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ORIGINAL PAPER

Morphophysiological Changes in *Genipa americana* Seedlings in Response to Root Deformation and Substrate Attributes

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Abstract

The establishment of tree seedlings in the field, particularly in acidic soils, is commonly restricted by the excess or low availability of nutrients, or the quality of the root system. This study aimed to evaluate the effects of root deformation and substrate attributes on the growth, biomass allocation, and photosynthesis of *G. americana* seedlings. Plants were grown in pots containing three substrates (one sandy and fertile substrate enriched with organic matter and two acidic and low fertility substrates differing in texture) and two root conditions (without and with deformation). Growth, biomass allocation, leaf gas exchange, and chlorophyll fluorescence were evaluated. Substrates significantly affected growth, biomass allocation, and photosynthesis of *G. americana* seedlings. Root deformation affected only growth and biomass allocation. Interactive effects of substrate attributes and root deformation were observed for individual leaf area (*ILA*) and leaf area ratio (*LAR*). The increases in *ILA* and *LAR* of *G. americana* seedlings with root deformation and growing in substrates with low natural fertility may cause an imbalance in the absorption and loss of water by evapotranspiration, making the plants more susceptible to environmental stress after planting in the field.

Keywords Biomass allocation · Cation exchange capacity · Chlorophyll fluorescence · Leaf gas exchange · Root system formation · Plant-soil interactions

1 Introduction

Reforestation with native trees for the production of timber and non-timber forest products provides profits to farmers and is a way of increasing biological diversity, in addition to helping to restore the structure and functionality of forest ecosystems (Rappaport and Montagnini 2014; Piotto and Rolim 2018). The success of forest plantations is directly dependent on the seedling quality and resources of the physical environment, such as the availability of water and nutrients in the soil (Chadwick and Asner 2018).

Soil is an environmental factor of fundamental importance for all terrestrial plants because it provides not only the substrate for the roots to grow in but also the water and nutrients. However, the soil system can become a stress factor in some situations, interfering with the seedling establishment in forest environments and plantations (Ford and HilleRis Lambers 2020). Tropical forests are increasingly threatened by natural and anthropic actions. Natural processes such as droughts and floods are occurring more frequently and more intensely due to climate change in recent years and can promote imbalances in forest ecosystems (Vido and Nalevanková 2021); rates of deforestation and frequency of fires have increased in Brazil in recent decades (Borrelli et al. 2017; Flores et al. 2019). In many cases, these processes cause soil degradation, altering characteristics such as texture, drainage, and fertility (Dubuis et al. 2013), which can affect the availability of mineral nutrients or even increase

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the concentration of toxic elements (White et al. 2013). The establishment of seedlings in the field, mainly in acidic soils, is commonly limited by excess Al, Mn, and Fe concentrations or by the low availability of P, K, Mg, and Ca (White et al. 2013). In forest environments or mineral extraction areas, the concentrations of Al and Fe in the soil can significantly increase and reach toxic levels for some plants growing in these areas (Kochian et al. 2015). For example, phytotoxicity due to excess Al in the soil can limit plant growth and development for non-tolerant species (Wulff-Zottele et al. 2014). High concentrations of Al in the soil can lead to decreased absorption of water and nutrients (Cartes et al. 2012) because of lesions in the root meristems and decreased root elongation (Wulff-Zottele et al. 2014). In flooded soils and Fe extraction areas, high concentrations of metals in the soil can inhibit root growth and cause foliar chlorosis in non-tolerant species, which negatively affects their survival (Schmidt and Fühner 1998; Moller et al. 2007; Xing et al. 2010).

Seedling vigor contributes to increased survival and early growth after being transferred from the nursery to the field (Grossnickle and MacDonald 2018). Plants with greater vigor should be robust and have a balanced relationship between height, diameter, and root biomass (Grossnickle and MacDonald 2017). In addition, the greater root growth potential, water, and nutritional status of plants ensures greater survival and satisfactory growth in the field, even under stressful conditions (Grossnickle and MacDonald 2018; Riikonen and Luoranen 2018). In the nursery stage, the quality of the root system is one of the main aspects that requires attention. Root deformation can originate during pricking out or repotting seedlings. The damage during this process is irreversible and leads to the folding of the pivoting root in the form of a “loop” or “J” (Duboc 2014). Changes in the integrity of the root system contribute to decreased absorption and distribution of nutrients in various organs of the plant (Santos et al. 2022), which may decrease seedling survival and growth under environmentally stressful conditions.

