Physiological and biochemical plasticity as a driver of invasiveness in Syzygium jambos (L.) Alston

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Abstract

Purpose

This study explores the physiological and biochemical plasticity of *Syzygium jambos*, an invasive tree species native to Tropical Asia, under contrasting light intensities, fertilization regimes, and water availability. The aim is to elucidate the mechanisms underlying its ecological success and to address how these mechanisms may inform strategies for managing invasive plants under changing climate scenarios.

Methods

A factorial experiment was conducted using seedlings grown in two substrates – control (soil and sand), and organic amendment (aged bovine manure) – and exposed them to three light environments: very low radiation (VLR), low radiation (LR), and high radiation (HR). Experiments were conducted under controlled conditions at the Federal University of Juiz de Fora (Minas Gerais, Brazil). Physiological assessments included gas exchange, chlorophyll *a* fluorescence, antioxidant enzyme activities, osmotic stress markers, and foliar nutrient profiling.

Results

Plants under HR exhibited elevated protein content and lipid peroxidation levels, alongside reduced superoxide dismutase (SOD) and polyphenol oxidase (PPO) activities. Organic fertilization enhanced nutrient availability and modulated stress responses. Despite reduced photosynthetic rates under HR, *S. jambos* maintained photochemical efficiency and water-use balance, with rapid recovery following drought stress. Nutrient analyses revealed significant differences between control and fertilized plants, with fertilized seedlings showing elevated levels of nitrogen (N), phosphorus (P), and potassium (K).

Conclusion

These findings reveal that *S. jambos* possesses high ecophysiological plasticity, enabling it to adapt to heterogeneous tropical environments and recover from abiotic stress. Such versatility likely contributes to its invasive potential and ecological dominance. By linking functional traits to invasion success, this study provides a predictive framework for managing exotic species and assessing their impact under climate variability.

Introduction

Invasive plant species are among the most transformative agents in tropical ecosystems, often reshaping community structure and ecosystem function. Their ecological success is frequently

attributed to their ability to tolerate and thrive under a wide range of environmental conditions (Moura et al. 2021; Hernández-Fernández et al. 2025). *Syzygium jambos* (L.) Alston (Myrtaceae), commonly known as rose apple, exemplifies this adaptability. Native to Tropical Asia, this fast-growing tree species can exceed 12 meters in height and is widely recognized for its capacity to colonize both disturbed and undisturbed tropical habitats. Its rapid establishment in open areas and mature forests has led to significant alterations in native plant assemblages, particularly through the formation of dense canopies that suppress light-dependent species (Horvitz et al. 1998; Aide et al. 2000; Lugo 2004; Brown et al. 2006; Cramer et al. 2008; Morales 2020).

In tropical forests, where light is a limiting and heterogeneously distributed resource, the ability to optimize light use is crucial for plant performance. Light availability drives key physiological processes, including photosynthesis, antioxidant metabolism, and nutrient uptake (Valladares et al. 2000; dos Anjos et al. 2015; Liu et al. 2016). The interplay between light intensity and soil nutrient availability can significantly shape competitive interactions among species, particularly in environments where resource partitioning is crucial for growth and survival (Ferreira et al. 2009). While native species have evolved strategies to cope with such variability, invasive plants often exhibit enhanced phenotypic plasticity, enabling them to outperform native flora under fluctuating conditions (Davidson et al. 2011; Chen et al. 2024).

Invasive plants also tend to exhibit physiological and biochemical traits that enhance their resilience under environmental stress, contributing to their competitive success. Traits such as increased photosynthetic efficiency, flexible stomatal regulation, and robust antioxidant systems enable these species to maintain functional performance across diverse light, nutrient, and water conditions (McAlpine et al. 2008; Pintó-Marijuan and Munné-Bosch 2013; Sanders et al. 2025). Chlorophyll fluorescence is a sensitive tool for assessing photochemical efficiency and has been widely used to assess stress responses in invasive taxa (Zhou et al. 2024). Additionally, the activity of antioxidant enzymes – including superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and polyphenol oxidase (PPO) – plays a central role in mitigating oxidative damage caused by reactive oxygen species (ROS), which tend to accumulate under abiotic stress such as drought, nutrient limitation, and excess light (Wang et al. 2023). These physiological mechanisms, when coupled with phenotypic plasticity, may explain the ability of *S. jambos* to persist and dominate in diverse tropical environments.

Beyond ecological disruption, biological invasions impose substantial economic costs. A global synthesis estimated that the cumulative cost of invasive species reached at least USD 1.28 trillion between 1970 and 2017, with annual costs tripling every decade and peaking at USD 162.7 billion in 2017 alone (Diagne et al. 2021). Notably, damage-related expenses – such as loss of ecosystem services and agricultural productivity – far exceed management investments, particularly for plant taxa, which remain underrepresented in economic assessments. In Brazil, the economic burden of biological invasions has recently been quantified for the first time, revealing a minimum cost of USD 105.53 billion over 35 years, with an overwhelming 99% of this amount attributed to damages and losses rather than management efforts (Adelino et al. 2021). Given that only 16 invasive species were included in this

estimate – out of at least 460 recognized invaders – the actual economic impact is likely much higher. An updated national inventory has since identified 444 invasive non-native species in Brazil, including 188 plants, with trees being the most frequent life form among them (Zenni et al. 2024). This reinforces the relevance of investigating arboreal invaders such as *S. jambos*.

These findings underscore the urgency of understanding the physiological mechanisms that underpin invasion success, especially in species like *S. jambos*, whose ecological dominance is matched by its potential economic impact. This study aimed to investigate the physiological and biochemical traits of *S. jambos* under varying environmental conditions, in order to identify the features most closely associated with its invasive behavior. By linking ecophysiological performance to invasion potential, we seek to contribute to a more predictive framework for managing exotic species in tropical forest ecosystems.

