Acta Botanica Brasilica, 2024, 38: e20240072
doi: https://doi.org/10.1590/1677-941X-ABB-2024-0072

Original Article

Assessing the feasibility of using *Acrocomia aculeata* (Arecaceae) for the rehabilitation of iron ore tailings

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ABSTRACT

The objective of this work was to evaluate the effects of iron mining tailings on seed germination, photosynthetic capacity, and biomass accumulation of macaúba palm (*Acrocomia aculeata*) seedlings. After operculum removal, seed germination tests were conducted on two substrates: iron mining tailings and vermiculite (control). No significant difference was observed between treatments in the total percentage of germinated seeds, 68% and 65% for vermiculite and tailings, respectively. In a second essay, the macaúba palm seedlings were grown using four different substrates: a reference soil (mixture of red oxisol and sand), tailings, fertilized reference soil, and fertilized tailings. No significant differences were observed for the chlorophyll indices. Plants in the reference soil showed significantly higher net photosynthesis, stomatal conductance, and transpiration rate. However, plants in fertilized tailing showed greater photochemical efficiency compared to those without fertilization. The study concludes that *A. aculeata* maintains its germination capacity in iron mining tailings. Tailing fertilization increased macaúba seedling dry mass and leaf area with greater CO_2 assimilation and photochemical efficiency. Thus, the macaúba palm is a promising plant component for rehabilitating degraded areas impacted by iron ore mining activities.

Keywords: Macaúba; Mining tailings; Oilseed; Photosynthesis; Restoration of degraded areas.

Introduction

The human impact on biodiversity loss mainly through ecosystem degradation has driven the the Paris and Bonn Challenge agreements, aiming to restore 350 million hectares of forests and degraded areas worldwide by 2030, with 12 million hectares in Brazil (Cooke *et al.*, 2019; Strassburg *et al.*, 2020). A successful restoration initiative must consider the ecological complexity of the reference ecosystem (Holl & Brancalion, 2020) and the physiological requirements of the selected species (Valliere *et al.*, 2021) that would contribute to achieving self-sustaining sites undergoing restoration at a long-term functional level.

Palms (Arecaceae) are essential components of tropical forest structure (Benchimol *et al.*, 2017) but are commonly neglected in restoration initiatives. Some palm species, such as the macaúba palm (*Acrocomia aculeata* (Jacq.) Lodd. ex. Mart.) present a remarkable resistance to abiotic stresses

Received Mar 12, 2024; Accepted Aug 27, 2024
Editor-in-Chief: Thaís Elias Almeida; Associate Editor: Marina Scalon

How to cite:
Alves MC, Neves DGA, Bicalho EM, Kuki KN, Pereira EG *et al.* 2024. Assessing the feasibility of using *Acrocomia aculeata* (Arecaceae) for the rehabilitation of iron ore tailings. Acta Botanica Brasilica 38: e20240072.
doi: 10.1590/1677-941X-ABB-2024-0072

(Pires, *et al*. 2013; Bicalho, *et al*. 2016; Dias, *et al*. 2018; Rosa, *et al*. 2019; Oliveira, *et al*. 2022) that would explain their broad geographic distribution (Bjorholm *et al.,* 2005; Eiserhardt *et al.,* 2011; Renninger & Phillips, 2016). The oleaginous macaúba palm has high productivity, generating approximately five tons of oil per hectare per year from the pulp of its fruit (Navarro-Díaz *et al.,* 2014). Also, it has a great capacity to generate income for local communities due to its exploratory versatility (Costa *et al.,* 2018) and significant economic potential for the production of vegetable oil (Oliveira *et al.,* 2022). Being a pioneer and heliophyte species, this palm is also a promising plant component in the restoration of degraded areas, due to its significant resistance to drought, pests, fires, and great acclimation capacity to different edaphoclimatic conditions (Pires *et al.,* 2013; Bicalho *et al.,* 2016 ; Rosa *et al.,* 2019). In the state of Minas Gerais (MG, Brazil), research and cultivation of macaúba palm stand out and receive incentives from Law No. 19,485/2011, also known as the Pro-Macaúba Law, which mainly aims to stimulate the production, research, and use of macaúba palm as a source of renewable energy.