Genipa americana L. is a tree species native to South and Central America and is widely distributed throughout Brazil. The species occurs in different soils, including the Cerrado (Bailão et al. 2015; Ruzza et al. 2018), where the soil Al content is high, or in floodplains in the Amazon (Pires et al. 2018), which may present phytotoxic concentrations of Fe (Schmidt and Fühner 1998). Belonging to the Rubiaceae family, it is popularly known as “Jenipapo” or “Jenipapeiro” (Zappi 2016). It has great ecological and economic importance, with significant potential for reforestation as a medicinal and food plant. In addition, it stands out for its physiological and morphological characteristics, being recommended for phytoremediation, the recovery of degraded areas, and the restoration of riparian forests (Lima et al. 2010; Santos et al. 2022). There are different studies in the literature on the versatility and high potential of *G. americana* for various possibilities of use related to the morphophysiological behavior of flooding tolerance (Santos et al. 2022), seed and seedling production (Raupp et al. 2020), medical and pharmaceutical properties (Alves et al. 2017), seed quality (Virgens et al. 2019), breeding and conservation (Cardoso et al. 2019), and ethnobotany (Tomchinsky and Ming 2019). Because of the countless possibilities associated with using this species, *G. americana* was included in a list of 39 priority species in the “Plants for the Future” program in the International Treaty on Plant Genetic Resources for Food and Agriculture (FAO 2017). *G. americana* is also indicated as one of the fifteen priority species for silvicultural research and for plantations in the Brazilian Atlantic Forest (Rolim et al. 2019).

Considering the attention that reforestation with native trees has received in recent years, and given the ecological and economic importance of *G. americana*, further studies on the changes that occur in the ecophysiological traits of this species due to the excess or low availability of nutrients in naturally degraded soils and root deformation, are required to increase the efficiency of initial plant establishment after planting. Thus, this study aimed to evaluate the effects of root deformation and substrate attributes on the growth, biomass allocation, and photosynthesis of *G. americana* seedlings. We tested the hypothesis that root deformation exacerbates the negative effects of low natural fertility and the high concentrations of heavy metals in the soil on the growth, biomass allocation, and photosynthesis of *G. americana* seedlings.

2 Materials and Methods

2.1 Study Area and Plant Material

The study was performed at the Universidade Estadual de Santa Cruz (UESC), Ilhéus, Bahia, Brazil (39°13′59"W; 14°45′15"S). Seeds were obtained from fruits sold in a free market in the city of Ibicaraí, Bahia, Brazil. The fruits were manually pulped and washed with running water. After washing, the seeds were dried in the shade on paper towels for 24 h and were germinated and grown in seedbeds containing washed sand for 63 days, according to the methodology described by Santos et al. (2021).

The experiment was conducted in the UESC’s nursery, which is a 12 m long, 6 m wide, and 3 m high hyphenation structure, covered with a shade screen that allows the passage of approximately 60% of solar radiation in full sun. After germination, 58 seedlings, 4 cm long with fully expanded cotyledon leaves, were collected. Of which 10 plants were destined to determine the initial biomass, and

48 were transferred from the seedbeds to 90 mL plastic tubes containing Carolina Soil® commercial substrate. At the time of pricking out, two root conditions were induced, that is, without and with deformation. Root deformation was manually induced in half of the seedlings by making holes in the substrate to accommodate only 50% of the total root length. This results in an elbow bend of the seedlings' tap root, deforming further root growth. This procedure was performed by a single person to avoid variations due to the handling of the plants by different operators. After a period of 60 days of growth, the plants were transferred to 1.5 L plastic bags containing the three substrates with different chemical and physical characteristics (see Supplementary Fig. S2). In the transplant, the substrate that adhered to the roots of the plants was maintained, corresponding to approximately 20% of the total capacity of the plastic bag. During the experiment, daily average temperatures of 27 ℃ were recorded. The average daily vapor pressure deficit was 1.35 kPa, and the average daily light integral was 16 mol photons m^{-2} day^{-1}, varying between 8 and 28 mol photons m^{-2} day^{-1}. The experiment lasted 90 days.

