



Photosynthetic responses and growth dynamics of *Allagoptera arenaria* (Gomes) Kuntze (Arecaceae) in a chronosequence in a Restinga restoration area

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Abstract

Knowledge about plant species' growth dynamics is essential in restoring degraded environments. In this study, we evaluated the growth dynamics of *Allagoptera arenaria* (Gomes) Kuntze in a chronosequence of plantations in the Restinga. The sampling was taken from three populations with different planting ages ($n = 12$): group GI – 8 months; GII – 4 years; GIII – 7 years. We analyzed biometric measurements, leaf traits, photosynthetic pigments, and chlorophyll *a* fluorescence. The GI group's maximum quantum yield of primary photochemistry was significantly higher. On the other hand, the energy dissipation by heat was significantly higher in GIII. Our findings demonstrate that *A. arenaria* has high ecophysiological plasticity as it can adjust its photosynthetic machinery to avoid permanent damage to the proteins and structures of the photosystems. GI plants group can invest in greater carbon allocation, which is essential for survival in the field, as observed in groups GII and GIII.

Keywords: ecological facilitation; ecophysiology; establishment of planting; photosynthetic plasticity.

Introduction

The principles and practices of quantitative analysis of plant growth aim to describe and interpret the performance of a given species under natural or controlled

environmental conditions over time (Mendes *et al.* 2022, Abebe *et al.* 2023, Ribeiro 2023). Growth can be measured by the height, diameter, or count of parts or organs of the plant (linear growth), or even through the phytomass of a community, in a significant sampling of

Highlights

- *Allagoptera arenaria* adjusts photosynthesis to survive in adverse environments
- Photosynthetic efficiency was higher in younger plants
- Slow growth and accumulation of biomass are survival strategies

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Abbreviations: ABS/RC – absorption flux per active reaction center; Car – total carotenoid content; Chl *a* – chlorophyll *a*; Chl *a/b* – the ratio between chlorophyll *a*/chlorophyll *b*; Chl *b* – chlorophyll *b*; Chl total – total chlorophyll content; DI₀/RC – total energy dissipated as heat per active reaction center; DM_{aerial part} – aerial part dry mass; DM_{underground} – underground dry mass; DM_{underground}/DM_{aerial part} ratio – the ratio between underground and aerial dry mass; ET₀/RC – electron flux transported by active reaction center; ETR – electron transport rate; F₀ – minimum fluorescence; F_m – maximum fluorescence; F_v/F_M – maximum efficiency of PSII; LDM – leaf dry mass; LMA – leaf mass per unit area; PAR – photosynthetically active radiation; RDM – root dry mass; RWC – relative water content; SDM – stem dry mass; SI – sclerophylly index; SUC – succulence; TDM – total dry mass; THI – thickness; TR₀/RC – energy flux captured by the active reaction center; WUE – water-use efficiency; φNPQ – quantum yield of regulatory light-induced nonphotochemical quenching.

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plants in greenhouse or field conditions (Abebe *et al.* 2023, Ribeiro 2023, Mendes *et al.* 2025). Other techniques, such as plant leaf traits, can be applied to evaluate their adaptation to different environments and how they adapt to environmental variations (Mendes *et al.* 2022, Gong *et al.* 2023). It is essential to understand the growth patterns and ecophysiology of plant species, as this can help explain the establishment, richness, and abundance of species in coastal environments, such as Restinga (Gessler *et al.* 2008, Hwang and Choo 2017, Pereira and Menezes 2023, Zani *et al.* 2023, Carvalho *et al.* 2025, Menezes *et al.* 2025, Silva *et al.* 2025).

Leaf traits are also used to measure plant growth because of the recognition of the functional significance of leaves, such as leaf mass per unit area (LMA), succulence (SUC), and leaf blade thickness (THI) (Kluge and Ting 1978, Reich 2014, Mendes *et al.* 2022). Some studies have demonstrated the importance of interpreting and understanding the functional relationships between plants from a foliar perspective to understand how plant establishment and growth are affected by environmental changes (Gessler *et al.* 2008, de la Riva *et al.* 2016, Mendes *et al.* 2025, Menezes *et al.* 2025, Silva *et al.* 2025). In addition, ecophysiological evaluations, such as the quantification of photosynthetic pigments and measurement of chlorophyll fluorescence parameters, allow us to infer the photosynthetic potential of plants and, consequently, their growth, in addition to revealing aspects of their adaptability to different environments (Kalaji *et al.* 2016, Mendes *et al.* 2025). Chlorophyll *a* fluorescence can also be used to estimate the efficiency of electron transport through PSII (Strasser *et al.* 2004, Kalaji *et al.* 2016, Bussotti *et al.* 2020).

The palm *Allagoptera arenaria* (Gomes) and Kuntze (Arecaceae) is distributed along the coastal plains of Brazil (Moraes and Martins 2017, Pereira and Menezes 2023, Zani *et al.* 2023). This palm can reach 1.5 m in height and 2.0 m in canopy diameter (Menezes *et al.* 2018, Pereira and Menezes 2023, Zani *et al.* 2023), and can be associated with thickets forming dense populations featuring a phytophysiognomies of Restinga (Moraes and Martins 2017, Pereira and Menezes 2023, Zani *et al.* 2023). In addition, *A. arenaria* has a high regenerative success mainly after burning, as a geophyte, and the ability to accumulate organic matter in the soil from its senescent leaves. Also, this species provides microclimatic modifications under its canopy and ecologically facilitates the establishment of other species in Restinga (Menezes *et al.* 2018, Pereira and Menezes 2023, Zani *et al.* 2023, Carvalho *et al.* 2025). However, few studies have focused on the growth dynamics and colonization of palm trees in Restinga environments. One such study compared the physiological performance of *Clusia hilariana*, *Andira legalis*, and *A. arenaria*, seeking to understand how the physiological mechanisms of these species could explain their colonization of Restinga environments (Gessler *et al.* 2008).

Restinga are ecosystems with limited characteristics for the establishment and development of plants, such as high temperatures, strong winds, salinity, and limited

availability of water and nutrients in the soil (Hwang and Choo 2017, Menezes *et al.* 2018, Pereira and Menezes 2023, Ribeiro 2023, Menezes *et al.* 2025, Silva *et al.* 2025). Thus, ecological facilitation processes have been identified as important in niche occupation strategies in Restinga, and *A. arenaria* is reported as a key element in secondary succession processes (Menezes *et al.* 2018, Pereira and Menezes 2023, Zani *et al.* 2023). From this perspective, *A. arenaria* contributes to the conservation of coastal ecosystems by promoting greater stability in this environment and increasing biodiversity (Menezes *et al.* 2018, Pereira and Menezes 2023, Zani *et al.* 2023, Carvalho *et al.* 2025). According to Pereira and Menezes (2023), studies on coastal vegetation associated with Quaternary sediments have been conducted in all Brazilian coastal states. However, as the Restinga ecosystem comprises different phytophysiognomies, the successful colonization of these environments involves species-specific physiological adaptations (Gessler *et al.* 2008).

