic rate (A), stomatal conductance to water vapor (gs) and the ratio

Table 1. List of whole-plant and leaf scale variables used in this study with symbols and unities.

Bioprocess scale	Variable	Symbol	Unity
Whole-plant growth	Relative growth rate	RGR	mg g^{-1} day^{-1}
Whole-plant carbon balance	Net assimilation rate	NAR	mg cm^{-2} day^{-1}
Whole-plant biomass allocation	Leaf area ratio	LAR	dm^2 g^{-1}
	Leaf dry mass ratio	LMR	g g^{-1}
	Stem dry mass ratio	SMR	g g^{-1}
	Root dry mass ratio	RMR	g g^{-1}
Leaf biomass allocation	Individual leaf area	LA	cm^{-2}
	Leaf mass per area	LMA	g m^{-2}
Leaf carbon balance (photochemistry)	SPAD index	SPAD	-
	Maximum photochemical efficiency of photosystem II	Fv/Fm	-
	Performance index	PIabs	-
	Performance index for energy conservation from exciton to the reduction of PSI end acceptors	PItotal	-
Leaf carbon balance (biochemistry)	Net photosynthetic rate	A	μmol CO$_2$ m^{-2} s^{-1}
	Stomatal conductance to water vapor	gs	mol m^{-2} s^{-1}
	Ratio of intercellular to atmospheric CO$_2$ concentration	Ci/Ca	-

of intercellular to atmospheric CO_2 concentration (Ci/Ca) were performed at the end of the 198 days of the experiment. Meaurements of leaf gas exchange were always carried out between 7 and 11 am, on the third mature and fully expanded leaf, on five plants for each progeny. Measurements were performed using a portable photosynthesis system, LI6400 (Li-Cor Bioscience, USA), set to a PAR value of 1000 µmol m^{-2} s^{-1}, the temperature was maintained between 27°C and 28°C, relative humidity between 60% and 65%, and ambient CO_2 concentration (± 390 ppm).

2.5. Chlorophyll index and chlorophyll fluorescence

At the end of the experiment, evaluations of the SPAD index and chlorophyll fluorescence emission were carried out in all 120 plants. The evaluations were made right after the measurements of leaf gas exchange, always on the same leaf. To determine the SPAD index, a SPAD-502 portable chlorophyll meter (Minolta, Japan) was used. Chlorophyll fluorescence was measured using a Pocket PEA chlorophyll fluorimeter (Hansatech Instruments, UK). After measuring the SPAD index, a clip was placed on the same leaf, keeping the region in the dark for at least 30 minutes, in order to guarantee the total oxidation of the electron transport chain. Then, the leaf were exposed to a pulse of saturating light (3500 µmol photons m^{-2} s^{-1}, wavelength 650 nm, for 1 s). Chlorophyll a transient fluorescence was analyzed by the JIP test (Strasser and Strasser, 1995), which relates the electron transport steps of chlorophyll a transient fluorescence (OJIP) to the energy flux associated with photosystem II (PSII). From the chlorophyll fluorescence emission measurements, we calculated the maximum photochemical efficiency of photosystem II (Fv/Fm), the absorption-based performance index (PIabs) and the energy conservation performance index (PItotal). These parameters were selected because they are indicators of the PSII absorption, capture and energy transfer efficiency, and because they indicate the loss of photochemical efficiency of the photosynthetic apparatus (Strasser et al., 2010).

2.6. Statistical analysis

The data were submitted to analysis of variance (two-way ANOVA), followed by the *Scott-Knott test* (*p < 0.05*), for comparisons between the analyzed variables and the different progenies. Spearman's correlation coefficients were also calculated for the bivariate cross-correlations of growth variables, biomass allocation and carbon balance in relation to RGR. Statistical analyzes were performed using the R software platform (R Core Team, 2020).

For the analysis of genetic parameters, data were submitted to Pearson's (*r*) correlation analysis, with coefficient significance tested by *Student's t test*. To evaluate the divergence between the progenies, a cluster analysis was performed, with a distance matrix by the Euclidean dissimilarity measure, and the UPGMA (*Unweighted Pair Group Method with Arithmetic Mean*) clustering method. The validation of the clusters was determined by the cophenetic correlation coefficient (CCC), with significance by the Mantel test. The definition of the group number was established by the methods of the Pseudo t^2 and silhouete

index. Subsequently, intergroup analysis was performed using the Kruskal-Wallis test. All statistical analyzes were performed in an R environment (R Core Team, 2020). The genetic parameters of heritability (h²mp), coefficient of genetic variation (CV$_g$%), coefficient of experimental variation (CV$_e$%), and coefficient of relative variation (CV$_g$/CV$_e$) were determined based on the methodology of mixed models, using the software Selegen-REML/BLUP (Resende, 2016).