2.2 Substrate Characterization and Analysis

The substrates were collected from different locations in the southern region of the state of Bahia, Brazil. The substrates were selected based on their chemical and physical characteristics. Soil samples were collected at a depth of 20 to 40 cm. Substrate S1 was collected from a rustic agroforestry system (cacao trees cultivated with several native and exotic trees) in the district of Salobrinho in the municipality of Ilhéus (39°10′0″W; 14°48′0″S), substrate S2 was collected in the municipality of Uruçuca (39°17′29″W; 14°35′12″S), and substrate S3 was collected at the Experimental Station of Almada in the municipality of Ilhéus (39°10′00″W; 14°38′00″S). The physicochemical characteristics of the substrates were analyzed at the Soil, Plant Tissue, and Fertilizers Analyses Laboratory of the Universidade Federal de Viçosa (UFV), Viçosa, MG, Brazil. The substrates were analyzed according to the methodology described by Teixeira et al. (2017) which consisted of pH in water and $CaCl_2$ (substrate: solution ratio 1:2.5) determined by potentiometry. P and K contents were extracted with Mehlich-1 solution and determined by spectrocolorimetry and flame photometry, respectively. The contents of Ca, Mg, and Al were extracted with KCl 1.0 mol L^{-1}; Ca and Mg were determined by complexometric titration with EDTA and Al by acid/base neutralization titration. Organic matter (OM) was digested with potassium dichromate and determined by Walkley Black titration. The granulometric analysis was performed using the densimeter method. The micronutrients Zn, Mn, Cu, and Fe were extracted with Mehlich-1 solution and determined by atomic absorption spectrometry. The three substrates used in the experiment contrasted in terms of texture and the fertility attributes of acidity, total organic matter, cation exchange capacity (CEC), and nutrient availability (Table 1). S1 had high organic matter and total nitrogen content, high CEC, and good nutrients availability of all. In contrast, S2 and S3 were acidic, with low organic matter content, low CEC, and low availability of nearly all nutrients. However, S2 and S3 also showed the following differences: S2 was siltier, poorer in macronutrients, and more acidic than S3. Therefore, S2 had greater availability of micronutrients Cu, Mn, and Zn than S3 (Table 1).

2.3 Growth and Biomass Allocation

At the beginning of the experiment, of the 58 plants that were collected, 10 plants were used to determine the diameter (*D*), height (*H*), number of leaves (*LN*), leaf area (*LA*), leaf dry mass (*LDM*), stem dry mass (*SDM*), root dry mass (*RDM*), and total dry mass (*TDM*), the initial time. The *LA* was measured using an automatic leaf area meter, LI-3000 (Li-Cor Bioscience, Lincoln, NE, USA). To determine the dry mass, the plants were separated into roots, stems, and leaves and the samples were dried in a forced ventilation oven at 50 ℃ until a constant mass was obtained. At the end of the 90 days of the experiment, all 48 plants that were cultivated with different treatments were collected for growth and biomass analysis. After counting the *LN*, *LA* was obtained and the dry mass leaf was determined. Subsequently, the individual leaf area (*ILA*) and leaf mass per area (*LMA*) were calculated. From the dry mass and LA data, the following variables were calculated: root mass ratio (*RMR*),

Table 1 Results of the chemical and granulometric analyses$^{1/}$ of the three substrates studied

S	Cy	St	Sd	pH	OM	N	Ca	Mg	Al	CEC	BS	P	K	Cu	Fe	Mn	Zn
	g kg^{-1}				g kg^{-1}		$mmol_c$ dm^{-3}				%	mg dm^{-3}					
S1	95	97	808	5.9	42	1.2	130	33	0	192	86	107	90	1.1	41	160	14.5
S2	239	388	373	5.0	3	0.2	5	2	8	36	20	2	6	0.7	13	12	0.5
S3	294	13	693	5.2	7	0.3	8	6	2	38	40	2	15	0.4	62	2	0.4

1/ S (substrate); Cy (clay), St (silt), Sd (sand); pH in water 1:2.5; OM (total organic matter); N (total nitrogen); P, K, Cu, Fe, Mn, and Zn – Mehlich-1; Ca^{2+}, Mg^{2+}, and Al^{3+} – KCl 1.0 mol L^{-1}; CEC (cation exchange capacity at pH 7.0); BS (base saturation) (Teixeira et al., 2017) stem mass ratio (*SMR*), leaf mass ratio (*LMR*), leaf area ratio (*LAR*), relative growth rate (*RGR*), and net assimilation rate (*NAR*), according to Hunt (2017).