A. arenaria plays an important role in the secondary succession process in Restinga, and these environments are naturally stressful for the establishment and development of plants. Biometric measurements, biomass partition, leaf traits, photosynthetic pigments, and chlorophyll *a* fluorescence in three populations of different planting ages were analyzed to evaluate and understand the growth dynamics of this species in Brazilian Restinga.

Materials and methods

Study area: After the installation of the terrestrial gas area in the region of Cacimbas, Linhares, ES, an area of 0.4 ha of vegetation of the non-flooding open shrub and shrub formations was suppressed. The State Institute of Environment (IEMA) issued condition no. 17, linked to installation license no. 222/2004, requesting the recovery of the degraded area. To fulfill this condition and restore the landscape, two plantations of *A. arenaria* were carried out in the area, one in 2011 and the other in 2014 (Fig. 1).

Climate: The climate of the region is tropical hot and humid (Aw), characterized by rainy and dry seasons, with the rainy season coinciding with the hottest months of the year (October to April) and the dry season with the coldest months (May to September) (Alvares *et al.* 2013). The total precipitation is greater than 1,200 mm per year and is more concentrated in the period from October to March, with the rainiest months being November and December (Fig. 2).

Sampling: The sampling was taken from three populations with different planting ages, consisting of 12 individuals from each population ($n = 12$). In our experiment, three treatments/groups of plants were established according to the age of the individuals: Group 1 (GI) – 8 months commercial seedling, kept under nursery conditions in plastic pots (3.6 L) with a substrate formed by a mixture of subsoil, sand, and clay in the proportion of 2:2:1; Group 2 (GII) individuals with 4 years of growth planting in a natural environment; and Group 3 (GIII) individuals

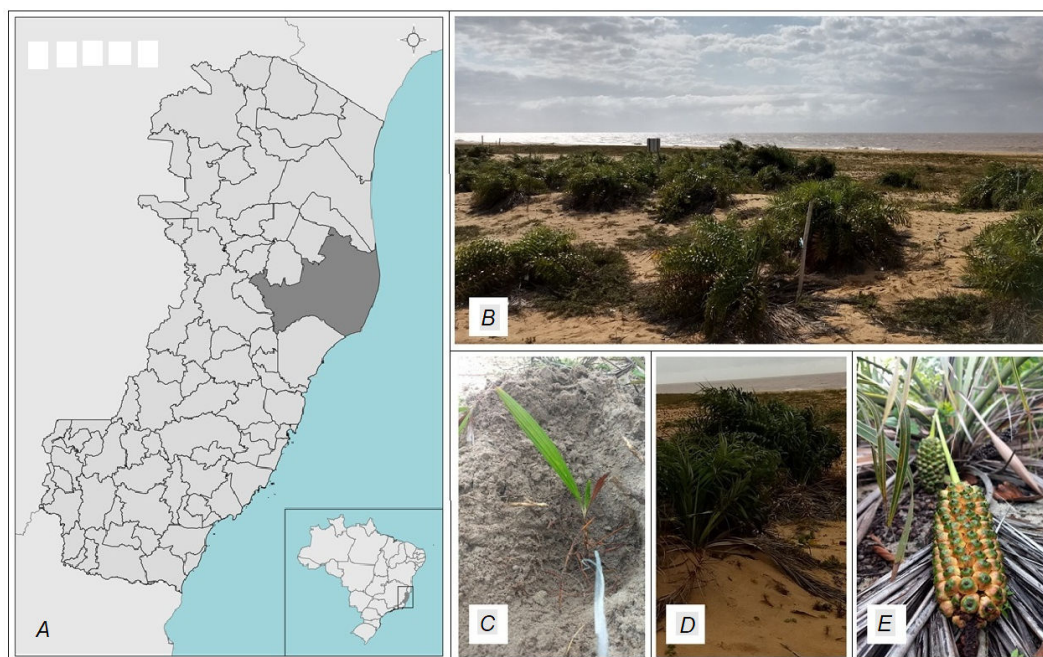


Fig. 1. (A) Linhares, Espírito Santo, Brazil. (B) Location of study area, Cacimbas (latitude -19.479442° , longitude -39.736216°). (C) Young *Allagoptera arenaria* plants in field conditions. (D) Adult *A. arenaria* plants (more than 7 years old). (E) Fruits of *A. arenaria* plants.

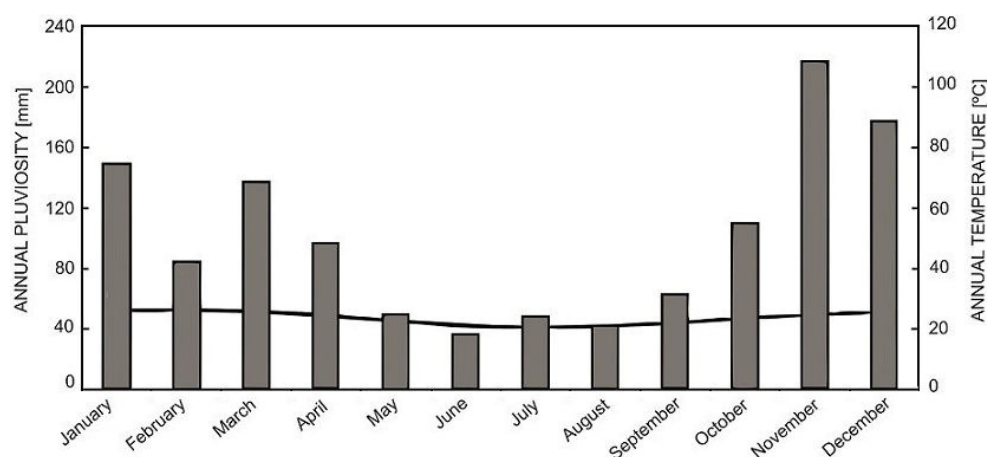


Fig. 2. Average precipitation (rainfall) and temperature in the Linhares region, during the experimental period.

with 7 years of growth planting in a natural environment. The seedlings used in the planting of Groups II and III had the same characteristics as those in Group GI. Measurements were performed in September 2018.