Understanding the ecophysiological responses of palms to environmental conditions and stressors is crucial to restoring harsh and stress-prone degraded areas, such as those affected by mining. The Quadrilátero Ferrífero region in the center-south portion of the Minas Gerais state is one of the largest iron ore exploration centers in Brazil (IBRAM 2023) and is one of the macaúba palm natural regions of occurrence. The mining activity has a considerable impact on the environment, as it alters the landscape and biodiversity of the mined area and also affect indirectly the neighboring areas. Expanding mining sites requires deforestation, besides the long-term impacts due to tailing storage facilities, waste rock dumps, and on-site ore processing (Giljum *et al.,* 2022). The tailings resulting from the processing of iron ore, commonly found in huge dams, are a dense material, with low nutrient and high metal concentrations (Guerra *et al.,* 2017; Cruz *et al.,* 2020; Rios *et al.,* 2021). These tailings can cause additional environmental contamination when these dams break. This has happened in recent years with the Fundão dam breach in the city of Mariana, in 2015 and the Mina do Feijão dam collapse in the city of Brumadinho in 2019, both in Minas Gerais state. These incidents resulted in incalculable damage to the environment due to contamination of soils, vegetation, and watercourses, as well as of economic and social orders, mainly due to the loss of human lives and livelihood (Silveira *et al.,* 2019).

The use of macaúba palm as a contribution to the recovery of these areas impacted by the collapse of dams has advantages because it is an indigenous species adapted to the climatic conditions of the region. In this way, it is possible to preserve local biodiversity and accelerate the restoration process (Gastauer *et al.,* 2019). The establishment of macaúba palm in the tailings would allow improvement of physical, chemical, and biological aspects of the soil, with an increase in organic matter, decompaction of the tailings by the roots, and, consequently, an increase in the microbiota (César *et al.,* 2015; Moreira *et al.,* 2019).

Although promising, the use of macaúba palm in areas impacted by tailings is limited by its propagation, since its spontaneous germination can take approximately two years. To overcome seed dormancy in macaúba palm, mechanical scarification can be used to accelerate the germination process (Motoike *et al.,* 2007). However, it is important to determine, with the application of this technique, if macaúba palm seeds maintain their germination capacity in areas contaminated by iron ore tailings. Other important factors to be observed when indicating macaúba palm for recovering impacted areas with iron ore tailings are its nutritional requirements (Pimentel *et al.,* 2016), morphological adjustments, and biomass allocation (Freschet *et al.,* 2015). Palm species have different nutritional requirements compared to dicotyledon trees (Broschat, 2009). The nutrient deficiency in tailings can directly impact root development, plant growth, and photosynthetic metabolism (Cruz *et al.,* 2020; Rios *et al.,* 2021).

Based on this set of characteristics, it is hypothesized that macaúba palm is a viable species for the recovery of areas degraded by iron mining, by being capable of germinating and establishing in the tailings, overcoming its physicochemical limitations, and adjusting the photosynthetic metabolism, biomass accumulation and partitioning when grown in the iron ore tailing. The objective of this work was to evaluate the germination potential of *Acrocomia aculeata* seeds, and the photosynthetic responses of seedlings established in iron ore tailings.

Material and Methods

Seed collection and preliminary procedures

The experiments were carried out at the Federal University of Viçosa in the city of Florestal (19°53’22’’S, 44°25’57’’W), Minas Gerais, Brazil. Mature fruits of macaúba palm (*Acrocomia aculeata* (Jacq.) Lodd. ex. Mart.) were provided by the Germplasm Bank BAG-Macaúba registered under the number 084/2013 – SECEX/CGEN (Madeira *et al.,* 2024) from Federal University of Viçosa (UFV), located in Araponga (20° 39′ S, 42° 31′ W, 1040 m altitude), Minas Gerais, Brazil. The seeds were collected from *A. aculeata* parent plants (UFV herbarium reference voucher VIC 16416) from different municipalities of Minas Gerais: Itaúna (20°04’32’’S, 44°34’35’’W; BGP26), Jaboticatubas (19°30’50’’S, 43°44’46’’W; BGP83) and Pará de Minas (19°51’36’’S, 44°36’28’’W; BGP33 and BGP22). After three months of storage in a shaded and ventilated shed, the drupes were cracked up using a table vise to remove the seeds. The seeds were then washed with detergent, rinsed under running water, and dried in the shade. Those seeds with ruptured tegument, malformation, absence of embryo, and visible presence of bacterial colonies in the embryo were discarded. The seeds selected for the experiment were disinfected with 5% sodium hypochlorite for about 5 minutes and washed in running water. Then, the seeds were soaked for seven days in a beaker, at room temperature, and without sunlight, with the deionized water being changed daily (Ribeiro *et al.*, 2011). After imbibition, the seeds were scarified, which consisted of manually removing the operculum with a scalpel (Motoike *et al.,* 2007). Scarified seeds were treated with fungicide (Vitavax Thiram 200 SC, 250 ml for each 100 kg of seed).