Materials and Methods

Plant material and experimental design

Fruits of *S. jambos* were collected from two specimens at the Institute of Biological Sciences (ICB) of the Federal University of Juiz de Fora (UFJF), Minas Gerais, Brazil. Seeds were extracted, placed in Petri dishes with filter paper, and moistened with 20 mL of distilled water to induce imbibition and germination. Germinated seeds were transplanted into 200 mL plastic cups containing Plantmax Hortaliças HT® substrate, kept in shade, and irrigated twice weekly. All seeds developed into seedlings, which were standardized by height (10–12 cm) and leaf count (8–10 leaves) prior to experimental setup.

Seedlings were transferred to 25 L pots filled with one of three substrate treatments: 1) control – soil and sand (3:2, v/v); 2) bovine manure – soil, sand, and aged bovine manure (3:2:1, v/v/v); and 3) chemical fertilizer – soil and sand (3:2, v/v) + 50 g of Forth Frutas® (12% N, 5% P, 15% K). The pots were placed in a greenhouse under shade conditions (4% of ambient light, ~ 100 µmol photons m^{-2} s^{-1} of photosynthetically active radiation – PAR), achieved using Sombrite® screens of different mesh densities. Full sunlight (~ 2,400 µmol photons m^{-2} s^{-1} of PAR on clear days) was used as the reference for 100% irradiance. Plants remained in this environment for ~ 8 months to allow growth and tissue development. All plants in the chemically fertilized treatment died during this period, leaving only the control group and the bovine manure groups.

For the new experimental setup, plants from these two groups were standardized by height (30–50 cm, mean of 40 cm) and the number of leaves (12–18 leaves, mean of 16). They were then assigned to three light treatments: very low radiation (VLR) – 4% of ambient light (~ 100 µmol photons m^{-2} s^{-1} PAR); low radiation (LR) – 9% of ambient light (~ 220 µmol photons m^{-2} s^{-1} PAR); and high radiation (HR) – full sunlight (~ 2,400 µmol photons m^{-2} s^{-1} PAR). The experiments were conducted using a completely randomized factorial design (2 fertilization types × 3 light levels), totaling six treatments. All plants were irrigated at least twice a week and maintained under these conditions for 11 months, after which leaf samples were collected for biochemical analysis.

Physicochemical properties and fertility assessment of substrates

Prior to the experiment, random samples of the three substrates were collected to assess particle size distribution and nutrient composition. After 11 months of plant growth, three samples from each of the six final treatments were collected and analyzed for their nutritional and chemical attributes. Nutrient extraction followed standard protocols: Mehlich 1 (0.05 M HCl + 0.0125 M H_2SO_4) for K, P, Zn, Fe, Mn, and Cu; 1M KCl for Ca, Mg, and Al; hot water for B; monocalcium phosphate in acetic acid for S; pH in SMP buffer solution for potential acidity (H + Al). Additional parameters included: pH in water (1:2.5), sum of exchangeable bases (SB), cation exchange capacity at pH 7.0 (T), effective cation exchange capacity (t), base saturation index (V), aluminum saturation index (m), organic matter (OM; via oxidation with 4N $Na_2Cr_2O_7$ + 10N H_2SO_4), and remaining phosphorus (P-Rem).

Biochemical and enzymatic analysis

Crude extracts for total protein and enzymatic activity determinations – superoxide dismutase (SOD; EC 1.15.1.1), catalase (CAT; EC 1.11.1.6), peroxidase (POD; EC 1.11.1.7), and polyphenol oxidase (PPO; EC 1.10.3.1, EC 1.10.3.2, and EC 1.14.18.1) – were obtained by macerating four leaf discs (0.8 cm^2; 0.07–0.1 g each) in liquid nitrogen, followed by homogenization in 5 mL of buffer containing 0.1 M potassium phosphate (pH 6.8), 0.1 mM EDTA, and 1 mM PMSF (Peixoto et al. 1999). The homogenate was filtered through gauze and centrifuged (10,000 *g*, 15 min, 4°C). Soluble protein content was determined using the method of Lowry et al. (1951), with the Folin-Ciocalteu reagent. The protein concentration in each replicate was used to calculate the specific activity of the enzymes. SOD activity was measured according to Del Longo et al. (1993), with reactions conducted at 25°C under illumination by a 15W fluorescent lamp (Giannopolitis and Ries 1977). Photoreduction of nitro blue tetrazolium (NBT) was monitored at 560 nm, and one unit of activity was defined as the amount of enzyme required to inhibit 50% of NBT reduction (Beauchamp and Fridovich 1971). CAT activity was measured by monitoring H_2O_2 decomposition at 240 nm (Havir and McHale 1987), using a molar extinction coefficient of 36 M^{-1} cm^{-1} (Anderson et al. 1995). POD and PPO activities were estimated according to Kar and Mishra (1976), with absorbance measured at 420 nm. A molar extinction coefficient of 2.47 mM^{-1} cm^{-1} was used for calculations (Chance and Maehley 1954). Proline quantification was performed according to Bates et al. (1973). Six leaf discs (0.8 cm^2; 0.1–0.16 g each) were macerated in liquid nitrogen and homogenized in 10 mL of 3% (w/v) sulfosalicylic acid, then filtered through Whatman No. 2 paper. For each sample, 2 mL of filtrate was combined with 2 mL of acidic ninhydrin and 2 mL of acetic acid, then incubated at 100°C for 1 hour. After cooling in an ice bath, the chromophore was extracted with toluene and separated by decantation. Absorbance was measured at 520 nm, and proline concentration was determined using a standard curve. Hydrogen peroxide (H_2O_2) content was determined using a modified ferrous ammonium sulfate/xylenol orange (FOX) assay, with absorbance measured at 560 nm (Gay and Gebicki 2000). Approximately 0.2 g of leaf tissue (7–11 disks, 0.8 cm^2 each) was used, and H_2O_2 concentration was calculated from a standard curve prepared with authentic H_2O_2 solutions. Superoxide anion (O_2^{-}.)