Biometry: In the biometric evaluation, height (cm), stem diameter (mm), and number of leaves were measured. Plant height was measured using a tape measure from the stem to the largest expanded leaf. Stem diameter was measured with a digital caliper (± 0.01 mm) in the largest region of the stem of the plant, and the number of leaves was counted by direct observation of the individuals. For biomass assessment, individuals were dissected into roots, stems, and leaves, packed in paper bags, and placed in a greenhouse with forced air circulation (70°C for

72 h). The material was then weighed on a digital precision scale (0.01 g) to determine root dry mass (RDM), stem dry mass (SDM), and leaf dry mass (LDM). The total dry mass ($\text{TDM} = \text{RDM} + \text{SDM} + \text{LDM}$), dry mass of the underground part ($\text{DM}_{\text{underground}} = \text{RDM} + \text{SDM}$), aerial part dry mass ($\text{DM}_{\text{aerial part}} = \text{LDM}$), and the ratio between the underground dry mass and aerial part dry mass were calculated ($\text{DM}_{\text{underground}}/\text{DM}_{\text{aerial part}}$) along with the robustness coefficient (height/stem diameter).

Leaf traits: To calculate leaf traits, three leaf discs (0.84 cm^2) were removed from the middle of the leaf blade, totaling 24 repetitions per treatment. The leaf discs were obtained using a metal cutter. The discs were weighed on a precision scale (0.01 g) to determine the fresh mass (g).

To determine the turgid mass (g), the leaf discs were hydrated in distilled water for 24 h and weighed again. Thickness (mm) was measured using a digital caliper (± 0.01 mm) on the turgid discs. After hydration, the leaf discs were packed in paper envelopes, placed in an oven at 60°C for 72 h, and weighed again to determine dry mass (g). The following leaf traits were calculated: succulence (SUC in g m^{-2}) – difference between saturated mass and dry mass divided by area (Kluge and Ting 1978); leaf mass per leaf area (LMA in g m^{-2}), estimated by the ratio between the dry mass and leaf area of the discs; sclerophylly index (SI), calculated as $\text{dry mass (g)} / 2 \times \text{leaf area (dm}^2\text{)}$; relative water content (RWC %): $(\text{fresh mass} - \text{dry mass}) / (\text{saturated mass} - \text{dry mass}) \times 100$ (Barrs and Weatherley 1962).

Photosynthetic pigments: For the quantification of photosynthetic pigments, 300 mg of plant material was obtained from a fully expanded leaf. The plant material was placed in test tubes containing 5 ml of 80% acetone and kept in the dark at 4°C for 72 h for spectrophotometric analysis. The readings were taken at 480, 645, and 665 nm for carotenoids, chlorophyll *b* (Chl *b*), and chlorophyll *a* (Chl *a*). In addition, the total Chl and Chl *a/b* were calculated. The contents of photosynthetic pigments expressed in mg g^{-1} (FM) were calculated according to the equation of Lichtenthaler (1987).

Chlorophyll *a* fluorescence: The chlorophyll *a* fluorescence transient was measured using a portable fluorometer (Handy-PEA, Hansatech, UK). Leaves were adapted to the dark for 30 min using leaf clips (Hansatech) for complete oxidation of the photosynthetic system. The light intensity reaching the leaf was $3,000 \mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$, which was sufficient to generate the maximum fluorescence for all samples. Measurements were performed at 7:00 h. The JIP-test parameters were calculated using the formula described by Strasser *et al.* (2004).

Statistical analysis: The data obtained were subjected to analysis of variance (ANOVA), and when significant ($p < 0.05$), the means were compared using Tukey's test. Before performing the variance analysis, the Shapiro-Wilk test was applied, and the data showed a normal distribution. Another analysis was carried out using principal component analysis (PCA) to verify the main parameters and associated groups. All analyses were performed using the R Core Team software (R Foundation for Statistical Computing, Vienna, Austria), version 4.3.1 (R Core Team 2023). The complete list of morphophysiological parameters evaluated in this experiment can be seen in Table 1S (supplement).

Results

A. arenaria showed a significant increase in biometric variables over seven years. The plants grew by 19 cm, demonstrating an average increase of 2.7 cm per year. The stem increased by 20.18 mm, representing an average increase of 2.88 mm per year. In the GIII group, the average number of leaves increased from 2.3 leaves in the GI group to 5.6 leaves in the GIII group. The robustness quotient showed a significant reduction with planting age (Table 1). The biomass of the roots, stems, and leaves increased significantly with age at planting. Over time, the *A. arenaria* showed a greater accumulation of biomass in underground parts (roots and stem) than in the aerial parts (leaves). The ratio between underground and aerial parts was significantly higher in the GII group (Table 1).

The GI group showed a significantly higher mean for leaf thickness (THI), and a reduction in GII and GIII was observed compared to group GI. The succulence (SUC) did not show variation between the groups (Table 2). The leaf mass per unit area (LMA) demonstrated a marked increase (GI→GIII), even as the sclerophylly index (SI) increased, and the relative water content (RWC) demonstrated a total increase in general; all these were significantly higher in GIII compared to the other groups analyzed.

Table 1. Height (cm), stem diameter (mm), number of leaves, robustness coefficient, root dry mass (RDM, g), stem dry mass (SDM, g), leaf dry mass (LDM, g), total dry mass (TDM, g), underground dry mass ($\text{DM}_{\text{underground}}$, g), aerial part dry mass ($\text{DM}_{\text{aerial part}}$, g), ratio between underground and aerial dry mass ($\text{DM}_{\text{underground}}/\text{DM}_{\text{aerial part}}$) in *Allagoptera arenaria* populations with different planting ages (GI – 8 months; GII – 48 months; GIII – 84 months). Data (mean $\pm$ standard deviation) with different letters indicate significant differences considering $p \leq 0.05$ between GI, GII, and GIII, Tukey's test ($n = 12$).