Germination experiment

The substrates used in the germination test, vermiculite (control) and iron ore tailings, were previously autoclaved to eliminate possible contaminating microorganisms such as fungi and bacteria. The total porosity was calculated using the indirect method proposed by Embrapa (Teixeira *et al.,* 2017), with 48% for vermiculite and 17% for tailings. These values were used to determine the water retention capacity and to moisten the respective substrates. The germination test was conducted in open plastic trays containing 480 g of the respective substrates with 25 seeds in each tray, 14 repetitions (trays) with vermiculite, and 13 trays with iron ore tailings. The trays were placed in a germination chamber at 25ºC with a photoperiod of 12 hours (40 μmol photons m^{-2} s^{-1}). Seeds were evaluated daily for 56 days and the number of germinated seeds in both substrates was recorded. The replacement of water in the trays and the disposal of seeds affected by fungi or bacteria occurred when necessary. The protrusion of the cotyledonary petiole was used as a criterion for germination.

When no further germination was observed in the treatments for four days, the tetrazolium test (Ribeiro *et al.,* 2010) was performed on the seeds that did not germinate, using 10 replicates (trays) of each treatment with five embryos selected at random, totaling 50 seeds of each substrate, to verify the mortality of these seeds and determine the end of the germination test. The germination test was carried out in a completely randomized design, with an unequal number of repetitions, for the tailings and vermiculite treatments, with 13 and 14 repetitions, respectively.

Initial growth and photosynthetic responses of macaúba palm in tailings

For the second essay, seedlings of macaúba palm, with approximately 2 centimeters of protrusion of the cotyledonary petiole were used. The seedlings were placed in 290 mL tubes, containing commercial substrate (Tropstrato®), or iron mining tailings. They remained shaded by 50% irradiance under greenhouse conditions (Dias *et al.*, 2018). After two months, when the seedlings had developed eophylls, 16 seedlings were selected and transplanted to 3-liter pots containing tailings (8 seedlings) or 2:1 latosoil and sand mixture (eight seedlings from the commercial substrate), being irrigated when necessary, and followed up for 14 months until the end of the experiment. The chemical composition of the reference soil was P and K 2.4 and 65 mg dm^{-3}, respectively; Ca^{2+}, $Mg^{2+,}$ and Al^{3+} of 0.62, 0.21, and 1.34; the sum of exchangeable bases (SB) was 1; effective (t) and total (T) cation exchange capacity of 2.34 and 4.5 cmol c /dm^3, respectively; saturation index (V) and aluminum saturation index (m) of 22.2 and 57.3%, respectively; remaining phosphorus of 7.7%. The tailings used throughout the experiment came from the dam at the Mina de Fábrica (20°25'02''S, 43°51'57''W), owned by Vale S.A. The physicochemical characterization of the tailing was the same as presented by Rios *et al.,* (2021), with a loam texture and levels of Fe and Mn of 83.03 and 259.90 mg dm^{-3}, respectively. In the eighth month, half of the seedlings in the respective substrates were fertilized (Pimentel *et al.,* 2016) as follows: 1 kg m^{-3} of limestone, 6 kg m^{-3} of simple superphosphate, 1 kg m^{-3} of ammonium sulfate, and 0.3 kg m^{-3} of potassium chloride. On the 10th month, the remaining seedlings were transplanted into 8-liter pots and fertilized again following the same methodology. The experiment consisted of four treatments: reference soil (RS, control), tailings (T), fertilized reference soil (FRS), and fertilized tailings (FT), with four replications.

All photosynthetic evaluations were carried out in the central portion of the second fully expanded leaf, in the morning period, between 9 am and 12 am. The evaluations were carried out in the eighth month after planting and four months later; after the fertilization of the treatments, they were submitted to the same evaluations.

For leaf gas exchange measurements, an infrared gas analyzer (IRGA) model LI-6400xt (Li-Cor Inc., Lincoln, Nebraska, USA) was used, with an irradiance of 1500 μmol m^{-2} s^{-1} provided by LEDs in the leaf chamber (model 6400-02B, Li-Cor Inc.). All evaluations were carried out with a CO_2 concentration of 400 μmol mol^{-1} provided by the CO_2 control system (model 6400-01, Li-Cor Inc.), with a temperature of 28ºC and 45% relative humidity. From the measurements, the following variables were obtained: net photosynthetic rate (A), stomatal conductance to water vapor (g_s) transpiration rate (E), and instantaneous water use efficiency (*WUE*), which was calculated as the ratio between A and E.

Chlorophyll indices were obtained with the portable ClorofiLOG meter (Falker, Brazil) from the average of three measurements performed on the same leaf used for gas exchange analyses.

Initial fluorescence (F_0) and maximum fluorescence (F_m) measurements were performed with a pulse-modulated Mini-Pam fluorometer (Heinz Walz, Effeltrich, Germany) with measuring light (<1 μmol m^{-2} s^{-1}) and saturating light pulse (12000 μmol m^{-2} s^{-1}), after acclimation in the dark for 30 minutes. With the results, the maximum quantum efficiency of photosystem II (PSII) was determined as $F_v/F_m = (F_m - F_0)/F_m$ (Genty *et al.* 1989).