3. Results

Based on the analysis of variance, there was a significant difference among *G. americana* progenies for growth and biomass allocation at whole plant scale (Table 2). For biomass allocation at leaf scale (LA and LMA), it was possible to observe significant differences (Table 2). There were no significant effects for leaf scale carbon balance (photochemical and biochemical) (Table 2).

Analysis of genetic parameters revealed experimental coefficient of variation (CVe) ranging from 4.16% to 43% for Fv/Fm and Piabs, respectively. The values of coefficient of genetic variation (CV$_g$) showed genetic variation found among the progenies, considering twelve mother plants, the variables LAR (21.17%), NAR (20.08%) and PIabs (17.04%), were the ones that most contributed to this genetic variation. On the other hand, Fv/Fm (0.17%) and Ci/Ca (0.36%) did not show relevant contribution to variation between progenies (Table 3). The heritability

Table 2. Summary of analysis of variance (ANOVA) comparing the performance of *G. americana* progenies from twelve mother plants at different scales of bioprocesses in southern Bahia, Brazil.

Bioprocess scale	Variable	p (Anova)
Whole-plant growth	RGR	**0.0000**
	LAR	**0.0000**
	NAR	**0.0000**
Whole-plant biomass allocation	LMR	**0.0000**
	SMR	**0.0100**
	RMR	**0.0000**
Leaf biomass allocation	LA	**0.0000**
	LMA	**0.0010**
Leaf carbon balance (photochemistry)	SPAD	0.1030
	Fv/Fm	0.8100
	PIabs	0.0857
	PItotal	0.4480
Leaf carbon balance (biochemistry)	A	0.4010
	gs	0.1341
	Ci/Ca	0.6030

Bold values indicate significant correlations. See abbreviature in Table 1.

Table 3. Estimated genetic parameters for morphological and physiological variables of *G. americana* progenies from twelve mother plants.

Variable	Mean	CV_e (%)	CV_g (%)	CV_g/CV_e	h^2_{mp}
LA	1614.53	16.30	10.58	0.64	**0.80**
LAR	0.66	26.13	**21.17**	0.81	**0.86**
LMA	48.46	18.70	10.54	0.56	0.76
LMR	0.30	13.34	11.26	0.85	**0.87**
SMR	0.19	24.24	11.19	0.45	0.67
RMR	0.50	9.73	6.28	0.64	**0.80**
RGR	31.96	4.81	6.68	**1.38**	**0.95**
NAR	0.44	21.30	**20.08**	0.94	**0.89**
Fv/Fm	0.80	**4.16**	0.17	0.04	0.01
PIabs	2.07	**43.00**	**17.04**	0.40	0.62
PItotal	1.08	39.38	10.82	0.27	0.43
A	9.52	15.67	4.36	0.27	0.28
gs	0.24	27.02	9.62	0.35	0.38
Ci/Ca	0.76	5.82	0.36	0.06	0.02
SPAD	50.07	15.10	5.49	0.36	0.39

Bold values indicate significant correlations. Abbreviations: CV_e - experimental variation coefficient; CV_g - genetic variation coefficient; h^2_{mp} - mean progeny heritability scalel. abbreviature in Table 1.

estimates (h^2_{mp}), showed lower values for Fv/Fm (0.01) and Ci/Ca (0.02) and higher values for LA (0.80), LAR (0.86), LMR (0.87), RMR (0.80), RGR (0.95) and NAR (0.89). This indicates greater genetic control over the environment in phenotypic expression, especially for RGR. the only variable that presented the CV_g/CV_e ratio greater than one (Table 3).

We observed a high correlation between growth variables, whole-plant and leaf biomass allocation in relation to RGR. In addition, a correlation was observed for leaf-scale carbon balance (PIabs; *rs* = 0.61) (Table 4). No correlation was observed for LAR, LMR, Fv/Fm and PItotal in relation to RGR (Table 4).