Growth parameters	GI	II	GIII
Height [cm]	15.8 $\pm$ 3.2 ^c	23.1 $\pm$ 3.7 ^b	34.8 $\pm$ 8.4 ^a
Stem diameter [mm]	4.7 $\pm$ 1.0 ^c	13.1 $\pm$ 0.8 ^b	24.9 $\pm$ 1.1 ^a
Number of leaves	2.3 $\pm$ 1.9 ^c	3.7 $\pm$ 3.8 ^b	5.7 $\pm$ 4.5 ^a
Robustness coefficient	3.8 $\pm$ 1.6 ^a	1.9 $\pm$ 0.6 ^b	1.4 $\pm$ 0.3 ^b
RDM [g]	0.3 $\pm$ 0.1 ^c	6.7 $\pm$ 3.9 ^b	19.2 $\pm$ 8.1 ^a
SDM [g]	0.1 $\pm$ 0.0 ^b	3.8 $\pm$ 2.0 ^b	12.8 $\pm$ 9.4 ^a
LDM [g]	0.2 $\pm$ 0.1 ^b	3.5 $\pm$ 2.0 ^b	18.3 $\pm$ 13.0 ^a
TDM [g]	0.5 $\pm$ 0.3 ^c	13.8 $\pm$ 6.4 ^b	48.7 $\pm$ 21.8 ^a
$\text{DM}_{\text{underground}}$	0.3 $\pm$ 0.2 ^b	10.3 $\pm$ 4.9 ^b	34.5 $\pm$ 17.6 ^a
$\text{DM}_{\text{aerial part}}$	0.2 $\pm$ 0.1 ^b	3.5 $\pm$ 2.0 ^b	18.3 $\pm$ 13.0 ^a
$\text{DM}_{\text{underground}}/\text{DM}_{\text{aerial part}}$ ratio	1.5 $\pm$ 0.4 ^b	3.4 $\pm$ 1.4 ^a	2.2 $\pm$ 1.1 ^b

Table 2. Thickness (THI, mm), succulence (SUC, g m⁻²), leaf mass per unit area (LMA, g m⁻²), sclerophylly index (SI, g mm²), relative water content (RWC, %) in *Allagoptera arenaria* populations with different planting ages (GI – 8 months; GII – 48 months; GIII – 84 months). Data (mean ± standard deviation) with different letters indicate significant differences considering $p \leq 0.05$ between GI, GII, and GIII, Tukey's test ($n = 12$).

Leaf traits parameters	GI	II	GIII
THI	0.4 ± 0.04 ^a	0.3 ± 0.05 ^b	0.3 ± 0.02 ^b
SUC	191.0 ± 21.0 ^a	182.5 ± 21.3 ^a	179.7 ± 22.8 ^a
LMA	80.0 ± 10.8 ^b	92.1 ± 16.1 ^b	128.5 ± 24.5 ^a
SI	0.3 ± 0.03 ^b	0.3 ± 0.05 ^b	0.5 ± 0.08 ^a
RWC	82.9 ± 8.5 ^b	87.1 ± 7.1 ^{ab}	90.9 ± 11.8 ^a

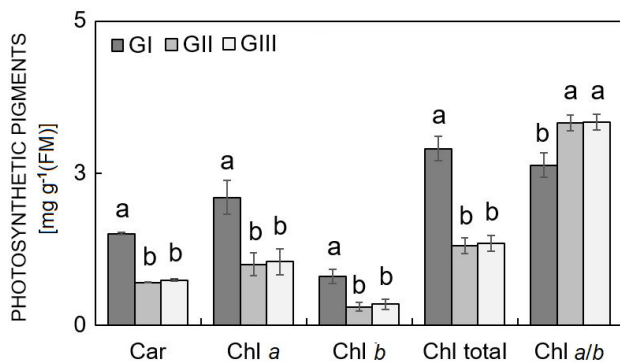


Fig. 3. Carotenoids (Car), chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), chlorophyll total (Chl total), chlorophyll ratio *a/b* (Chl *a/b*) in *Allagoptera arenaria* populations with different planting ages (GI – 8 months; GII – 48 months; GIII – 84 months). Data (mean ± standard deviation) with different letters indicate significant differences considering $p \leq 0.05$ between GI, GII, and GIII; Tukey's test ($n = 12$).

Overall, the GI group presented the highest mean values for photosynthetic pigments: carotenoids, Chl *a*, Chl *b*, and Chl total being statistically significant with the other groups (Fig. 3). On the other hand, groups GII and GIII did not show significant differences between them for photosynthetic pigments but showed a significant difference for Chl *a/b* compared to GI. *A. arenaria* plants that grew up in GII and GIII showed a decrease of approximately 53.3 and 50.6% for the carotenoids contents (Car), 52.3 and 50.4% for the Chl *a*, 62.5 and 57.5% for the Chl *b*, 55.1 and 53.7% for the Chl total, respectively,

compared with *A. arenaria* plants in GI group. However, for the ratio of Chl *a/b*, increases of 26.6 and 26.9% were observed.

The transient fluorescence measured in the leaves of the individuals of *A. arenaria* in each group is shown in Table 3. The JIP-test parameters differed between the groups (GI, GII, and GIII). The initial fluorescence (F_0) did not differ significantly between groups. However, the maximum fluorescence (F_M) values and the maximum quantum yield of primary photochemistry (F_V/F_M) were significantly higher in the GI group compared to the GII and GIII groups. Also, the values of specific energy flows showed that for the total number of photons absorbed (ABS/RC) and for the energy flow captured per reaction center at $t = 0$ (TR_0/RC), there were no significant differences between the groups. However, the transport flow (ET_0/RC) and electron dissipation per reaction center at $t = 0$ (DI_0/RC) were significantly higher in GII and GIII compared to the other groups (Table 3).

In our study, the first axis of PCA (Dim1) explained 61% of the total variation of the data, and the second axis (Dim2) explained 13.6% of the entire variation (Fig. 4). For the GI group, the main components were associated with chlorophyll, photochemical efficiency, THI, SUC, and the robustness coefficient. On the other hand, GII appears as an intermediate group and is associated with the ratio $DM_{\text{underground}}/DM_{\text{aerial part}}$. Finally, the GIII group showed an association with the accumulation of biomass both in the aerial part and in the underground part (growth traits); this group also was more correlated with JIP-test parameters that indicate low use of trapped energy

Table 3. Minimum fluorescence (F_0), maximum fluorescence (F_M), maximum quantum yield of primary photochemistry (F_V/F_M), energy flow of electron absorption (ABS/RC), captured (TR_0/RC), transported (ET_0/RC), and energy dissipation (DI_0/RC) in *Allagoptera arenaria* populations with different planting ages (GI – 8 months; GII – 48 months; GIII – 84 months). Data (mean ± standard deviation) with different letters indicate significant differences considering $p \leq 0.05$ between GI, GII, and GIII, Tukey's test ($n = 12$).