At the end of the experiment, the plants were separated into leaves, roots, pseudobulb, and petiole. The leaves were digitalized with a scanner and the total leaf area was calculated using the ImageJ software (Abramoff *et al.*, 2004). The leaves, roots, pseudobulb, and petiole dry mass were determined after 72 hours in an oven at 65ºC. The leaf mass per area (LMA) was calculated as the total leaf dry mass divided by the total leaf area. The leaf area ratio (LAR) was calculated as leaf area divided by total plant biomass. The leaf mass fraction (LMF), root mass fraction (RMF), and pseudobulb mass fraction (PMF) were calculated as the mass of the respective organ divided by total plant biomass. The dried material was used to analyze the iron concentration in plant tissues by atomic absorption spectrophotometry (AA-7000, Shimadzu, Japan) after wet digestion with a solution of nitric-perchloric acid (3: 1) at 200 °C.

Statistical analyses

The first trial, concerning the germination of macaúba palm seeds, was carried out in a completely randomized design with two treatments, vermiculite and tailings, with 14 and 13 repetitions, respectively. The second trial was carried out in a randomized block design, with four treatments: reference soil (RS, control), tailings (T), fertilized reference soil (FRS), and fertilized tailings (FT), with four replications. For all trials, data were submitted for analysis of variance (ANOVA). The data significance in the first trial was compared by the F-test ($P < 0.05$) and Tukey test ($P < 0.05$) for the second trial. Before ANOVA, data were tested for normality of residuals and homogeneity of variance. Data on the germination percentage were transformed in arcsin $\sqrt{x}/100$ before statistical analysis. All analyses were performed using the R program, version 3.6.1 (R Core Team 2019).

Results

Germination of macaúba palm seeds in iron ore tailings

There was no significant difference for all sampling times in the germination percentage of seeds in iron ore tailings (65% of maximum germination) compared to the seeds in vermiculite (68% of maximum germination) (Fig. 1).

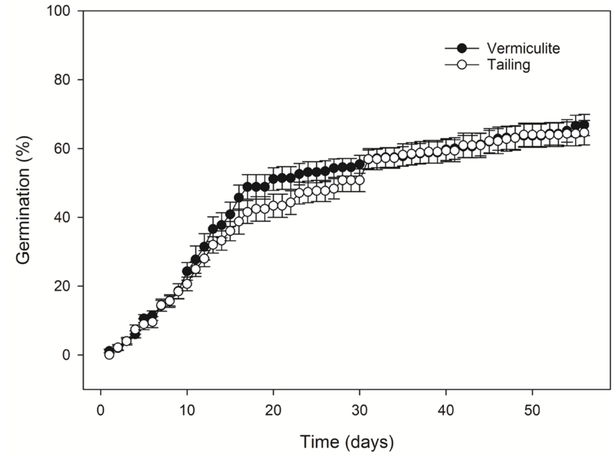

Figure 1. Germination percentage of macaúba palm seeds in iron ore tailings and vermiculite (control) over 56 days of the experiment. Data are the means and standard deviations of 14 replicates for vermiculite and 13 replicates for tailings. There was no significant difference between treatments.

Photosynthetic and growth responses of macaúba seedlings in iron ore tailings and reference soil

No significant differences were observed for the total chlorophylls, chlorophyll *a* and *b,* and chlorophyll *a*/*b* ratio (Fig. 2) in *A. aculeata* seedlings, regardless of the treatments.

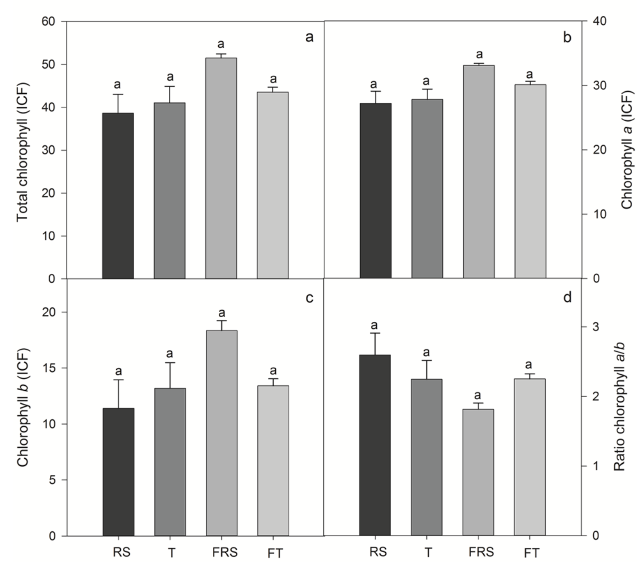

Figure 2. Index of chlorophyll Falker (ICF) for total chlorophyll (a), chlorophyll *a* (b), chlorophyll *b* (c), and chlorophyll *a*/*b* ratio (D) in *A. aculeata* seedlings grown in reference soil (RS), tailings (T), fertilized reference soil (FRS) and fertilized tailings (FT). Values are mean and standard error of four repetitions. There was no significant difference between treatments according to the Tukey test ($p > 0.05$).