content was measured following Mohammadi and Karr (2001), with modifications. Leaf samples (0.3 g; 40 discs, 0.2 cm² each) were incubated in reaction medium, and superoxide production was quantified based on adrenochrome formation (Misra and Fridovich 1971), using a molar extinction coefficient of 4.0 x 10^3 M^{-1} cm^{-1} (Boveris 1984). Lipid peroxidation was assessed by quantifying malondialdehyde (MDA) produced after reaction with thiobarbituric acid (TBA) (Cakmak and Horst 1991). Approximately 0.2 g of leaf tissue (25–38 disks, 0.2 cm^2 each) was used per sample. Absorbance was recorded at 532 and 600 nm. MDA-TBA concentration was calculated using a molar extinction coefficient of 155 mM^{-1} cm^{-1} (Heath and Packer 1968).

Gas exchange and chlorophyll fluorescence

Gas exchange and chlorophyll *a* fluorescence measurements were conducted after 11 months of plant exposure to different light environments. Analyses were performed between 08:00 and 12:00 h using an infrared gas analyzer (LI-6400XT, Li-Cor, Lincoln, NE, USA) with an LED fluorescence chamber (6400-02B, Li-Cor). Fully expanded, healthy leaves from the fourth or fifth node were selected for use. The leaf chamber was set to a photon flux density of 1,000 µmol photons m^{-2} s^{-1} and ambient CO_2 concentration (~ 400 µmol mol^{-1}). Leaf temperatures averaged 29 ± 1°C under HR and 34 ± 2°C under VLR and LR. Measured parameters included net photosynthetic rate (A), transpiration rate (E), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i). Derived indices estimated were the ratio of intercellular to external CO_2 concentration (C_i/C_a), water-use efficiency (WUE = A/E) (Ou et al. 2015), intrinsic WUE (WUE_{int} = A/g_s), and carboxylation efficiency (A/C_i). Fluorescence was assessed on light-adapted leaves exposed to a saturating pulse (6,000 µmol photons m^{-2} s^{-1}, 0.8 s) to determine steady-state fluorescence (F_s) and maximum fluorescence under light (F_m'). Far-red light was then applied to measure the minimum fluorescence of light-adapted leaves (F_o'). Based on Genty et al. (1989), the following parameters were calculated: effective quantum yield of PSII electron transport (Φ_{PSII} = (F_m' – F_s)/F_m'), efficiency of excitation energy capture by open PSII reaction centers (F_v'/F_m' = (F_m' – F_o')/F_m'), the photochemical quenching (q_P = (F_m' – F_s)/(F_m' – F_o')), and the apparent electron transport rate (ETR = Φ_{PSII} × PAR × 0.5 × 0.84, where PAR is the photosynthetically active radiation incident on the leaf, 0.5 represents the fraction of photons allocated to photosystem I and photosystem II, and 0.84 is the average fraction of incident light absorbed by the leaf).

Leaf nutrient contents

Macro- and micronutrient contents in leaves were determined at the end of the experiments. Samples were dried at 65°C to constant weight, ground, and analyzed using standardizing methodologies. The nutrients evaluated included N, P, K, Ca, Mg, S, B, Cu, Mn, Zn, and Fe. Nitrogen (N) content was determined using the sulfuric digestion method followed by quantification via the Kjeldahl procedure. For K, S, Fe, Ca, Zn, Mg, Cu, and Mn, tissue samples were digested in a nitric-perchloric solution (3:1; v:v).

Boron (B) was extracted using a hydrochloric acid (HCl) solution. Nutrient concentrations were determined by atomic absorption spectrophotometry (for K, Ca, Mg, Fe, Cu, Mn, and Zn) and colorimetric spectrophotometry (for P, S, and B).

Drought stress experiment

After 11 months of growth, plants from the control group under the two most contrasting light conditions – VLR and HR – were selected for a drought stress experiment. These plants were subjected to a progressive dehydration protocol, in which irrigation was withheld for 10 or 20 days, while a well-watered control group continued to receive daily irrigation. This design resulted in six distinct treatments. Following the drought phase, all plants were rehydrated and maintained under optimal watering conditions.

Leaf samples were collected at the end of each drought period (10 or 20 days without irrigation) and one week after rehydration for physiological assessments. These included measurements of gas exchange parameters and antioxidant enzyme activities, as previously described. Soil moisture and temperature were continuously monitored throughout the experiment. Predawn leaf water potential was determined during both dehydration and rehydration phases using a Scholander-type pressure chamber, as described by Turner (1988).

Statistical analysis

Data were first tested for homogeneity of variances (Cochran-Bartlett test) and normality (Lilliefors). Once these assumptions were met, data were subjected to analysis of variance (ANOVA), and means were grouped using the Scott-Knott test at a 5% probability level, performed with SAEG software (version 9.1).

Results

Chemical analyses of substrates

Before the cultivation, the substrate pH was near neutral in the control group (6.9) and slightly acidic in the bovine manure-fertilized group (6.2). In contrast, the chemically fertilized substrate was much more acidic (pH 4.5) (Table 1). Potential acidity (H + Al) was also markedly higher in the chemically fertilized material – 4.5 times greater than the control and 3.6 times greater than the manure-fertilized group. Macronutrient (K, P, Ca, Mg, S) and micronutrient (Mn, B) levels were highest in the chemically fertilized substrate, followed by the manure-fertilized and control groups. Fe and Cu contents decreased in the order: chemically fertilized, control, and manure fertilized. Zn and organic matter (OM) were most abundant in the manure-fertilized substrate. Despite differences in P levels, P-Rem and base saturation (V) were similar across treatments. Confirmed by the aluminum saturation index (m), Al was detected only in the chemically fertilized substrate. Although classified as different soil types – medium texture

(control and chemical) and clayey texture (manure) – the proportions of clay, silt, and sand were similar among them, with sand predominating.