Fluorescence parameters	GI	II	GIII
F_0	583.8 ± 46.2 ^a	550.8 ± 126.8 ^a	531.4 ± 69.3 ^a
F_M	3,206.0 ± 243.9 ^a	2,133.9 ± 373.2 ^b	2,194.0 ± 228.4 ^b
F_V/F_M	0.82 ± 0.02 ^a	0.74 ± 0.03 ^b	0.76 ± 0.01 ^b
ABS/RC	2.1 ± 0.2 ^a	2.2 ± 0.2 ^a	2.4 ± 0.3 ^a
TR_0/RC	1.6 ± 0.1 ^a	1.6 ± 0.2 ^a	1.7 ± 0.2 ^a
ET_0/RC	0.8 ± 0.1 ^b	0.7 ± 0.2 ^b	1.0 ± 0.2 ^a
DI_0/RC	0.4 ± 0.1 ^b	0.6 ± 0.1 ^a	0.7 ± 0.1 ^a

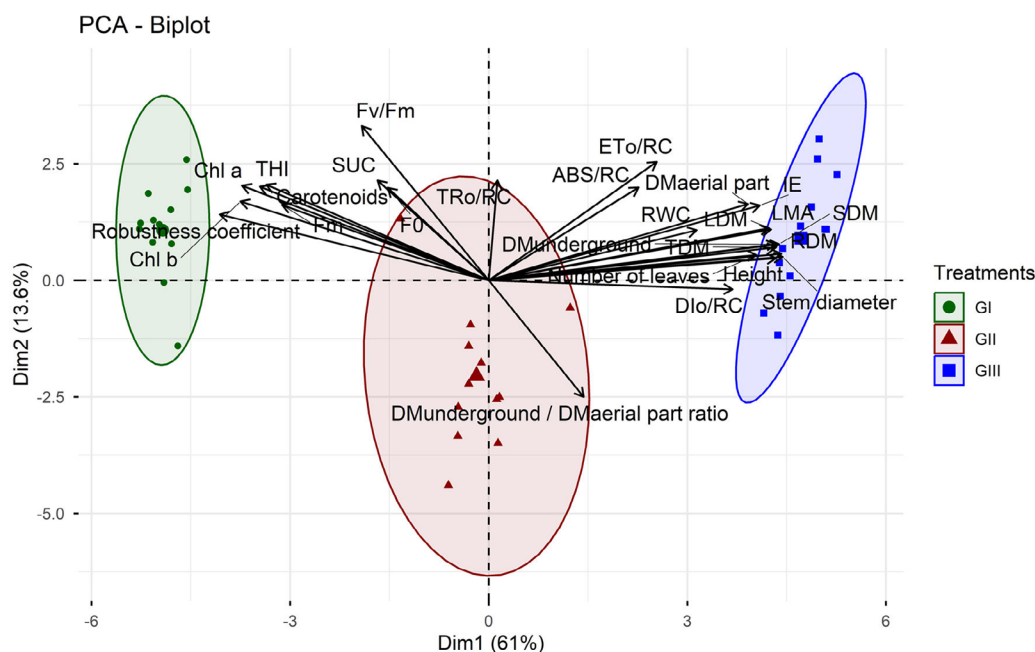


Fig. 4. Principal component analysis (PCA) for the robustness quotient, underground dry mass ($DM_{\text{underground}}$) and aerial part ($DM_{\text{aerial part}}$), the ratio between the subsurface mass and the aerial mass ($DM_{\text{underground}}/DM_{\text{aerial part}}$), leaf mass per leaf area (LMA), maximum photochemical efficiency of PSII (F_v/F_m), electron absorption energy flow per reaction center (ABS/RC), electron capture (TR_o/RC), of electron transport (ET_o/RC), and energy dissipation (DI_o/RC) in populations of *Allagoptera arenaria* with different planting ages (GI – 8 months; GII – 48 months; GIII – 84 months).

(ABS/RC , TR_o/RC , ET_o/RC , DI_o/RC), and the following leaf traits: SI, LMA, and RWC (Fig. 4).

In our study of *A. arenaria* plants, we verified that the youngest individuals (GI) presented the highest values for robustness quotient, indicating resistance and ability to adapt to adverse environmental conditions, and the higher F_v/F_m , reflecting the condition of cultivation in a nursery. The groups GII and GIII were more correlated with the accumulation of biomass and specific energy flows (Fig. 4).

Discussion

A. arenaria plants showed low growth in height, stem diameter, and number of leaves for seven years. This may be linked to the slow growth characteristic of palm species and the environmental characteristics of the planting site, such as dystrophic soils and high light (Rossatto and Franco 2017, Collins *et al.* 2022, Zani *et al.* 2023). Studies conducted with other species of palm trees show that growth is impaired in poor and very bright soils, those of Restinga (Rossatto and Franco 2017, Collins *et al.* 2022, Zani *et al.* 2023). The reduction in the values for the robustness quotient with the longest planting time is a positive aspect and indicates the development of the seedlings since the increase in the number of leaves is not the most characteristic indicator to represent differences in plant growth, as we must consider the constant abscission and emission of this structure (Carvalho *et al.* 2014).

Carvalho *et al.* (2014), when studying the variation of the aboveground biomass of *A. arenaria* (Gomes

O. Kuntze (Arecaceae) in a Palmae shrub community in the Marambaia Restinga-RJ, observed that this palm enriches the soil by increasing organic matter arising from its growth traits. In our study, this statement can be corroborated. In our findings, 7-year-old *A. arenaria* plants showed higher RDM, SDM, LDM, TDM, $DM_{\text{underground}}$, $DM_{\text{aerial part}}$, and $DM_{\text{underground}}/DM_{\text{aerial part}}$. This promotes the accumulation of nutrients and the creation of microclimates, facilitating the establishment of other species, as was observed by Carvalho *et al.* (2014). On the other hand, species like *Euterpe edulis*, growing in full sunlight, showed a significant reduction in the accumulation of dry mass, demonstrating that this condition is no longer ideal for its cultivation (Nakazono *et al.* 2001). The behavior shown by *E. edulis* is found in other palm species where prolonged exposure to high irradiance can be harmful to seedlings that absorb more photons of light than they can use, leading to photoinhibition of photosynthesis or even death due to damage caused to the photosynthetic apparatus by the excess amount of photons of light (Lavinsky *et al.* 2014, Kalaji *et al.* 2016). According to Mendes *et al.* (2022), plants can also change their leaf traits to adapt to resource-scarce environments.

Leaf traits such as thickness and succulence represent the ability to store water in leaf tissues (Melo Júnior and Torres Boeger 2016). These parameters are higher in cultivated plants under high solar radiation (Melo Júnior and Torres Boeger 2016). In *A. arenaria*, thickness (THI) and succulence (SUC) were greater in the GI group, which was younger and cultivated in a nursery, compared to the GII and GIII groups. However, when we checked the relative

water content (RWC), the opposite occurred, indicating that the leaf may be a water reserve organ in field conditions (Mendes *et al.* 2022). The sclerophylly index (SI) was below 0.6 g mm⁻² for all groups, classifying this species as mesophilic concerning its water requirements (Barrs and Weatherley 1962). However, Guerra and Scremin-Dias (2018), when studying leaf traits, sclerophylly, and growth in plant species of a dry environment, found that different species have different adaptations to the dry environment, although not all of them are sclerophyllous.