For the growth variables on a whole plant scale (RGR, LAR and NAR), significant differences were observed between the groupings than in relation to the progenies themselves (Figure 1). In general, after applying the Scott-Knot mean separation test, in relation to RGR, the progenies were grouped into four groups, one for an average RGR of 38 mg g^{-1} day^{-1}, eight for RGR between 31 and 32 mg g^{-1} day^{-1}, two for RGR of 30 mg g^{-1} day^{-1} and one with the lowest value of RGR 29 mg g^{-1} day^{-1} (Figure 1). On the other hand, for LAR, it was possible to observe only two clusters among the progenies, four with LAR between 0.79 and 0.81 dm^2 g^{-1} and eight pair average LAR of 0.55 dm^2 g^{-1}. For NAR, the progenies were grouped into two groups, eight with NAR between 0.44 and 0.55 mg cm^{-2} day^{-1} and four with NAR between 0.28 and 0.34 mg cm^{-2} day^{-1} (Figure 1).

There were significant differences for biomass allocation variables at the whole plant scale, in relation to the grouping of progenies (Figure 2). For LMR, it was possible to observe three groups, four with LMR between 0.32 and 0.43 g g^{-1}, four with LMR between 0.28 and 0.30 g g^{-1} and four with LMR between 0.24 and 0.27 g g^{-1} (Figure 2). On the other

Table 4. Correlations between all measures of *G. americana* progeny (growth, biomass allocation, and physiological variables at whole plant and leaf scale), correlated with relative growth rate (RGR).

Variable	RGR
LAR	-0.97
NAR	**0.98*****
LMR	-0.96
SMR	**0.97*****
RMR	**0.72***
LA	**0.91*****
LMA	**0.98*****
Fv/fm	0.36
PIabs	**0.61***
PItotal	0.36

Spearman's correlations coefficients of bivariate cross-correlations (*n*= 120). Bold values and with asterisk (*) indicate significant correlations. (*: P<0.05; **: P<0.01; and ***: P<0.001). See abbreviature in Table 1.

hand, for SMR, two groups were observed, eight with SMR between 0.18 and 0.22 g g^{-1} and four with SMR between 0.15 and 0.16 g g^{-1} (Figure 2). For RMR the progenies were grouped into two groups, three with RMR between 0.50 and 0.81 g g^{-1} and nine with RMR between 0.47 and 0.52 g g^{-1} (Figure 2).