2.4 Leaf Gas Exchange

Measurements of the net photosynthetic rate per unit leaf area (A_{area}), stomatal conductance to water vapor (*gs*), and leaf transpiration rate (*E*) were performed at the end of the experiment. Measurements of leaf gas exchange were performed between 7 and 10 am, on the third mature and fully expanded leaf, on eight plants per treatment. Measurements were performed using a portable photosynthesis system, LI6400 (Li-Cor Bioscience, USA), adjusted to a PAR value of 1000 μmol m^{-2} s^{-1}, the temperature of 28 ℃, relative humidity between 60 and 65%, and ambient CO_2 concentration (± 390 ppm). The net photosynthetic rate per unit mass (A_{mass}) was calculated as the ratio between A_{area} and *LMA* (Prado and de Moraes 1997). The water use efficiency (*WUE*) was calculated as the ratio between A_{area} and *E*.

2.5 Chlorophyll Index and Chlorophyll Fluorescence

After the leaf gas exchange measurements on the same leaf, measurements of the chlorophyll index (*ISPAD*) were performed using a portable chlorophyll meter model SPAD-502 (Minolta, Japan). Chlorophyll fluorescence was measured using a portable fluorescence emission meter Pocket Pea (Hansatech Instruments, UK). After measuring the chlorophyll index, a clip was placed on the same leaf to maintain dark conditions for at least 30 min, ensuring total oxidation of the electron transport chain of the photosynthetic system. Thereafter, the leaves were exposed to a saturating pulse light (3500 μmol photons m^{-2} s^{-1}, wavelength of 650 nm, for 1 s). The transient fluorescence of chlorophyll a was analyzed by the JIP test (Strasser and Strasser 1995), which consists of the evaluation of the electron transport steps of the transient fluorescence of chlorophyll a (OJIP) from the energy flow associated with photosystem II (PSII). From the chlorophyll fluorescence measurements, we calculated the maximum quantum yield of PSII photochemistry (F_v/F_m), the reaction center density (*RC/ABS*), the performance index (PI_{ABS}), and the total performance index (PI_{total}). These parameters were selected because they are indicators of the efficiency of absorption, capture, and energy transfer of PSII, which can express the loss of photochemical efficiency of the photosynthetic apparatus under conditions of environmental stress (Modolo et al., 2020; Guimarães et al. 2022).

2.6 Statistical Analysis

The experiment was conducted in a completely randomized 3 × 2 factorial design, with three substrates and two root conditions (with and without root deformation), with eight replicates and one plant per experimental unit. Prior to the analyses, to meet the assumptions of homogeneity and normality, the data were submitted to the Shapiro–Wilk normality test and the Levene Test. The data were subjected to analysis of variance (two-way ANOVA), followed by Tukey's test ($p < 0.05$) for comparisons among substrates and *T*-test ($p < 0.05$) for comparisons between root conditions. Statistical analyses were performed using the R software platform (R Core Team 2020).

3 Results

Among the twenty-one variables analyzed in this study, eighteen were significantly affected by substrates and seven by root deformation (Supplementary Table S1). With the exception of *LMR*, *RMR*, and *LAR*, the substrates significantly affected all growth, biomass allocation, leaf gas exchange, and chlorophyll fluorescence variables analyzed, but root deformations significantly affected only growth and biomass allocation variables. Interactive effects of substrate attributes and root deformation were observed for individual leaf area (*ILA*) and leaf area ratio (*LAR*).

Most of the variables analyzed were significantly affected by the characteristics of the substrates; the mean values for S1 were significantly higher than the mean values for the substrates S2 and S3 (Table 2). The only exceptions were *SMR*, whose mean was significantly higher in S3 compared to *S1* and *S2*, and PI_{ABS}, which did not differ significantly between S1 and S2. In general, the highest mean values were obtained for *S1*, followed by *S2* and *S3*. Some variables showed very large differences between *S1* and *S2*. For example, the mean values of *H*, *LA*, *ILA*, *WUE*, A_{area}, A_{mass}, *RC/ABS*, and PI_{total} were more than twice as high in *S1* compared to *S2*. Among these variables, the greatest differences were obtained for *LA* and *RC/ABS*, whose mean values were more than three times higher in *S1* compared to *S2*.

The highest mean values of *LA*, *ILA*, *RGR*, *RMR*, and *LAR* were observed for plants with root deformations, and the highest mean values of *SMR* and *LMA* were observed for plants without root deformation (Table 3). Contrary to what was observed for the substrates, none of the variables presented in Table 2 showed differences greater than twice between plants without and with root deformation.