The F_0 was significantly lower in plants grown in the fertilized reference soil and fertilized tailing compared to those in the control (RS) treatment, although, the plants cultivated in the tailings without fertilization did not diverge from the other treatments (Fig. 3A). There were no significant differences in F_v/F_m values in plants from the RS, tailings, and fertilized control treatments, however, the plants in the fertilized tailings showed significantly higher values compared to the RS and T treatments (Fig. 3B).

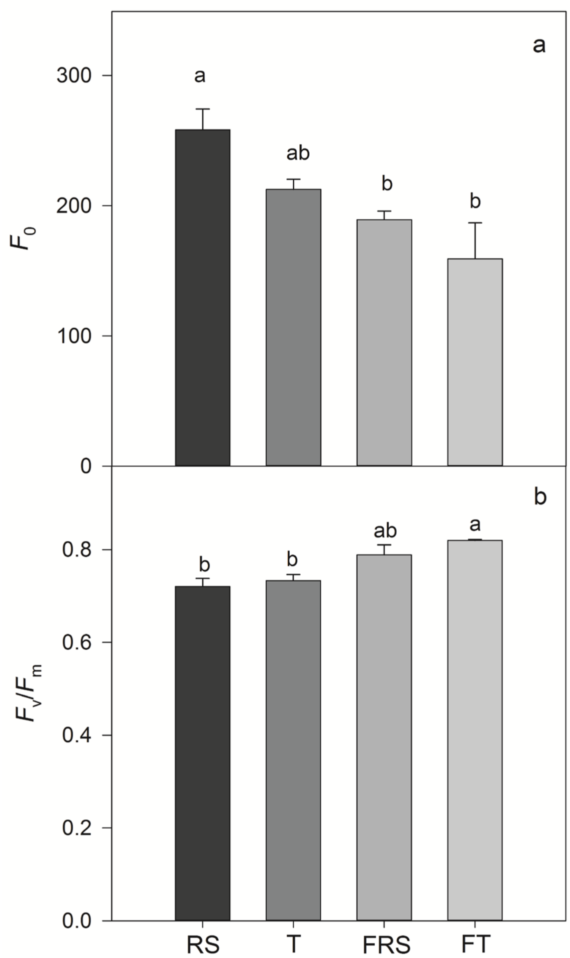

Figure 3. Initial fluorescence (F_0, a) and maximum quantum efficiency of photosystem II (F_v/F_m, b) in *A. aculeata* seedlings grown in reference soil (RS), tailings (T), fertilized reference soil (FRS) and fertilized tailings (FT). Values are mean and standard error of four repetitions. Distinct letters indicate significant differences according to the Tukey test ($p < 0.05$).

The macaúba palm seedlings growing in the reference soil showed significantly higher *A* than in the other treatments. Plants cultivated in tailing and fertilized reference soil, on the other hand, presented considerably lower *A* compared to other treatments. The g_s and *E* (Fig. 4) showed significantly higher values in the plants grown in the reference soil but showed no difference between the tailings, fertilized reference soil, and fertilized tailings. The seedlings of macaúba palm did not differ in terms of *WUE* when growing in the reference soil, tailings, and fertilized tailings. However, the seedlings established in the fertilized reference soil and fertilized tailings were considerably more efficient concerning the use of water (Fig. 4).

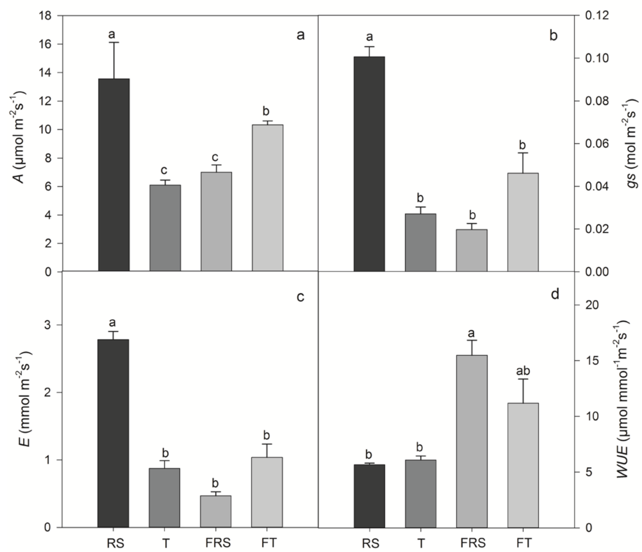

Figure 4. Net photosynthesis (*A*, a), stomatal conductance (g_s, b), transpiration (*E*, c), instantaneous water use efficiency (*WUE*, d), in *A. aculeata* seedlings grown in reference soil (RS), tailings (T), fertilized reference soil (FRS) and fertilized tailings (FT). Values are mean and standard error of four repetitions. Distinct letters indicate significant differences according to the Tukey test ($p<0.05$).