Significant difference was observed for allocation of biomass in leaf scale (LA and LMA), in relation to the grouping of progenies. For LA, the progenies were grouped into three
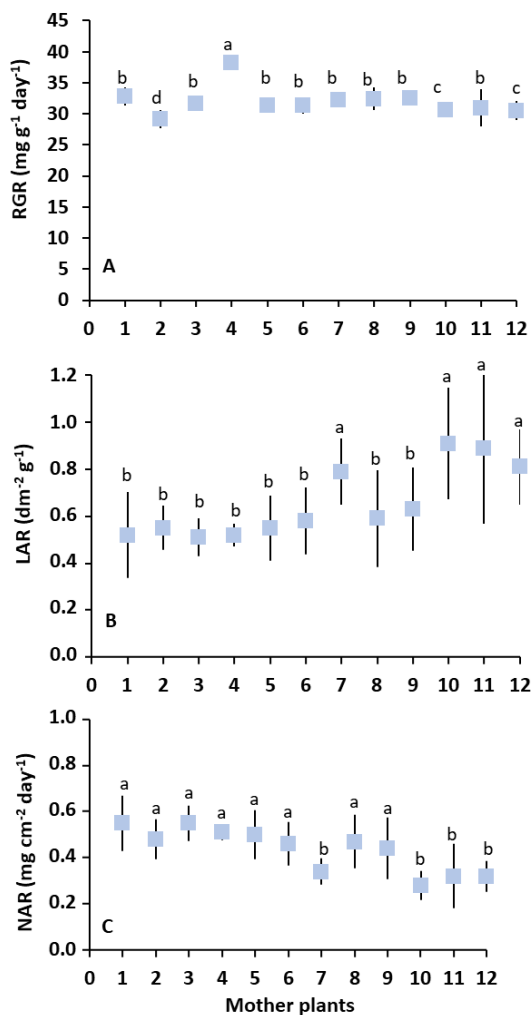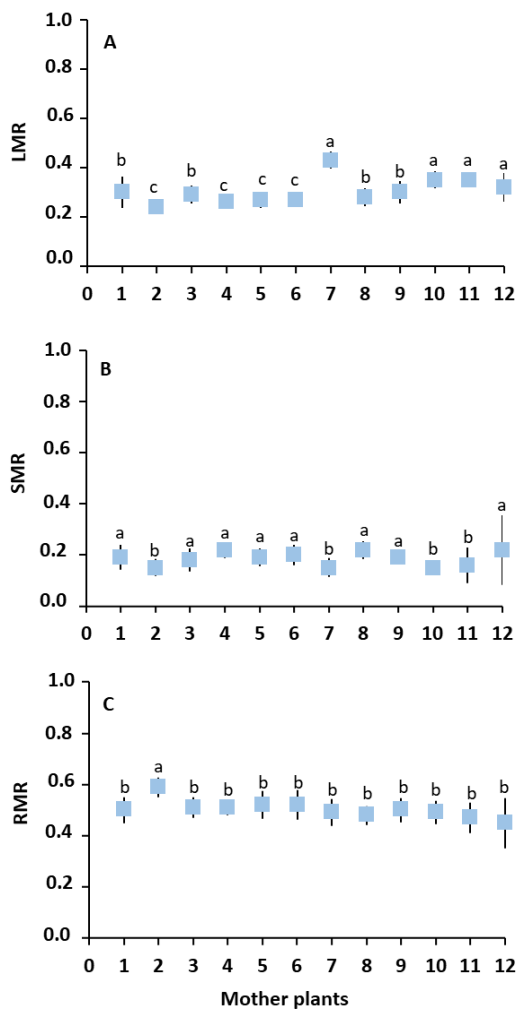
Figure 1. Mean values of relative growth rate (*RGR*), leaf area ratio (*LAR*) and net assimilation rate (*NAR*) of *G. americana* progenies from twelve mother plants in southern Bahia, Brazil. At 198 days of age. (N = 10). Equal letters indicate no statistical difference between *G. americana* progenies (P>0.05. Scott-Knott Test). Bars represent standard deviations.

Figure 2. Mean leaf mass ratio (*LMR*) values. stem mass ratio (*SMR*) and root mass ratio (*RMR*) of *G. americana* progenies from twelve mother plants in southern Bahia. Brazil. At 198 days of age. (N = 10). Equal letters indicate no statistical difference between *G. americana* progenies (P>0.05. Scott-Knott test). Bars represent standard deviations.

groups, one for average LA of 2033.7 cm^{-2}, six for LA between 1626.2 and 1800.9 cm^{-2}, and five for LAR between 1626.2 and 1800.9 cm^{-2} (Figure 3). For LMA, the progenies presented three groupings, two for an average LMA of 62.0 g m^{-2}, seven for LMA between 44.30 and 51.62 g m^{-2} and three for LMA between 39.94 and 44.21 g m^{-2} (Figure 3).

Multivariate analysis revealed the existence of high phenotypic variability among the *G.americana* progenies of twelve mother plants, with the formation of two clusters (*Cluster I and II*), consisting of 58.3% and 41.7%, respectively (Figure 4).

4. Discussion

In this study, we compared growth and carbon balance related characteristics of young *G. americana* plants from