Table 1
Chemical characterization and granulometry of substrates used in the experiment. Parameters: pH of the substrates (pH); contents of potassium (K), phosphorus (P), calcium (Ca), magnesium (Mg), aluminum (Al), zinc (Zn), iron (Fe), manganese (Mn), copper (Cu), boron (B), sulfur (S), remaining phosphorus (P-Rem), organic matter (OM); potential acidity (H + Al); sum of exchangeable bases (SB), effective cation exchange capacity (CEC) (t), and CEC at pH 7.0 (T); base saturation index (V) and aluminum saturation index (m); clay, silt, and sand. Soil type 2 – medium texture; soil type 3 – clayey texture

Parameter	Substrate		
	Control	Chemical fertilization	Bovine manure
pH	6.9	4.5	6.2
K (mg dm^{-3})	30.00	720.00	396.00
P (mg dm^{-3})	10.24	121.49	18.58
Ca (cmol dm^{-3})	4.10	12.71	5.30
Mg (cmol dm^{-3})	1.00	4.58	2.20
Al (cmol dm^{-3})	0.00	0.20	0.00
Zn (mg dm^{-3})	26.41	58.29	102.24
Fe (mg dm^{-3})	82.67	96.36	66.68
Mn (mg dm^{-3})	33.22	67.55	59.86
Cu (mg dm^{-3})	0.77	5.96	0.68
B (mg dm^{-3})	0.17	0.84	0.50
S (mg dm^{-3})	37.91	135.64	91.28
P-Rem (mg L^{-1})	15.94	12.93	14.17
O.M (dag kg^{-1})	1.87	2.61	3.84
H + Al (cmolc dm^{-3})	1.55	7.04	1.94
SB (cmolc dm^{-3})	5.18	19.14	8.52
t (cmolc dm^{-3})	5.18	19.34	8.52
T (cmolc dm^{-3})	6.73	26.18	10.46
V (%)	76.92	73.09	81.41

Parameter	Substrate		
	Control	Chemical fertilization	Bovine manure
m (%)	0.00	1.03	0.00
Clay (dag kg^{-1})	28	34	37
Silt (dag kg^{-1})	3	5	4
Sand (dag kg^{-1})	69	61	59
Classification	Type 2	Type 2	Type 3

Since plants treated with chemical fertilizer died before the start of light intensity treatments, only the control and bovine manure-fertilized substrates were evaluated. Performed 11 months after plant development, nutritional analyses of the substrates showed that in the control group, radiation intensity had no significant effect on most soil parameters, except for S levels, which decreased with increasing light intensity (Table 2). In contrast, bovine manure-fertilized substrates showed marked differences in the concentration of essential elements across light environments. After nearly one year of cultivation, substrate pH under HR was significantly higher (mean 7.03) than in LR and VLR. Under VLR, levels of K, P, Mg, B, sum of exchangeable bases (SB), and cation exchange capacity (CEC) at pH 7.0 (T) were significantly more elevated, with no differences between LR and HR. Ca, Zn, Fe, Mn, remaining phosphorus (P-Rem), organic matter (OM), and base saturation index (V) showed no significant variation across light treatments. Cu was lower under HR, and potential acidity (H + Al) was reduced under VLR. S levels mirrored those in the control, decreasing with higher radiation. Al was not detected in any of the samples. No significant differences in pH or in the Zn, Fe, Cu, and S concentrations were found between control and bovine manure-fertilized substrates across light environments. After 11 months, substrates prepared with manure generally showed higher levels of K, P, Ca, Mg, P-Rem, OM, SB, T, and V. Compared to the control, higher concentrations of Mn and B were detected only in the fertilized material under VLR. In VLR and LR conditions, H + Al levels were higher in control than in those with organic amendment.

Table 2

Chemical attributes of substrates of *Syzygium jambos* plants after 11 months of development in three light environments (very low radiation – VLR, low radiation – LR, and high radiation – HR), subjected to two fertilization systems (control group and bovine manure-fertilized). Parameters: pH of the substrates (pH); contents of potassium (K), phosphorus (P), calcium (Ca), magnesium (Mg), zinc (Zn), iron (Fe), manganese (Mn), copper (Cu), boron (B), sulfur (S), remaining phosphorus (P-Rem), organic matter (OM); potential acidity (H + Al); sum of exchangeable bases (SB), cation exchange capacity (CEC) at pH 7.0 (T); and base saturation index (V). Uppercase letters compare the effect of radiation within each fertilization system, while lowercase letters compare the effect of fertilization within each light intensity. Data are presented as mean ± standard error. Means followed by the same letters do not differ significantly according to the Scott-Knott test at a 5% probability