In our study, the palm *A. arenaria* showed a greater biomass allocation in the underground portion than the aerial part, corroborating the literature, in general, plants invest more in roots when there is less availability of nutrients in the soil. According to Dias *et al.* (2006), Restinga plants, such as *C. hilariana*, can apply a conservative strategy (CAM metabolism), giving a high contribution to biomass stock in this nutrient-poor coastal vegetation. In our findings, 7-year-old *A. arenaria* plants showed a strong correlation between DM_{underground}, DM_{aerial part}, and leaf traits such as LMA, SI, and RWC. The leaf mass per unit area (LMA) also increased with planting age, reflecting environmental conditions at the planting site. Species that occur in environments that are poor in nutrients and/or subject to less water availability tend to have leaves with higher values for LMA, leaf longevity, and efficiency in the use of nutrients (Melo Júnior and Torres Boeger 2016, Mendes *et al.* 2022, Ren *et al.* 2024). Still, a broader approach is needed to understand growth dynamics in resource-scarce environments such as Restinga.

Mustafa *et al.* (2015) observed that Chl *a* content in oil palm tree leaves (*Elaeis guineensis*), young leaves' age stage had higher values than the old stage. Similar findings were obtained in our study, a higher Chl *a*, Chl *b*, and carotenoid content was observed in young *A. arenaria* plants at the age of 8 months (GI). Plants under stress promote physiological adjustments in their metabolism to survive the harsh conditions of the environment (Sharma *et al.* 2020). In our study, the reduction in all photosynthetic pigments was accompanied by an increase in the Chl *a/b* ratio. This is an example of the ecophysiological adjustment that *A. arenaria* is capable of making to adapt and establish itself in environments with such stressful conditions as Restinga.

However, this reduction in our study is merely a necessary adjustment to the survival of *A. arenaria* plants at the age of 3 (GII) and 7 years (GIII) under the environmental conditions of the Restinga. According to Shevela *et al.* (2021), the antenna complex system, also known as light-harvesting complexes (LHCs), consists of protein complexes spatially organized around light-absorbing molecules, such as chlorophylls or phycobilins, and other accessory pigments. The lower pigments in *A. arenaria* plants (GII and GIII) are important to reduce the spectrum of visible light absorbed by the antenna system and avoid damage to photosystems. Reduction in the chlorophyll content can contribute to the protection of photosynthetic machinery against the effects of high light radiation as it minimizes the light collection capacity and,

consequently, the PSII excitation (Shevela *et al.* 2021). One way to better understand these reactions is through chlorophyll *a* fluorescence transient (Strasser *et al.* 2004).

The highest F_M, observed in the GI group, indicates a greater stock of electron acceptors in the PSII than in the GII and GIII groups (Strasser *et al.* 2004, Kalaji *et al.* 2016, Bussotti *et al.* 2020). The plants in the GII and GIII groups showed a reduction in the maximum photochemical efficiency of the PSII (F_v/F_M), which is the most frequently used fluorescence parameter, and it is used in several studies to characterize the photosynthetic efficiency in plants, mainly under stress conditions. These parameters are good indicators of the effect of environmental stress on the photosynthetic apparatus (Kalaji *et al.* 2016, Bussotti *et al.* 2020). In our study, the results indicate the occurrence of a chromatic adaptation of *A. arenaria* that possibly helps its photosynthetic performance. The congener species *Allagoptera campestris* can also survive and perform well in sites disturbed by photosynthesis and leaf plasticity (Lopes *et al.* 2024).

Björkman and Demmig (1987) compared chlorophyll fluorescence characteristics for 44 species of vascular plants; from their findings, they claim that values of F_v/F_M between 0.75 and 0.85 demonstrate no damage in photochemical reactions through an efficient conversion of light energy at the PSII level. Overall, leaves have typical F_v/F_M values around, or just below, 0.8; for shadow sheets, these values are between 0.83 and 0.85 with a difference of around 4% (Critchley 1998, Kalaji *et al.* 2016). The authors also reported that at values below 0.725, the leaves would be subjected to photoinhibitory damage, which was not observed here among the groups analyzed. In our study, the decreases observed in F_v/F_M certainly cause an increase in energy dissipation as heat, which results in the conversion of active PSII RCs into heat dissipation centers (Pinheiro *et al.* 2023). A fact observed in the individuals of the groups GII and GIII, which also presented the highest values for the flow of transport and energy dissipation. The photosynthetic adjustments observed in the energy flow of electron absorption (ABS/RC), captured (TR₀/RC), transported (ET₀/RC), and energy dissipation (DI₀/RC) in *A. arenaria* (GIII) can explain the current geographic distribution of this species in Restinga areas.

Restinga ecosystems are affected by several abiotic factors, such as sandy soil (Ren *et al.* 2024), high light intensity (Hwang and Choo 2017, Mendes *et al.* 2025), high temperatures (Zani *et al.* 2023, Ressaissi *et al.* 2025), high salinity (Vineeth *et al.* 2023), wind intensity (Menezes *et al.* 2025), and water seasonality (Zani *et al.* 2023). These combined factors create an inhospitable environment that shapes vegetation adaptation, enabling plants to establish themselves under these conditions (Zani *et al.* 2023, Menezes *et al.* 2025). In our study, groups GII and GIII of *A. arenaria* were exposed to all these factors. Therefore, we believe that the combination of these abiotic factors, common to virtually all Restinga environments, could explain the observed results in the specific energy fluxes per reaction center. According to Kalaji *et al.* (2018), most plants dissipate excess excitation

energy by heat (DI_0/RC), alongside a downregulation of PSII activity (F_v/F_m). This serves to protect the photosynthetic apparatus against abiotic environmental stressors that could otherwise cause damage to it.

Gessler *et al.* (2008), when comparing the ecophysiological performance of *C. hilariana*, *Andira legalis*, and *A. arenaria*, state that a variety of physiological adaptations, including F_v/F_m , ϕNPQ (quantum yield of regulatory light-induced nonphotochemical quenching), ETR (electron transport rate), PAR (photosynthetically active radiation), WUE (water-use efficiency from gas exchange), soluble carbohydrates, and photosynthetic light-response curves of net CO_2 uptake, as well as morphological adaptations, are related to the carbon balance. The authors further suggest that water and nitrogen availability may have favored the success of these plants in migrating from the mesophilic Atlantic Forest to colonize the extreme Restinga habitats. Our study corroborates the authors' findings for *A. arenaria* and further reveals that plant age is a determining factor for the successful establishment of this species in Restinga ecosystems.