The seedlings from the fertilized reference soil showed higher dry mass and leaf area. The seedlings established in non-fertilized tailings by contrast had a lower leaf dry mass compared to those established in the fertilized reference soil (FRS) treatments and fertilized tailings (Table 1). The petiole and root dry mass was higher in plants from the fertilized reference soil, and in the other treatments, they did not diverge. The pseudobulb from seedlings in fertilized reference soil had the highest values of dry mass. The tailings promoted lower pseudobulb dry mass, which showed no significant difference between the other treatments. The leaf area was significantly greater only in seedlings growing on the FRS, compared to the other treatments. However, the leaf mass-to-area ratio (LMA) and the leaf area ratio (LAR) were not affected by the treatments (Table 1). In the same way, the root mass fraction (RMF) did not change in response to the treatments. However, the fertilization of reference soil (FRS) or tailings (FT) promoted an increase in the leaf mass fraction (LMF) of *A. aculeata* seedlings, in comparison to the other treatments. The pseudobulb mass fraction (PMF) was lower in plants grown in the fertilized reference soil in comparison to no fertilized plants and did not differ from those in fertilized tailings (Table 1).

Table 1. Dry mass of plant, leaf blade, petiole, pseudobulb and roots, leaf area, and mass-to-leaf area ratio (LMA), leaf area ratio (LAR), leaf mass fraction (LMF), root mass fraction (RMF), pseudobulb mass fraction (PMF) in *Acrocomia aculeata* seedlings grown in reference soil (RS), tailing (T), fertilized reference soil (FRS), and fertilized tailings (FT). Values are mean and standard error of four repetitions. Distinct letters in the lines indicate significant differences according to the Tukey test ($p < 0.05$).

	RS	T	FRS	FT
Plant dry mass (g)	21.638 ± 9.25b	7.497 ± 3.19c	72.865 ± 1.87a	15.200 ± 5.06bc
Leaf blade dry mass (g)	3.235 ± 0.28bc	1.170 ± 0.28c	13.46 ± 1.09a	3.695 ± 0.46b
Petiole dry mass (g)	1.857 ± 0.17b	0.823 ± 0.20b	15.51 ± 0.73a	1.745 ± 0.25b
Root dry mass (g)	4.364 ± 0.58b	1.247 ± 0.21b	14.515 ± 1.37a	2.362 ± 0.75b
Pseudobulb dry mass (g)	12.181 ± 0.60b	4.256 ± 1.42c	29.38 ± 3.05a	7.397 ± 1.68 bc
Leaf area (cm^2)	391.21 ± 56.47b	181.70 ± 35.35b	1559.45 ± 248.27a	438.22 ± 45.53b
LMA ($mg\ cm^{-2}$)	8.863 ± 1.69a	6.264 ± 0.39a	8.970 ± 0.80a	8.402 ± 0.60a
LAR ($cm^2\ g^{-1}$)	18.119 ± 2.65a	25.498 ± 2.25a	21.114 ± 2.21a	31.627 ± 5.21a
RMF ($g\ g^{-1}$)	0.201 ± 0.02a	0.185 ± 0.03a	0.200 ± 0.02a	0.142 ± 0.02a
LMF ($g\ g^{-1}$)	0.235 ± 0.01b	0.268 ± 0.02b	0.399 ± 0.01a	0.377 ± 0.04a
PMF ($g\ g^{-1}$)	0.564 ± 0.03a	0.547 ± 0.05a	0.401 ± 0.02b	0.481 ± 0.02ab

Seedlings from both treatments with reference soil (RS and FRS) had a significantly lower iron concentration in leaves compared to the plants growing in fertilized tailings, with no significant differences in petiole and pseudobulb between the 4 treatments (Fig. 5). The roots presented higher iron concentrations among plant structures. Especially, in those plants that did not receive a fertilization treatment (Fig. 5).