Parameter	Control			Bovine manure		
	VLR	LR	HR	VLR	LR	HR
pH	6.60 ± 0.06 Aa	6.87 ± 0.33 Aa	6.80 ± 0.06 Aa	6.37 ± 0.30 Ba	6.70 ± 0.10 Ba	7.03 ± 0.03 Aa
K (mg dm^{-3})	26.67 ± 1.76 Ab	26.00 ± 0.00 Ab	25.33 ± 2.40 Ab	199.33 ± 37.81 Aa	110.00 ± 12.49 Ba	64.67 ± 6.77 Ba
P (mg dm^{-3})	10.25 ± 0.46 Ab	9.08 ± 0.66 Ab	8.44 ± 0.50 Ab	21.37 ± 2.01 Aa	16.83 ± 0.17 Ba	16.02 ± 0.76 Ba
Ca (cmolc dm^{-3})	4.13 ± 0.15 Ab	3.93 ± 0.13 Ab	3.97 ± 0.09 Aa	4.87 ± 0.37 Aa	4.53 ± 0.13 Aa	4.23 ± 0.13 Aa
Mg (cmolc dm^{-3})	1.10 ± 0.06 Ab	1.00 ± 0.06 Ab	0.97 ± 0.03 Ab	2. 07 ± 0.18 Aa	1.77 ± 0.07 Ba	1.57 ± 0.07 Ba
Zn (mg dm^{-3})	24.73 ± 1.09 Aa	22.08 ± 2.82 Aa	26.51 ± 1.32 Aa	24.64 ± 1.98 Aa	26.35 ± 0.88 Aa	22.38 ± 2.88 Aa
Fe (mg dm^{-3})	54.52 ± 0.90 Aa	60.00 ± 5.25 Aa	64.85 ± 12.98 Aa	69.93 ± 2.64 Aa	69.93 ± 5.88 Aa	65.70 ± 5.54 Aa
Mn (mg dm^{-3})	28.20 ± 2.75 Ab	32.49 ± 2.93 Aa	32.74 ± 1.88 Aa	43.16 ± 5.03 Aa	43.45 ± 2.24 Aa	42.02 ± 6.51 Aa
Cu (mg dm^{-3})	0.64 ± 0.06 Aa	0.57 ± 0.07 Aa	0.56 ± 0.03 Aa	0.68 ± 0.03 Aa	0.68 ± 0.02 Aa	0.52 ± 0.07 Ba
B (mg dm^{-3})	0.14 ± 0.01 Ab	0.19 ± 0.01 Aa	0.15 ± 0.02 Aa	0.23 ± 0.04 Aa	0.16 ± 0.01 Ba	0.14 ± 0.01 Ba
S (mg dm^{-3})	57.47 ± 5.76 Aa	43.18 ± 6.99 Ba	19.24 ± 0.98 Ca	68.05 ± 5.99 Aa	31.66 ± 1.50 Ba	16.90 ± 1.85 Ca
P-Rem (mg L^{-1})	14.65 ± 1.00 Ab	14.75 ± 0.29 Ab	13.34 ± 0.41 Ab	18.04 ± 0.60 Aa	17.05 ± 0.43 Aa	17.37 ± 0.28 Aa
OM (dag kg^{-1})	2.11 ± 0.00 Ab	2.19 ± 0.08 Ab	2.07 ± 0.04 Ab	2.53 ± 0.08 Aa	2.61 ± 0.15 Aa	2.79 ± 0.21 Aa
H + Al (cmolc dm^{-3})	1.82 ± 0.08 Aa	1.89 ± 0.08 Aa	1.65 ± 0.09 Aa	1.36 ± 0.06 Bb	1.60 ± 0.04 Ab	1.68 ± 0.13 Aa

Parameter	Control			Bovine manure		
	VLR	LR	HR	VLR	LR	HR
SB (cmolc dm^{-3})	5.30 ± 0.21 Ab	5.00 ± 0.19 Ab	5.00 ± 0.12 Aa	7.44 ± 0.63 Aa	6.58 ± 0.22 Ba	5.96 ± 0.22 Ba
T (cmolc dm^{-3})	7.12 ± 0.20 Ab	6.89 ± 0.18 Ab	6.65 ± 0.17 Ab	9.14 ± 0.59 Aa	8.18 ± 0.26 Ba	7.65 ± 0.16 Ba
V (%)	74.39 ± 1.24 Ab	72.51 ± 1.24 Ab	75.14 ± 1.05 Aa	81.40 ± 3.29 Aa	80.42 ± 0.17 Aa	77.99 ± 1.80 Aa

Comparisons between initial and post-cultivation substrate fertility revealed notable shifts (Tables 1 and 2). pH decreased in unfertilized substrates but increased in those with bovine manure, mirroring trends in potential acidity (H + Al). Macronutrients (K, P, Ca, Mg, S) and parameters SB, t, and T declined more sharply in manure-amended substrates, proportionally to light intensity. Micronutrient levels (Zn, Fe, Mn, Cu, B) fluctuated without consistent patterns. After 11 months, OM increased in control but declined in substrates with manure addition, while P-Rem showed the opposite trend.

Foliar nutrient concentrations

The results for foliar nutrient concentrations are summarized in Table 3. In the control group, the concentrations of P, K, Ca, Mg, B, Mn, and Fe did not vary significantly with light intensity. However, foliar N decreased as light radiation increased, with significant differences observed in both control and manure-fertilized plants. In control plants, S was highest under VLR, while Cu and Zn peaked under HR. In manure-fertilized plants, most nutrients varied significantly across light treatments, except for Fe, which remained stable. HR conditions favored the accumulation of P, Mg, B, Cu, and Zn, while the opposite was observed for K, Ca, and S (higher concentrations in VLR). Across all light environments, S, Zn, and Fe showed no significant differences between control and fertilized groups. In general, fertilized plants showed higher levels of N, P, and K, although these differences were not always statistically significant. Notably, B and Cu were significantly higher in fertilized plants under HR. Control plants had higher Ca and Mg overall, except for Mg under HR.