The highest mean values for *ILA* and *LAR* were obtained in *S1* and *S3*, respectively, independent of the root conditions (Fig. 1). Non-significant differences between root conditions were observed in *S1* and *S2*, but the mean values of *ILA* and *LAR* were significantly higher for plants with root deformations in comparison with plants without root deformations

Table 2 Mean values of morphological, biomass allocation, growth, and physiological variables for young plants of *G. americana* growing in substrates with different characteristics attributes (*S*) for 90 days (*N* = 8)

Variable	Substrate		
	S1	S2	S3
H (cm)	15.26 ± 1.29 a	7.31 ± 0.83 b	6.12 ± 0.78 b
D (mm)	7.51 ± 0.40 a	4.53 ± 0.43 b	3.70 ± 0.19 b
LA (cm^{-2})	310.90 ± 18.37 a	104.69 ± 7.55 b	79.56 ± 10.46 b
ILA (cm^{-2})	24.21 ± 1.35 a	11.70 ± 0.94 b	10.99 ± 1.65 b
RGR (mg g^{-1} day^{-1})	55.93 ± 0.84 a	42.90 ± 1.14 b	36.49 ± 1.42 c
NAR (mg cm^{-2} day^{-1})	1.22 ± 0.06 a	0.83 ± 0.05 b	0.58 ± 0.04 c
SMR (g g^{-1})	0.17 ± 0.01 b	0.18 ± 0.01 b	0.20 ± 0.01 a
LMA (g m^{-2})	118.94 ± 5.84 a	99.66 ± 5.57 b	82.34 ± 5.59 c
E (mmol H_2O m-^{2} s-^{1})	2.64 ± 0.17 a	1.98 ± 0.18 b	1.96 ± 0.09 b
WUE (μmol CO_2 mmol H_2O^{-1})	3.60 ± 0.20 a	1.74 ± 0.19 b	1.32 ± 0.13 c
A_{area} (μmol m^{-2} s $^{-1}$)	9.34 ± 0.44 a	3.25 ± 0.24 b	2.63 ± 0.31 b
A_{mass} (μmol CO_2 Kg^{-1} s $^{-1}$)	80.78 ± 6.85 a	33.12 ± 2.53 b	32.18 ± 3.48 b
gs (mol m^{-2} s^{-1})	0.20 ± 0.02 a	0.13 ± 0.02 b	0.12 ± 0.01b
ISPAD	43.68 ± 2.07 a	26.58 ± 2.19 b	19.25 ± 1.59 c
Fv/*Fm*	0.75 ± 0.01 a	0.66 ± 0.02 b	0.61 ± 0.03 b
RC/*ABS*	0.43 ± 0.07 a	0.14 ± 0.05 b	0.08 ± 0.03 b
PI_{ABS}	4.53 ± 0.42 a	3.94 ± 0.23 a	2.26 ± 0.13 b
PI_{total}	0.48 ± 0.08 a	0.24 ± 0.08 b	0.27 ± 0.11 b

Means followed by the same letter on the line do not differ statistically from each other by the Tukey test at a 5% probability

H, height; *D*, diameter; *LA*, leaf area; *ILA*, individual leaf area; *RGR*, relative growth rate; *NAR*, net assimilation rate; *SMR*, stem mass ratio; *LMA*, specific leaf mass; *E*, leaf transpiration rate; *WUE*, water use efficiency; A_{area}, net photosynthetic rate per unit area; A_{mass}, net photosynthetic rate per unit mass; *gs*, stomatal conductance to water vapor; *ISPAD*, chlorophyll index; *Fv*/*Fm*, potential of quantum efficiency of photosystem II; *RC*/*ABS*, density of the reaction center for chlorophyll; PI_{ABS}, performance index; PI_{total}, total performance index

Table 3 Mean values of the biomass allocation and growth variables of young plants of *G. americana* without and with root deformation (*RD*) (*N* = 8)

	Root (R)	
Variable	Without RD	With RD
LA (cm^{-2})	151.63 ± 37.45 b	178.47 ± 37.08 a
ILA (cm^{-2})	14.00 ± 2.54 b	17.27 ± 2.24 a
RGR (mg g^{-1} day^{-1})	43.95 ± 3.16 b	46.26 ± 2.74 a
SMR (g g^{-1})	0.19 ± 0.01 a	0.17 ± 0.01 b
RMR (g g^{-1})	0.42 ± 0.02 b	0.46 ± 0.02 a
LAR (dm^{-2} g^{-1})	0.37 ± 0.02 b	0.40 ± 0.02 a
LMA (g m^{-2})	105.53 ± 7.07 a	95.10 ± 7.64 b

Means followed by the same letter do not differ statistically from each other by the *T*-test test at 5% probability *LA*, leaf area; *ILA*, individual leaf area; *SMR*, stem mass ratio; *RMR*, root mass ratio; *LAR*, leaf area ratio; *RGR*, relative growth rate; *LMA*, leaf mass per area

in *S3*. In the *S3*, the mean values of *ILA* and *LAR* in plants with root deformation were about 2.0 and 1.3 times higher, respectively, in relation to plants without root deformation.