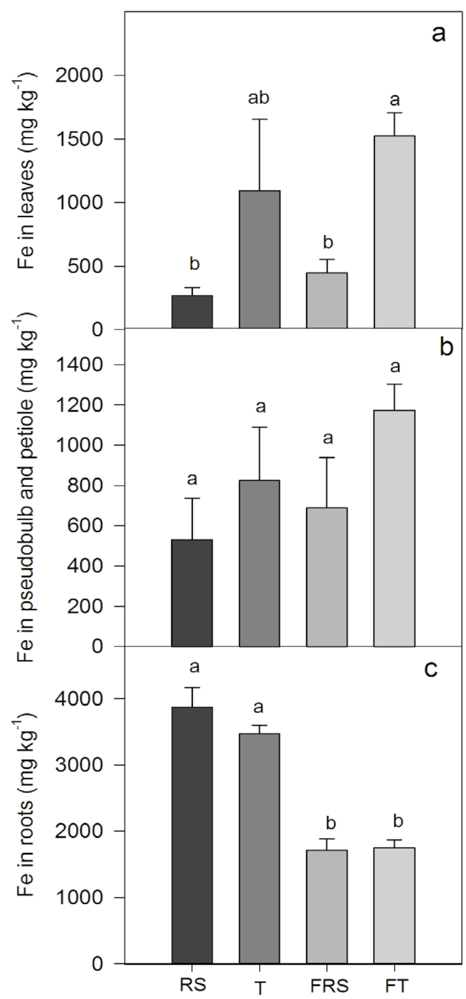

Figure 5. Iron concentration in leaf blades (a), pseudobulb and petiole (b), and root (c) of *A. aculeata* seedlings exposed to reference soil (RS), tailings (T), fertilized reference soil (FRS) treatments and fertilized tailings (FT). Values are mean and standard error of four repetitions. Distinct letters indicate significant differences according to the Tukey test ($p < 0.05$).

Discussion

The germination capacity of macaúba palm seeds proved to be indifferent to the chemical and physical limitations of the tailings. The iron ore tailings do not have toxicity to the point of hindering the germination process of macaúba palm seeds, as also found in other plant species (Scarpa *et al.,* 2022). Seeds, in general, have reserves that guarantee their germination and the initial development of seedlings, especially those of macaúba palm, which have a high concentration of lipids, proteins, and non-soluble carbohydrate compounds (Bicalho *et al.,* 2016; Oliveira *et al.,* 2022).

During the initial growth of macaúba seedlings in the tailing, the stomatal limitation was the main factor responsible for the decrease in CO_2 absorption in the photosynthetic process, when compared to plants from the reference soil without fertilization. Due to the low porosity and high density of the tailings (Rios *et al.,* 2021), the water is retained owing to the high tension force in the soil, detaining water absorption by the plants. There is a relationship between soil fertility and plant nutritional status, and with this, an increase in the concentration of nutrients in plant tissues improves various physiological processes (Ehrenfeld *et al.,* 2005), such as the increased photosynthetic capacity of plants grown in the fertilized tailing when compared to those grown in tailings without fertilization. Fertilization was also important to stomatal regulation and, consequently, balancing the seedling transpiration process, mainly with the increase in KCl, as also observed by Pimentel *et al.,* (2015), causing a greater water use efficiency (WUE) in fertilized plants.

The scarcity of essential elements in the tailings (Rios *et al.,* 2021), especially N, but also K, responsible for the stomatal opening, and Mg, the central atom of the chlorophyll molecule, could have contributed to the low carbon assimilation by plants grown in this substrate, and consequently, lower production of dry mass (Pimentel, 2012; Rosa *et al.,* 2019). Fertilizing the tailings made the plant that was under low nutritional status to invest in its recovery in vegetative growth through a greater increase in the photosynthetic processes (Cruz *et al.,* 2022; Santos *et al.,* 2022). However, even with good practices (Busch *et al.,* 2024) the gas exchange measurements possess several methodological limitations, especially sampling a small portion of the leaf during a short time in optimal conditions, which could not reflect the long-term gain in biomass production.

The lowest values of F_0 and the highest values of F_v/F_m are related to a favorable response to the establishment of macaúba palm seedlings in the fertilized tailings, as it demonstrates that the efficiency of energy conversion in the PSII under unfavorable substrate was not affected. Considering that there were no changes in chlorophyll indices, the greater F_0 in unfertilized treatments could be the result of PSII reaction centers impairment, or compromised energy transfer from the antenna complex to the reaction centers (Rios *et al.*, 2024). Furthermore, the maintenance of chlorophyll levels even in the unfertilized tailings corroborates the efficiency of macaúba in environments with nutritional limitations. The opposite was observed in the establishment of seedlings of several tree species in the mining tailings, which presented lower chlorophyll content, and lower quantum yields of PSII (Cruz *et al.,* 2020; 2022).

Although the physical constitution of the tailings does not change significantly in the short period evaluated, the fertilization provided mitigation of the chemical limitation to the growth of macaúba palm seedlings. It is well known that macaúba palm (Pimentel *et al.,* 2015) and also other palm tree species with similar growing characteristics (Ares *et al.,* 2003; Broschat, 2009; El Kinany *et al.,* 2022; Dassou *et al.,* 2022), possess high efficiency in absorption and use of nutrients in the soil, including N, P, K, via inorganic or organic fertilization. Liming increases the availability of calcium and magnesium, nutrients that are scarce in the tailings (Rios *et al.,* 2021). Calcium induces root development and, consequently, provides a greater uptake of water and nutrients from the soil (Broschat, 2009; Jasim *et al.,* 2016; Pimentel *et al.,* 2016). N and Mg are constituents of the chlorophyll molecule, and K is directly related to the stomatal opening. Adequate availability of such minerals is essential to enhance photosynthesis and growth in palms (Broschat, 2009; Pimentel, 2012; Pimentel *et al.,* 2015).