Table 3

Foliar nutrient concentrations in *Syzygium jambos* plants after 11 months of growth under three light environments (very low radiation – VLR; low radiation – LR; and high radiation – HR) and two fertilization systems (control group and bovine manure-fertilized). Uppercase letters compare the effect of radiation within each fertilization system, while lowercase letters compare the effect of fertilization within each light intensity. Data are presented as mean ± standard error. Means followed by the same letters do not differ significantly according to the Scott-Knott test at a 5% probability

Parameter	Control			Bovine manure		
	VLR	LR	HR	VLR	LR	HR
N (%)	1.39 ± 0.04 Ab	0.99 ± 0.07 Bb	0.78 ± 0.04 Cb	1.67 ± 0.03 Aa	1.23 ± 0.06 Ba	0.97 ± 0.06 Ca
P (%)	0.08 ± 0.01 Aa	0.06 ± 0.00 Ab	0.06 ± 0.01 Ab	0.09 ± 0.01 Ba	0.10 ± 0.01 Ba	0.13 ± 0.02 Aa
K (%)	0.63 ± 0.04 Ab	0.52 ± 0.05 Ab	0.37 ± 0.02 Aa	1.33 ± 0.12 Aa	0.76 ± 0.04 Ba	0.54 ± 0.09 Ca
Ca (%)	0.88 ± 0.02 Aa	0.84 ± 0.03 Aa	0.77 ± 0.03 Aa	0.70 ± 0.03 Ab	0.56 ± 0.05 Bb	0.57 ± 0.02 Bb
Mg (%)	0.36 ± 0.02 Aa	0.35 ± 0.00 Aa	0.36 ± 0.01 Aa	0.27 ± 0.01 Bb	0.29 ± 0.01 Bb	0.33 ± 0.02 Aa
S (%)	0.17 ± 0.01 Aa	0.13 ± 0.00 Ba	0.11 ± 0.01 Ba	0.17 ± 0.01 Aa	0.14 ± 0.00 Ba	0.13 ± 0.00 Ba
B (ppm)	15.3 ± 2.5 Aa	11.7 ± 1.1 Aa	24.3 ± 6.8 Ab	19.4 ± 0.7 Ba	22.3 ± 4.5 Ba	35.8 ± 3.0 Aa
Cu (ppm)	0.53 ± 0.24 Ba	0.37 ± 0.12 Ba	1.33 ± 0.38 Ab	0.87 ± 0.20 Ba	1.03 ± 0.23 Ba	2.33 ± 0.28 Aa
Mn (ppm)	48.2 ± 35.2 Aa	14.8 ± 3.1 Ab	6.1 ± 2.8 Aa	10.7 ± 3.5 Ba	167.9 ± 76.6 Aa	21.5 ± 9.5 Ba
Zn (ppm)	13.1 ± 0.9 Ba	13.0 ± 0.3 Ba	20.4 ± 1.5 Aa	12.4 ± 0.5 Ba	11.3 ± 0.3 Ba	21.3 ± 1.2 Aa
Fe (ppm)	131.3 ± 19.3 Aa	131.3 ± 38.5 Aa	88.4 ± 4.0 Aa	129.7 ± 5.5 Aa	110.2 ± 6.2 Aa	93.6 ± 5.2 Aa

Biochemical analyses

Regardless of the fertilization method or measurement unit, plants under HR had significantly higher total protein content (Table 4). In the control group, proline accumulated more under HR, while in fertilized plants, it was higher under VLR. SOD and PPO activities were lowest under HR, especially in fertilized plants, which showed significant variation across light treatments. CAT activity remained unchanged in fertilized plants but decreased under LR in the control group, whereas POD activity peaked under LR in both groups. Overall, hydrogen peroxide (H_2O_2) and superoxide ($O_2.^-$) levels were lowest under HR, while MDA content was highest under HR, regardless of fertilization. Comparing control and

fertilized plants, protein content differed significantly only under HR, with higher values in the control group. Proline was higher in fertilized plants under VLR and in control plants under HR. SOD activity differed only under LR, being lower in fertilized plants. CAT activity varied under VLR and HR, with fertilized plants showing the lowest values. POD and PPO activities differed only under VLR, with higher POD in control and higher PPO in fertilized plants. Hydrogen peroxide, superoxide, and MDA levels were generally similar between groups, except for MDA under HR, which was higher in fertilized plants.

Table 4

Biochemical attributes of *Syzygium jambos* plants after 11 months of growth under three light environments (very low radiation – VLR, low radiation – LR, and high radiation – HR) and two fertilization systems (control group and bovine manure-fertilized). Total protein content is presented on a fresh mass basis (mg g^{-1} FM) and area basis (mg cm^{-2}); proline content (µmol g^{-1} FM); enzymatic activities of SOD (units mg^{-1} protein), CAT (µmol of H_2O_2 min^{-1} mg^{-1} protein), POD (µmol mg^{-1} protein), and PPO (µmol mg^{-1} protein); and contents of peroxide (nmol g^{-1} FM), superoxide (nmol g^{-1} FM), and malondialdehyde (MDA; µmol g^{-1} FM). Uppercase letters compare the effect of radiation within each fertilization system, while lowercase letters compare the effect of fertilization within each light intensity. Data are presented as mean ± standard error. Means followed by the same letters do not differ significantly according to the Scott-Knott test at a 5% probability.

Parameter	Control			Bovine manure		
	VLR	LR	HR	VLR	LR	HR
Proteins (/mass)	26.0 ± 1.8 Ba	23.9 ± 1.4 Ba	93.6 ± 2.5 Aa	20.3 ± 0.9 Ba	20.8 ± 0.3 Ba	81.8 ± 3.5 Ab
Proteins (/area)	0.60 ± 0.03 Ba	0.60 ± 0.04 Ba	3.23 ± 0.11 Aa	0.49 ± 0.02 Ba	0.53 ± 0.01 Ba	2.72 ± 0.16 Ab
Proline	0.54 ± 0.04 Bb	0.34 ± 0.05 Ba	0.82 ± 0.07 Aa	0.75 ± 0.12 Aa	0.43 ± 0.04 Ba	0.54 ± 0.07 Bb
SOD	24.47 ± 0.37 Aa	22.40 ± 0.95 Aa	1.17 ± 0.21 Ba	24.82 ± 2.35 Aa	18.05 ± 1.05 Bb	0.02 ± 0.01 Ca
CAT	2.81 ± 0.41 Aa	0.49 ± 0.31 Ba	2.91 ± 0.13 Aa	1.20 ± 0.38 Ab	0.49 ± 0.31 Aa	0.95 ± 0.13 Ab
POD	0.39 ± 0.04 Ba	0.60 ± 0.07 Aa	0.11 ± 0.01 Ca	0.08 ± 0.04 Bb	0.62 ± 0.10 Aa	0.16 ± 0.01 Ba
PPO	1.46 ± 0.22 Ab	1.75 ± 0.09 Aa	0.29 ± 0.01 Ba	2.27 ± 0.13 Aa	1.54 ± 0.09 Ba	0.28 ± 0.04 Ca
Peroxide	70.3 ± 17.1 Aa	65.5 ± 6.0 Aa	29.7 ± 3.2 Ba	53.7 ± 12.7 Aa	43.0 ± 1.5 Aa	27.4 ± 2.8 Aa
Superoxide	22.50 ± 6.30 Aa	21.41 ± 3.47 Aa	3.73 ± 1.47 Ba	32.20 ± 2.92 Aa	15.52 ± 4.26 Ba	6.67 ± 1.38 Ba
MDA	1.25 ± 0.05 Ba	1.31 ± 0.02 Ba	1.54 ± 0.07 Ab	1.34 ± 0.06 Ba	1.39 ± 0.01 Ba	1.89 ± 0.07 Aa