The principal component analysis (PCA) can help us identify patterns and relationships in complex data, detecting key variations that may not be evident from the original parameters (Jolliffe and Cadima 2016, Volponi *et al.* 2022, Martins *et al.* 2024, Mendes *et al.* 2025). In fact, over time, individuals tend to incorporate more biomass, but due to the environmental conditions, the biomass accumulation in plant tissues can be higher or lower depending on the available resources (Hwang and Choo 2017, Zani *et al.* 2023). Plants adapt to their light environment by adjusting their photosynthetic apparatus, and the response to this adaptation is also reflected in the growth of the plant (Lopes *et al.* 2024). Thus, growth efficiency is related to the plant's ability to adapt to the intensity of light radiation within the environment in which it develops (Pinheiro *et al.* 2023). Nakazono *et al.* (2001) also observed these relationships when studying the initial growth of *E. edulis* at 2% and 6% shading and in full sun, that the plants in the most shaded environments had lower TDM and lower $DM_{\text{underground}}/DM_{\text{aerial part}}$ when compared to plants developed in full light. Also, the plasticity in the ecophysiology of plants may favor their survival in the face of climate change (Volponi *et al.* 2022). Thus, the resilience and physiological plasticity observed in *A. arenaria* may explain not only its establishment in Restinga environments but also that of other species that depend on it for their establishment.

Conclusions: In our research, it was possible to understand more about the growth dynamics of the species *A. arenaria* in a Restinga restoration area with varying planting ages. Our results indicated that this palm tree presents considerable ecophysiological plasticity, adapting its photosynthetic system to extreme environmental conditions, which favors its survival and progressive growth. The research demonstrated that the youngest plants, aged 8 months, presented a higher photosynthetic efficiency, evidenced by high contents of pigments and better photosynthesis performance. However, over time

(7-year-old plants), a greater accumulation of biomass was observed in the roots and stem, which suggests an adaptive strategy for soil conditions with few nutrients, high heat, and solar radiation, typical characteristics of Restinga. The most relevant results indicate that *A. arenaria* can successfully establish itself in challenging environments, playing a crucial role in ecological succession and facilitating the growth of other species in Restinga areas.

References

- Abebe A.M., Kim Y., Kim J. *et al.*: Image-based high-throughput phenotyping in horticultural crops. – *Plants-Basel* **12**: 2061, 2023.
- Alvares C.A., Stape J.L., Sentelhas P.C. *et al.*: Köppen's climate classification map for Brazil. – *Meteorol. Z.* **22**: 711-728, 2013.
- Barrs H.D., Weatherley P.E.: A re-examination of the relative turgidity technique for estimating water deficits in leaves. – *Aust. J. Biol. Sci.* **15**: 413-428, 1962.
- Björkman O., Demmig B.: Photon yield of O_2 evolution and chlorophyll fluorescence characteristics at 77 K among vascular plants of diverse origins. – *Planta* **170**: 489-504, 1987.
- Bussotti F., Gerosa G., Digrado A., Pollastrini M.: Selection of chlorophyll fluorescence parameters as indicators of photosynthetic efficiency in large scale plant ecological studies. – *Ecol. Indic.* **108**: 105686, 2020.
- Carvalho D.C. de, Pereira M.G., Menezes L.F.T. de: [Biomass and nutrient input by *Allagoptera arenaria* in Restinga da Marambaia, Rio de Janeiro, RJ.] – *Floresta* **44**: 349-358, 2014. [In Portuguese]
- Carvalho G.A., Vargas L.B., Dias H.M.: [Structure and composition of the woody component of two Restinga forests in Caravelas, Bahia, Brazil.] – *Paubrasilia* **8**: e196s, 2025. [In Portuguese]
- Collins C., Wardle D.A., Andersen K.M.: Palm species traits determine soil nutrient effects on seedling performance. – *Front. For. Glob. Change* **5**: 733636, 2022.
- Critchley C.: Photoinhibition. – In: Raghavendra A.S. (ed.): *Photosynthesis: A Comprehensive Treatise*. Pp. 264-272. Cambridge University Press, Cambridge 1998.
- de la Riva E.G., Olmo M., Poorter H. *et al.*: Leaf mass per area (LMA) and its relationship with leaf structure and anatomy in 34 Mediterranean woody species along a water availability gradient. – *PLoS ONE* **11**: e0148788, 2016.
- Dias A.T.C., de Mattos E.A., Vieira S.A. *et al.*: Aboveground biomass stock of native woodland on a Brazilian sandy coastal plain: Estimates based on the dominant tree species. – *Forest Ecol. Manag.* **226**: 364-367, 2006.
- Gessler A., Nitschke R., de Mattos E.A. *et al.*: Comparison of the performance of three different ecophysiological life forms in a sandy coastal restinga ecosystem of SE-Brazil: a nodulated N_2 -fixing C_3 -shrub (*Andira legalis* (Vell.) Toledo), a CAM-shrub (*Clusia hilariana* Schltdl.) and a tap root C_3 -hemicryptophyte (*Allagoptera arenaria* (Gomes) O. Ktze.). – *Trees* **22**: 105-119, 2008.
- Gong H., Yang M., Wang C., Tian C.: Leaf phenotypic variation and its response to environmental factors in natural populations of *Eucommia ulmoides*. – *BMC Plant Biol.* **23**: 562, 2023.
- Guerra A., Scremin-Dias E.: Leaf traits, sclerophylly and growth habits in plant species of a semiarid environment. – *Braz. J. Bot.* **41**: 131-144, 2018.
- Hwang J.S., Choo Y.S.: Solute patterns and diurnal variation of photosynthesis and chlorophyll fluorescence in Korean coastal