4 Discussion

Seedling performance is mediated by morphological and physiological attributes (Grossnickle and Folk 1993), and the potential for survival in the first year after planting is influenced by the quality of the seedlings (Grossnickle 2012). Based on our results, many of the effects attributed to the chemical characteristics of the substrates and root conditions were associated with changes in the above-ground part of the plants, which negatively impacted photosynthesis and growth in different ways.

In this study, the highest growth rates were obtained in the substrate with higher organic matter content (*S1*) compared to the substrates *S2* and *S3*. The higher proportion of organic matter in *S1* may have contributed to the higher CEC and, consequently, the greater availability of cationic mineral nutrients (Krzyzanski et al. 2018). In contrast, exposure of roots to high concentrations of Al in *S2* may have caused damage and significant inhibition of root growth, thereby reducing water and nutrient uptake (Ryan et al. 2011). In many forest soils, the Al saturation index can reach values around 50% (Butterfield 1996) and even above 80% (Haridasan and Araújo 1988). Al-accumulating trees can survive

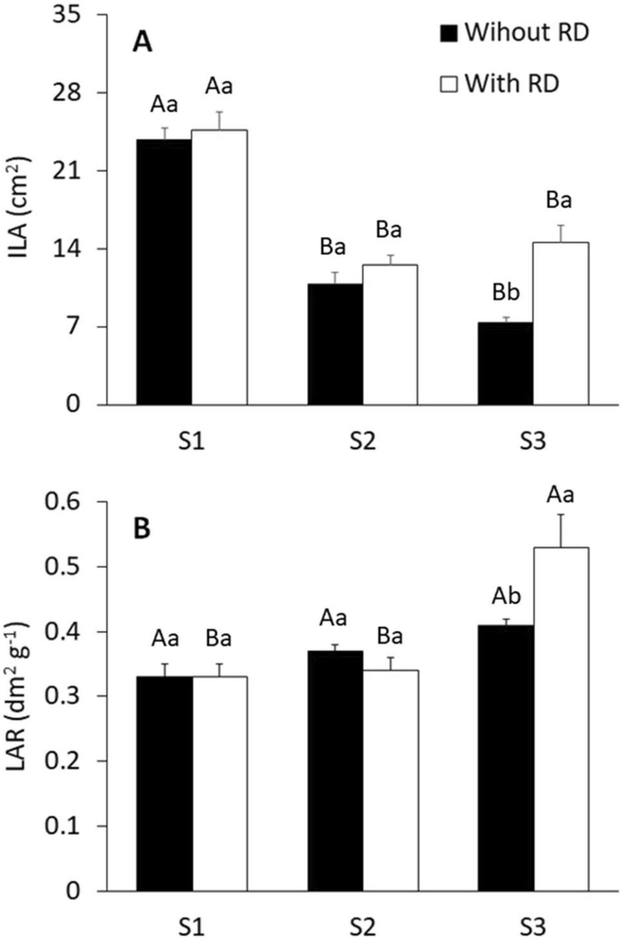

Fig. 1 Mean values of the individual leaf area (*ILA*) and the leaf area ratio (*LAR*) of *G. americana* plants without and with root deformation (*RD*), growing in substrates with different characteristics ($N = 8$). Capital letters represent comparisons between different substrates within different root conditions, and lower case letters represent comparisons between root conditions within substrates. For substrates, means followed by the same letter are not significantly different according to Tukey's test ($p < 0.05$). For root conditions, means followed by the same letter are not significantly different according to the *T*-test ($p < 0.05$). Bars represent the standard errors

and grow at very high Al saturation index values (Haridasan and Araújo 1988), including species from the Rubiaceae family (Haridasan 2008; Malta et al. 2016). Despite this, according to Ribeiro et al. (1999), Al saturation indexes above 20% cause limitations in perennial crops and above 50%, the soil presents high toxicity. In fact, Al content in S2 was 8 $\text{mmol}_c\ \text{dm}^{-3}$, which corresponds to an Al saturation index of 51%, above the limit considered toxic for most perennial plants.