Gas exchange and chlorophyll a responses

Higher light intensities significantly reduced net CO_2 assimilation (A), transpiration (E), stomatal conductance (g_s), and carboxylation efficiency (A/C_i) (Fig. 1). WUE increased with light intensity across all treatments, regardless of fertilization. In the control group, WUE_{int} followed the same pattern, while fertilized plants showed the opposite trend, with a peak under VLR. Fertilized plants showed reduced A, E, g_s, and C_i compared to controls, except for A under VLR and for E and C_i under HR, where differences were not significant. WUE and WUE_{int} were higher in fertilized plants under VLR but declined under HR, reversing the initial advantage. A/C_i remained higher in fertilized plants under VLR, while under HR, control plants surpassed them. Figure 2 presents the fluorescence parameters across treatments. Overall, F_v'/F_m' was lower in plants under HR compared to other light conditions. Φ_{PSII} and ETR followed a similar pattern, with the highest values under VLR, regardless of fertilization. Comparing control and manure-fertilized plants, F_v'/F_m' was significantly higher in the control group, while Φ_{PSII}, q_p, and ETR were consistently higher in fertilized plants across light intensities. The exception was under HR, where Φ_{PSII} and ETR showed no significant differences between groups.

Gas exchanges under dehydration and after rehydration

The most pronounced changes in gas exchange occurred across dehydration durations within each light environment (Table 5). Under VLR, A remained stable after 10 days but declined significantly after 20 days. Under HR, A dropped more sharply, especially after 20 days. E followed a similar trend, with greater reductions under HR. g_s decreased significantly in both light conditions after 20 days, with a more pronounced effect under HR. WUE and WUE_{int} means varied with dehydration time but showed no significant differences between treatments. A/C_i remained unchanged, except after 20 days in plants under HR, when values were lower. Following rehydration, differences among dehydration treatments diminished, and values of A, E, g_s, and A/C_i increased, particularly under HR, where the recovery was statistically significant. During the experiment, a significant decline in soil moisture was observed after 10 and 20 days of dehydration under both VLR and HR conditions (Table 6). Plant water potential also decreased with dehydration, particularly under HR, dropping from − 0.20 MPa in the control to -4.63 MPa after 20 days (Fig. 3). Following rehydration, plant water potential showed marked recovery, with no significant differences among treatments. Comparing plants subjected to 20 days of dehydration before and after rehydration, the increase in water potential was significant under HR.

Table 5

Gas exchange parameters in *Syzygium jambos* plants subjected to different dehydration durations (10 and 20 days) under very low radiation (VLR) and high radiation (HR), before and after rehydration. Parameters include CO_2 assimilation rate (A, μmol CO_2 m^{-2} s^{-1}), transpiration rate (E, mmol H_2O m^{-2} s^{-1}), stomatal conductance (g_s, mol H_2O m^{-2} s^{-1}), intracellular-to-ambient CO_2 ratio (C_i/C_a), water-use efficiency (WUE, μmol CO_2 $mmol^{-1}$ H_2O), intrinsic water use efficiency (WUE_{int}, μmol CO_2 mol^{-1} H_2O), and carboxylation efficiency (A/C_i, μmol m^{-2} s^{-1} Pa^{-1}). Uppercase letters indicate comparisons of dehydration duration within each light condition, while lowercase letters compare the effects of light conditions within each dehydration treatment. Data are presented as mean ± standard error. Means followed by the same letters do not differ significantly according to the Scott-Knott test at a 5% probability. Asterisks denote statistically significant differences between dehydration and post-rehydration values ($p < 0.05$)