The P is also directly linked to photosynthetic metabolism, but despite the tailings being rich in this mineral compared to the reference soil (Rios *et al.,* 2021), macaúba palm has a low P requirement (Pimentel *et al.,* 2015; 2016).

However, in addition to physical and nutritional limitations, the presence of heavy metals such as Fe at high concentrations in the tailings also influences plant establishment (Rios *et al.,* 2021). Despite nutritional limitations and physical constraints, Fe toxicity was considered one of the main causes of the decline in growth and photosynthesis as observed in tropical tree species in iron-ore tailings (Cruz *et al.,* 2022; Santos *et al.,* 2022). Fe is an essential micronutrient for plant development, however, when in excessive concentration in tissues can generate oxidative stress, the overproduction of reactive oxygen species (ROS), and, consequently, inhibits root growth and causes photosynthetic limitations (Nurmalasari *et al.,* 2016; Rios *et al.,* 2017). The ideal range for iron concentration in plant tissues varies according to the species. In oil palm, for example, the total Fe level commonly found in leaves is between 60 and 350 mg kg^{-1} (Rodrigues *et al.,* 2006). In the green dwarf coconut palm, the Fe value in leaves is on average 158 mg kg^{-1} (Santos *et al.,* 2004). In macaúba palm seedlings not exposed to Fe excess, it was reported a higher average Fe concentration in leaves of 295.63 mg kg^{-1} (Pimentel *et al.,* 2016) ranging from 151 to 517 mg kg^{-1} and from 1174 to 4601 mg kg^{-1} in the root and pseudobulb (Pimentel, 2012). Under field conditions (Pires *et al.,* 2013) the Fe concentration in leaves of macaúba palm reached up to 273.33 mg kg^{-1}. Information about Fe nutrition and sufficiency range in macaúba palm is still very scarce in the literature, however, it is known that the concentration of nutrients would be higher in younger seedlings (Pires *et al.,* 2013). The high Fe requirement of macaúba palm as observed in this study was also related to its high photosynthetic efficiency (Pires *et al.,* 2013).

Through the data of the leaf area, LMA, LAR, and LMF it is possible to understand the best functional adjustment of macaúba palm, regarding the dry mass allocation in the leaf. Even with greater production of dry mass and higher leaf area in fertilized reference soil, the maintenance of LMA values among all treatments demonstrates that, in the tailings treatments and the control without fertilizing, they invested more in leaf thickness than in expansion, as a way to regulate water loss (Rosa *et al.,* 2019). Moreover, the lack of significant difference in LAR indicates that macaúba palm maintains the partitioning of biomass according to the whole leaf area even under different conditions in reference soil and tailings. The higher LMF and lower PMF in plants from the fertilized treatments are related to the changes in plant biomass allocation strategy when grown in nutritional limitations, with higher investment in conservative traits (Ordoñez *et al.,* 2009).

Based on its tolerance capacity, as observed in this work, the use of macaúba palm as a component in areas impacted by iron-dam collapses in Brazil is a feasible strategy. The indigenous and pioneer status of this palm species (Dias *et al.,* 2018) makes an important contribution to the attempt to amend the impacts caused by mining on biodiversity loss and ecosystem functioning.

In conclusion, macaúba palm presented a high germination percentage and seedling establishment capacity in iron ore tailings. Tailing fertilization overcame the physical and mainly chemical limitations, resulting in an increase in leaf and total biomass due to greater CO_2 assimilation and photochemical efficiency. Therefore, as a native species from the semi-deciduous Atlantic Forest, *A. aculeata* is likely to be used for rehabilitation of areas impacted by tailings deposition, due to its physiological characteristics and great resistance.

Acknowledgments

The authors thank FAPEMIG (Minas Gerais State Foundation for Research Development), CAPES (Coordination for the Improvement of Higher Education Personnel – Brazil) and Vale S.A. for financial support and also CNPq for the scholarship granted to M. C. Alves. E. G. Pereira and E. M. Bicalho also thank the National Council for Scientific and Technological Development (CNPq) for the research productivity grants (305376/2023-3 to EGP and 307846/2022-9 to EMB).

Authors' Contributions

EGP: Funding acquisition and resources, project administration, supervision, conceptualization, formal analysis, writing-reviewing, and editing. MCA: investigation, formal analysis, writing-original draft. DGAN: investigation. EMB and KNK: conceptualization, formal analysis, writing-reviewing, and editing.

Conflict of Interest

The authors declare that they have no conflict of interest. All authors approved the manuscript.

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