The low availability of nutrients in S2 and S3 influenced the photosynthetic capacity of *G. americana* (Wang et al. 2018), which is reflected in the low growth rates observed in these substrates (Turner et al. 2018). This fact indicates that low fertility can cause an imbalance in the absorption of nutrients due to the low or high concentration of another nutrient present in the soil. The high concentration of Fe in S3, which is associated with lower concentrations of Cu, Zn, and mainly Mn, negatively impacts plant growth by inhibiting root growth and nutrient cycling (Briat et al. 2010). It is noteworthy that in the root absorption process, a high concentration of one nutrient can inhibit the absorption of another (Marschner 2012), and this phenomenon is more intense when competitive inhibition occurs; that is, when two nutrients compete for the same absorption, such as Fe and Mn (Malavolta 2006). The visual symptoms observed in *G. americana* plants in S3 (data not shown) were internerval foliar chlorosis (Becker and Asch 2005), probably indicating nutritional imbalance associated with restrictive effects on seedling growth (Santana et al. 2014) and low availability of nutrients, mainly Mn.

The effects of mineral nutrition on shoot growth and its relationship with the root system depend on the physicochemical properties of the soil, root specialization (Rao et al. 2016) and interactions with microorganisms (Tedersoo and Bahram 2019), which must ensure good availability of mineral nutrients, favoring the high physiological performance of plants. Under ideal conditions, more efficient uptake of nutrients by plants may be related to high photosynthetic rates and translocation of carbohydrates for cellular respiration in roots, providing energy for uptake or renewal of carrier proteins (Chapin 1980). This energy input for the absorption of macro and micronutrients guarantees the supply for the development of new leaves. Thus, soils with high fertility can provide high efficiency in carbon assimilation, resulting in high growth rates after planting the seedlings in the field (White et al. 2013). Compared to *S1*, the lower values of *LA* observed in *S2* and *S3* may have indicated that carbon assimilation was not sufficient for the production of new photosynthetic tissues, which also resulted in lower *RGR* values in these substrates. The leaf characteristics of young *G. americana* plants were highly responsive to acidic substrates with low fertility. The high or low concentration of any mineral nutrient can cause an imbalance in other nutrients, as seen with the high availability of Fe and low availability of Mn in *S3*. Among the different proteins that act in the transport of nutrients in plants, the NRAMP family of proteins can transport metallic cations, both Fe and Mn (Tian et al. 2021). Thus, the high ratio between Fe/Mn concentrations may affect the plants more negatively than in *S2*. This is because most proteins that transport Mn are not specific for the metal, which can lead to competitive inhibition with other divalent cations, such as Cu, Zn, and mainly Fe, in their absorption (Santiago et al. 2020).

LMA is a variable related to investments in photosynthetic tissues per unit of leaf area (Liu and Su 2016) and is directly related to trade-offs between carbon assimilation and leaf life-span (Reich 2014). The *LMA* values obtained in our study are within the range of results previously reported for *G. americana* and other tropical tree species (Lima et al. 2010). The lowest values for *LMA* were observed for plants grown in *S2* and *S3*, indicating thinner and less dense leaves. Lower values were also observed for *E* and *WUE* in *S2* and *S3*. These differences show a relationship between the variables *LMA*, A_{area}, *E*, and *WUE*, which could be explained by the fact that *LMA* is very sensitive to changes in resource availability, such as nutrients, water, and light (Poorter et al. 2009). Furthermore, *WUE* is calculated by the ratio between A_{area} and *E*. Plants grown in *S1*, even with a greater loss of water through transpiration (higher average values of E in relation to the other), also showed higher *LMA*, A_{area}, and consequently *WUE*.

Chlorophylls are the most important plant pigments because they capture light and convert physical light energy into chemical energy, directly influencing carbon assimilation (Li et al. 2018). Plants grown in *S2* and *S3* had lower values for A_{area} and A_{mass} compared to plants grown in *S1*. This could be attributed to the excess of Al in *S2* and the high ratio between Fe/Mn concentrations in *S3*, which may have caused the inhibition of chlorophyll biosynthesis (El-Khatib et al. 2020). Furthermore, under saturating induction, the *Fv/Fm* ratio was lower in plants grown in *S3* than in plants grown in *S1* and *S2*. The *Fv/Fm* ratio is an important indicator of environmental stress in plants (Pollastrini et al. 2014). The high concentration of Fe associated with the low availability of Mn in *S3* may have contributed to the increased biosynthesis of reactive oxygen species and greater oxidative stress (Silva et al. 2006). In the same substrate, low *RC/ABS* values were observed, indicating that the PSII reaction centers were possibly inactive. This may also be associated with Mn deficiency, which may have reduced the number of Mn complexes in the PSII nucleus, which leads to PSII complex disintegration and causes damage to the thylakoid structure, thereby promoting chlorophyll degradation. Low PI_{ABS} values, also found for plants growing in *S3*, may reflect a loss of photochemical efficiency (Thach et al. 2007). The high acidity and low availability of nutrients in *S2* and *S3* contributed to changes in the leaf characteristics of *G. americana* seedlings, compromising the efficiency of light interception and, consequently, photosynthetic capacity and growth.