twelve mother plants. Our results revealed high variability in relation to the growth rates associated with *G. americana* progenies. The high phenotypic differences observed in this study occurs between progenies than between mother plants, an expected result in allogamous species such as *G. americana* (Siqueira et al., 2021). In our study the RGR values are within the range of results previously reported in other studies with this same species (Lavinsky et al., 2007; Lima et al., 2010; Sousa-Santos et al., 2022). Plants can exhibit large differences in RGR even when grown under similar environmental conditions (Lambers and Poorter, 1992), and the plant species that exhibit higher growth rates are more competitive in acquiring resources (light, nutrients and water), resulting in faster area occupation and higher survival rates after planting (Shipley, 2006). The RGR is considered an excellent indicator of plant
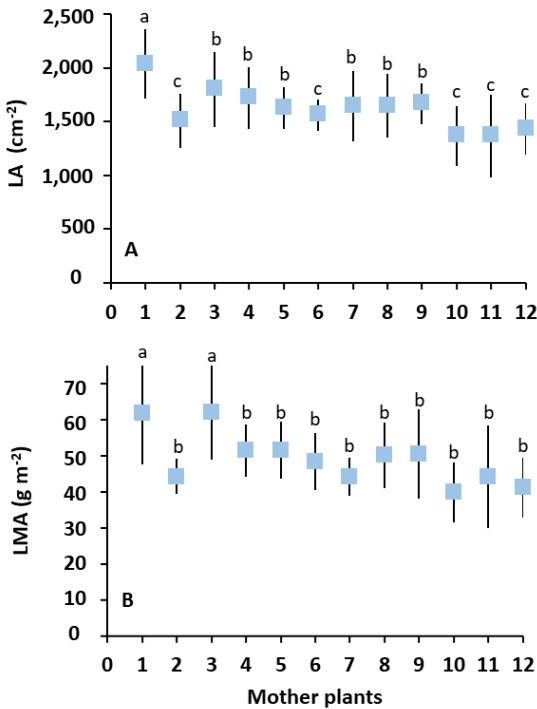
Figure 3. Mean values of total leaf area (*LA*) and leaf mass per area (*LMA*) of *G. americana* progenies, considering twelve mother plants, in southern Bahia. Brazil. At 198 days of age. (N = 10). Equal letters indicate no statistical difference between *G. americana* progenies (P>0.05. Scott-Knott test). Bars represent standard deviations.
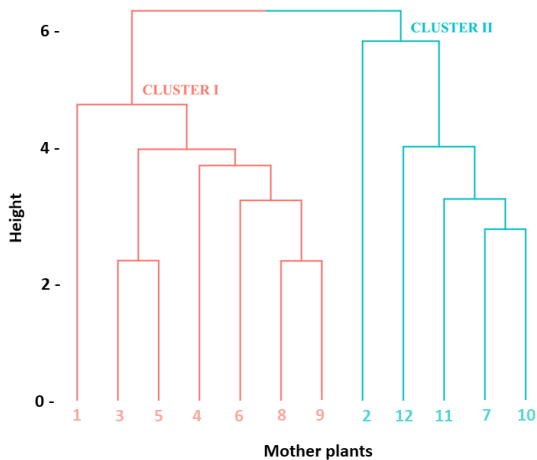
Figure 4. Dendrogram of cluster analysis among *G. americana* progenies, considering twelve mother plants. Unweighted Pair Group Method with Arithmetic Mean method (UPGMA).

acclimation to environmental conditions, representing the increase in growth per unit of biomass over time (Hunt, 2017). Differences in RGR are ecologically important because it is one of the main whole-plant variables that influence plant community dynamics and structure (Li et al.,

2016). Such variation possibly has an effect on the genetic composition between progenies, conditioned by genetic diversity. Pioneer species such as genipap tend to have greater genetic diversity (Lowe et al., 2018). Furthermore, the highest RGR values for *G. americana* progenies may indicate that the species occupies the initial stages of ecological succession (Lima et al., 2010).

Our results also showed that NAR was highly correlated with RGR, which was also observed in other studies (Lima et al., 2010; Sousa-Santos et al., 2022). Increases in NAR are associated with greater efficiency in the whole plant carbon balance, contributing to greater growth in high or low light availability (Poorter, 1999; Lima et al., 2010; Sousa-Santos et al., 2022). In this study, we also observed a clustering tendency among the *G. americana* progenies.

Plants allocate biomass to different organs and the differences of biomass allocation has profound implications for plant growth and seedlings survival (Poorter and Nagel, 2000). In this study, differences in RGR observed between *G. americana* progenies originating from different mother plants were associated with changes in biomass allocation at whole plant scale (LMR, SMR and RMR) and leaf scale (LA and LMA). Thus, plant growth may result from a greater allocation of biomass to photosynthetic tissues that allow the uptake of resources above ground (Poorter and Nagel, 2000), *ie* shoot growth increases photon capture by leaves. On the other hand, the greater allocation to roots allows the absorption of resources below ground (Grossnickle and MacDonald, 2018), that is, root growth increases competitiveness and capture of nutrients and water. Our results revealed that roots was the vegetative organ with the highest biomass allocation among progenies, followed by leaves and stems. During establishment, plants tend to allocate more biomass to roots in their initial seedling stages and the proportion of allocation to shoots tends to increase throughout growth in planting environments (Poorter and Nagel 2000: Niinemets, 2004). Furthermore, the higher RMR observed may be related to greater water absorption, due to greater transpiration demand in relation to high light availability (Claussen, 1996). Plants that grow in environments with greater light availability may experience increased leaf temperature, which results in greater evaporative demand (Lenhard et al., 2013). In addition, high RMR values, under high light availability, as found in *G. americana*, can be considered a strategy to maintain the high water supply and plant hydration (Markesteijn and Poorter, 2009; Cortina et al., 2013).