- sand dune plants. – *Photosynthetica* **55**: 107-120, 2017.
- Jolliffe I.T., Cadima J.: Principal component analysis: a review and recent developments. – *Philos. T. Roy. Soc. A* **374**: 20150202, 2016.
- Kalaji H.M., Jajoo A., Oukarroum A. *et al.*: Chlorophyll *a* fluorescence as a tool to monitor physiological status of plants under abiotic stress conditions. – *Acta Physiol Plant.* **38**: 102, 2016.
- Kalaji H.M., Rastogi A., Živčák M. *et al.*: Prompt chlorophyll fluorescence as a tool for crop phenotyping: an example of barley landraces exposed to various abiotic stress factors. – *Photosynthetica* **56**: 953-961, 2018.
- Kluge M., Ting I.P.: *Crassulacean Acid Metabolism: Analysis of an Ecological Adaptation*. Pp. 212. Springer, Berlin-Heidelberg 1978.
- Lavinsky A.O., Gomes F.P., Mielke M.S., França S.: Photosynthetic acclimation in shade-developed leaves of *Euterpe edulis* Mart (Arecaceae) after long-term exposure to high light. – *Photosynthetica* **52**: 351-357, 2014.
- Lichtenthaler H.K.: Chlorophylls and carotenoids: Pigments of photosynthetic biomembranes. – *Method. Enzymol.* **148**: 350-382, 1987.
- Lopes N.G.M., Campostrini E., França M.G.C.: Residues from the Fundão Dam accident in Brazil and their effects on photosynthetic efficiency of two restinga plant species. – *Arch. Environ. Contam. Tox.* **87**: 159-174, 2024.
- Martins J.P.R., Wawrzyniak M.K., Kalembe E.M. *et al.*: Differential morphophysiological and epigenetic responses during in vitro multiplication of *Quercus robur* depending on donor age and plant growth regulators. – *Plant Cell Tiss. Org. Cult.* **159**: 62, 2024.
- Melo Júnior J.C.F., Torres Boeger M.R.: [Leaf traits and plastic potential of plant species in a light-edaphic gradient from a Restinga in southern Brazil.] – *Acta Biol. Colomb.* **21**: 51-62, 2016.
- Mendes M.M., Pinheiro A.C.R., Pires F.R. *et al.*: Photosynthesis and leaf traits of tree species influenced by green manure associated with soil treatments. – *Commun. Soil Sci. Plant Anal.* **53**: 2064-2081, 2022.
- Mendes M.M., Ribeiro I.F., Santos V.F.D. *et al.*: Green manure can be an auxiliary factor against dynamic photoinhibition in *Dalbergia ecastophyllum* (L.) young trees in areas impacted by mining. – *Photosynthetica* **63**: 129-139, 2025.
- Menezes L.F.T. de, Pugnaire F.I., Matallana G. *et al.*: Disentangling plant establishment in sandy coastal systems: biotic and abiotic factors that determine *Allagoptera arenaria* (Arecaceae) germination. – *Acta Bot. Bras.* **32**: 12-19, 2018.
- Menezes L.F.T. de, Souza M. da C., Conde M.M.S. *et al.*: [Relationship between structure and topography in a dune forest in the Restinga da Marambaia, Rio de Janeiro state, Brazil.] – *Pau-brasil* **8**: e214s, 2025. [In Portuguese]
- Moraes R.M., Martins R.C.: *Allagoptera arenaria* (Gomes) Kuntze. Flora do Brazil. Botanical Garden of Rio de Janeiro, 2017. [In Portuguese] Available at: <http://reflora.jbrj.gov.br/reflora/floradobrasil/FB15666>.
- Mustafa N., Ya'acob N., Latif Z.A., Yusof A.L.: Quantification of oil palm tree leaf pigment (chlorophyll *a*) concentration based on their age. – *J. Teknol.* **75**: 129-134, 2015.
- Nakazono E.M., Costa M.C.D., Futatsugi K., Paulilo M.T.S.: [Early growth of *Euterpe edulis* Mart. in different light environments.] – *Braz. J. Bot.* **24**: 173-179, 2001. [In Portuguese]
- Pereira O.J., Menezes L.F.T.: [Restinga in Espírito Santo: Vegetation, Flora and Geographic Distribution of Species.] Pp. 19-20. Rupestre, Belo Horizonte 2023. [In Portuguese]
- Pinheiro C.L., Zampirolo J.B., Mendes M.M. *et al.*: Exposition of three *Cattleya* species (Orchidaceae) to full sunlight: effect on their physiological plasticity and response to changes in light conditions. – *Ornam. Hortic.* **29**: 57-67, 2023.
- R Core Team: *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna 2023. Available at: <https://www.R-project.org>.
- Reich P.B.: The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. – *J. Ecol.* **102**: 275-301, 2014.
- Ren H.R., Tao L., Ren J., Ren X.C.: Chlorophyll and growth performance of biological sand-fixing materials inoculated on sandy desert surface. – *Photosynthetica* **62**: 213-220, 2024.
- Ressaissi N., Mnafigui W., Maiza N. *et al.*: Synergistic effects of drought and heat stress on *Medicago truncatula*: understanding growth response and photosynthetic mechanisms. – *Photosynthetica* **63**: 151-161, 2025.
- Ribeiro I.F.: Facilitation between plants and the use of facilitating species as an ecological restoration strategy. – *Revista Científica Multidisciplinar Núcleo do Conhecimento* **01**: 151-169, 2023.
- Rossatto D.R., Franco A.C.: Expanding our understanding of leaf functional syndromes in savanna systems: the role of plant growth form. – *Oecologia* **183**: 953-962, 2017.
- Sharma A., Kumar V., Shahzad B. *et al.*: Photosynthetic response of plants under different abiotic stresses: a review. – *J. Plant Growth Regul.* **39**: 509-531, 2020.
- Shevela D., Kern J.F., Govindjee G. *et al.*: Photosystem II. – In: *Encyclopedia of Life Sciences*. Pp. 1-16. Wiley, Hoboken 2021.
- Silva T.R. da, Antunes T.J., Magnago L.F.S.: [Soil influence on species richness and composition along a Restinga phytophysiological gradient in Southeastern Brazil.] – *Pau-brasil* **8**: e206s, 2025. [In Portuguese]
- Strasser R.J., Tsimilli-Michael M., Srivastava A.: Analysis of the chlorophyll *a* fluorescence transient. – In: Papageorgiou G.C., Govindjee (ed.): *Chlorophyll *a* Fluorescence: A Signature of Photosynthesis*. Advances in Photosynthesis and Respiration. Pp. 321-362. Springer, Dordrecht 2004.
- Vineeth T.V., Krishna G.K., Pandesha P.H. *et al.*: Photosynthetic machinery under salinity stress: Trepidations and adaptive mechanisms. – *Photosynthetica* **61**: 73-93, 2023.
- Volponi F.C., Santos Junior R.N., Barreto F.M. *et al.*: The environmental gradient influences the concentrations of carbon compounds in the biomass of *Protium icariba* (DC.) Marchand in restinga area. – *Sci. For.* **50**: e3885, 2022.
- Zani L.B., Duarte I.D., Falqueto A.R. *et al.*: Changes in growth and reproductive phenology of *Allagoptera arenaria* (Arecaceae) under climate change scenarios. – *An. Acad. Bras. Ciênc.* **95**: e20220241, 2023.