In this study, three-month-old *G. americana* seedlings were affected by excess Al and a high [Fe] to [Mn] ratio, which is associated with lower contents of Cu, Zn in S3. Although plants grown in *S2* performed better for some variables than in *S3*, the very low Mn content and the higher Fe content in *S3* negatively affected plants grown on this substrate, which may be related to competitive inhibition. In this study, plants in *S2* and *S3* presented visible symptoms (data not shown) such as leaf chlorosis, necrotic spots, and leaf abscission, and negative effects on growth and photosynthesis. Notably, previous studies have reported that tropical tree species may have a high tolerance to metal accumulation in shoots and roots without visual symptoms (Verbruggen et al. 2009; Sun et al. 2020).

Contrary to expectations, the values of *LA*, *ILA*, *LAR*, and *RGR* were higher in plants with root deformation. Despite the greater *LA* observed in plants with root deformation, their leaves were thinner, as the mean value of *LMA* was significantly lower in plants with root deformations than in plants without root deformation. Thinner leaves may become a problem in situations of high light intensity or even water deficit during the seedling establishment phase in the field. This is because plants with thicker leaves have a greater amount of water per unit of leaf area, which can reduce the effects caused by possible photoinhibition, preventing overheating of the leaves (Takahashi and Murata 2008) and the risks of herbivory (Peeters et al. 2007). Structural changes in the leaves, particularly in leaf toughness (Wright et al. 2002), are among the main indicators of the ability of leaves to acclimatize to environmental conditions (Feng et al. 2004). Despite being a morphological characteristic, *LMA* is highly correlated with physiological processes. This is because *LA* and *LMA* connect growth (interception of light), allocation of biomass (*LMA*), and photosynthesis.

In this study, plants with root deformation had the highest *RMR* values. As previously reported by Figueiredo (2014), plants that grow in plastic tubes with the induction of root deformation may show an increase in root volume or even root volume similar to that of plants without root deformation. In our study, the higher values of *RMR* plants with root deformation may be related to an increase in the volume of the root system or increased root production. Other studies have also reported that the average diameter of roots with deformation becomes larger, which leads to an increase in their thickness (Gallegos et al. 2020). Thus, deformation followed by an increase in the average diameter of the roots may have contributed to the increase in volume observed in the root system.

5 Conclusions

Acidic substrates with a high concentration of Al (*S2*) or a high ratio of Fe/Mn concentrations (*S3*) significantly affected the growth, biomass allocation, and photosynthesis of *G. americana* young plants. Interestingly, root deformation increased *LA*, *ILA*, and *LAR*, increasing *RGR* , although no significant effects of root deformation on leaf gas exchange and chlorophyll fluorescence variables were observed. Interactive effects of substrates and root deformation were observed for *ILA* and *LAR*. The increases in *ILA* and *LAR* of *G. americana* seedlings with root deformation and growing in substrates with low natural fertility may cause an imbalance in the absorption and loss of water by evapotranspiration, making the plants more susceptible to environmental stress after planting in the field.

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Author Contribution All authors contributed to the study conception and design. Catriane Sousa Santos and Marcelo Schramm Mielke conceived this study. Catriane Sousa Santos, Álvaro Alves de Almeida, Natanielly Rodrigues Avelino, and Roberta Barreto dos Santos collected the data. Catriane Sousa Santos analyzed the data with contritbutions from Amanda Freitas Cerqueira, Ândrea Carla Dalmolin, Martielly Santana dos Santos, and José Olímpio de Souza Júnior. Catriane Sousa Santos wrote the manuscript with all co-authors contributing to the fnal version.

Availability of Data and Materials Supplementary Table S1 and Fig. S1.

Declarations

Ethics Approval and Consent to Participate All authors approved participation in the manuscript.

Consent for Publication All authors agree with the publication of the manuscript.

Competing Interests The authors declare no competing interests.

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