As observed in this study, LA and LMA were highly correlated among *G. americana* progenies, both variables are related to both growth, biomass allocation and photosynthesis. Higher LA values may represent greater photon capture and, consequently, direct effects on maintaining growth rates. In addition, plants that have thicker leaf have a greater amount of water per unit of leaf area, this fact contributes to the reduction of the effects caused by a possible photoinhibition and decreases the chance of overheating of the leaf (Takahashi and Murata, 2008) and predation of the leaf after planting (Peeters et al., 2007).

In humid tropics, different factors act to shape the growth and survival of tree seedlings after planting in the field (McDowell et al., 2022). Depending on the light environment conditions plants exhibit adjustments related to changes in carbon balance at leaf and whole-plant scale (Givnish, 1988; Valladares and Niinemets, 2008). At the leaf scale, the carbon balance is dependent on the processes of carbon assimilation (photosynthesis) and its loss (cellular respiration). At the whole plant scale, the carbon balance is related both to the ability of leaf to assimilate CO_2 from the atmosphere and to the efficiency in the allocation of biomass to leaves, roots and stems (Poorter et al., 2019). In this study, we did not observe significant differences in relation to photosynthesis at leaf scale between *G. americana* progenies. Furthermore, despite the absence of significant effects on the carbon balance at leaf scales (photochemical and biochemical), for *G. americana* progenies, the clustering pattern remains. In addition, the multivariate analysis also revealed the existence of phenotypic variability among the *G. americana* progenies, with a tendency to cluster. This behavior suggests greater genetic control over the environment in phenotypic expression, mainly for RGR, the only variable that presented a CVg/CVe ratio greater than one.

For the production of seedlings of tropical tree species with a view to forest restoration, the most used genetic material is seeds (Ruzza et al., 2018; Santos et al., 2021). The initial establishment, growth and survival of seedlings are also influenced by the genetic quality of the seeds used in plant propagation (Costa et al., 2021). The choice of mother plant (obtaining fruits and seeds) is considered one of the most influential variables that can determine the survival of plants after planting (Thomas et al., 2014; Atkinson et al., 2021). This is because more vigorous seedlings with fast growth, originating from good mother trees, have a greater capacity to establish themselves. From a practical point of view, seedlings of *G. americana* should be planted in open areas, such as abandoned pastures or in the formation of new agroforestry systems in areas that have been deforested. Seedlings that grow faster are more likely to establish themselves quickly, capture more resources and increase survival after planting. The results of this study can be useful to assist in the planning and selection of the best sources of material (mother trees) for forest restoration projects or even commercial plantations. Considering the high phenotypic variability among *G. americana* progenies in relation to RGR, our results showed the importance of selecting material sources based on this feature. In this study, it was possible to group the progenies based on the highest mean values of the studied variables. Thus, considering seedlings of *G. americana* for planting in agroecosystems, our results may contribute to greater genetic variability and consequent planting of more vigorous and resilient plants in the field.

5. Conclusions

Our results evidenced that the high variability in relation to growth rates among young *G. americana* seedlings originating from different mother plants. The RGR values

of *G. americana* seedlings were related to changes in biomass allocation at whole and leaf plant scale. With this study we aim to contribute important information about the *G. americana* species, which can be useful to assist in planning and selecting the best sources of material for seedlings propagation. From a practical point of view, we demonstrate that the selection of mother plants to produce seedlings with higher growth rates, and consequently greater establishment capacity in field plantings, can be made from the evaluations of growth and biomass allocation variables at the whole plant scale.

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Supplementary Material

Supplementary material accompanies this paper.

Table S1. Description of the sites where Genipa americana fruits were collected in Southern Bahia, Brazil. This material is available as part of the online article from https://doi.org/10.1590/1519-6984.281793