	Under dehydration					
	VLR			**HR**		
Parameter	**control**	**10 days**	**20 days**	**control**	**10 days**	**20 days**
A	5.04 ± 0.10 Aa	4.45 ± 0.45 Aa	0.60 ± 0.18 Ba	5.09 ± 0.30 Aa	2.35 ± 0.17 Bb	0.12 ± 0.01 Ca
E	1.19 ± 0.11 Aa	0.98 ± 0.10 Aa	0.07 ± 0.00 Ba	0.98 ± 0.03 Aa	0.38 ± 0.07 Bb	0.02 ± 0.00 Ca
g_s	0.097 ± 0.013 Aa	0.072 ± 0.010 Aa	0.004 ± 0.000 Ba	0.050 ± 0.002 Ab	0.018 ± 0.004 ABb	0.001 ± 0.000 Ba
C_i/C_a	0.76 ± 0.03 Aa	0.72 ± 0.03 ABa	0.33 ± 0.16 Ba	0.56 ± 0.01 Aa	0.42 ± 0.07 Aa	0.36 ± 0.12 Aa
WUE	4.33 ± 0.45 Aa	4.59 ± 0.52 Aa	8.59 ± 2.19 Aa	5.21 ± 0.13 Aa	6.49 ± 0.76 Aa	7.18 ± 1.55 Aa
WUE_{int}	54.0 ± 7.3 Aa	63.6 ± 7.5 Aa	162.1 ± 41.0 Aa	101.8 ± 1.8 Aa	137.6 ± 17.0 Aa	153.9 ± 31.4 Aa
A/C_i	0.017 ± 0.001 Aa	0.016 ± 0.002 Aa	0.008 ± 0.005 Aa	0.023 ± 0.002 Aa	0.015 ± 0.002 Aa	0.001 ± 0.000 Ba
	After rehydration					
A	4.90 ± 0.23 Aa	4.86 ± 0.33 Aa	3.68 ± 0.62 Aa*	4.81 ± 0.40 Aa	3.18 ± 0.28 Aa	3.66 ± 0.44 Aa*
E	1.18 ± 0.11 Aa	1.08 ± 0.04 Aa	0.73 ± 0.16 Aa	1.07 ± 0.20 Aa	0.61 ± 0.11 Aa	0.76 ± 0.06 Aa*
g_s	0.097 ± 0.013 Aa	0.063 ± 0.004 ABa	0.042 ± 0.010 Ba	0.075 ± 0.018 Aa	0.032 ± 0.006 Aa	0.040 ± 0.003 Aa*
C_i/C_a	0.77 ± 0.03 Aa	0.66 ± 0.01 Aa	0.59 ± 0.06 Aa	0.70 ± 0.04 Aa	0.55 ± 0.06 Aa	0.61 ± 0.02 Aa

	Under dehydration					
	VLR			HR		
Parameter	control	10 days	20 days	control	10 days	20 days
WUE	4.24 ± 0.52 Aa	4.50 ± 0.16 Aa	5.27 ± 0.53 Aa	4.71 ± 0.53 Aa	5.48 ± 0.73 Aa	4.81 ± 0.21 Aa
WUE_{int}	52.9 ± 8.2 Aa	77.3 ± 1.6 Aa	94.9 ± 14.1 Aa	69.5 ± 10.9 Aa	105.1 ± 13.9 Aa	91.5 ± 5.4 Aa
A/C_i	0.016 ± 0.001 Aa	0.018 ± 0.001 Aa	0.016 ± 0.002 Aa	0.017 ± 0.001 Aa	0.015 ± 0.001 Aa	0.015 ± 0.002 Aa*

Table 6
Soil temperature, soil moisture, and leaf water potential (Ψw) of *Syzygium jambos* plants subjected to dehydration for 10 and 20 days under very low radiation (VLR) and high radiation (HR), followed by rehydration. Uppercase letters indicate comparisons of dehydration duration within each light condition, while lowercase letters compare the effects of light conditions within each dehydration treatment. Data are presented as mean ± standard error. Means followed by the same letters do not differ significantly according to the Scott-Knott test at a 5% probability. Asterisks denote statistically significant differences between dehydration and post-rehydration values ($p < 0.05$)

	Under dehydration					
	VLR			HR		
Parameter	control	10 days	20 days	control	10 days	20 days
Soil temperature (°C)	21.8 ± 0.0 Ab	25.5 ± 0.1 Ab	25.8 ± 0.6 Aa	27.4 ± 1.2 Ba	33.5 ± 1.2 Aa	29.8 ± 1.5 ABa
Soil moisture (%)	8.1 ± 0.4 Aa	0.7 ± 0.1 Ba	0.7 ± 0.1 Ba	3.5 ± 0.5 Ab	0.6 ± 0.0 Ba	0.6 ± 0.1 Ba
Ψw (MPa)	-0.36 ± 0.03 Aa	-0.51 ± 0.05 Aa	-1.99 ± 0.54 Ba	-0.20 ± 0.01 Aa	-1.80 ± 0.25 Bb	-4.63 ± 0.09 Cb
	After rehydration					
Ψw (MPa)	-0.36 ± 0.03 Aa	-0.54 ± 0.10 Aa	-0.32 ± 0.06 Aa	-0.21 ± 0.04 Aa	-0.38 ± 0.11 Aa	-0.20 ± 0.01 Aa*

Discussion

Soil pH, or active acidity, reflects H^+ concentration in solutions. Based on classification of Soil Survey Staff (2024), the control treatment had pH within the “neutral” range (6.6–7.3), the bovine manure treatment had pH values within the “slightly acid” range (6.1–6.5), with the manure-amended substrate within the ideal range for plant growth (5.5–6.5), at pH 6.2 (Islam et al. 1980). The chemically fertilized

substrate falls within the “very strong acid” range (4.5-5.0), nearing the “extremely high” threshold (3.5–4.4). Excess acidity can increase the solubility of toxic elements, such as manganese and aluminum, which impair root function and cell development (Kochian 1995; Horst et al. 2010). This pH condition can potentially reduce yield, which may have been the primary factor in the death of plants observed in treatments supplemented with chemical fertilizer. Organic amendment (with bovine manure) enriched the substrates with nutrients and improved chemical attributes by increasing pH and base saturation while reducing acidity. The absence of Al indicates that the amendment effectively buffered soil acidity, preventing Al mobilization. Over the course of the experiment, pH values became more basic in fertilized substrates. This shift is likely linked to the decomposition of manure, which releases carbonates, bicarbonates, and organic acids – compounds that buffer acidity and raise substrate pH (Whalen et al. 2000; Holatko et al. 2022).

Before planting, manure-amended substrates contained higher levels of most macro- and micronutrients than the control (except Fe and Cu). This pattern largely persisted after cultivation for K, P, Ca, Mg, OM, SB, t, T, and V across all light environments. Thus, while manure improved substrate fertility and buffering capacity, the intensity of radiation determined the rate and direction of nutrient transformations in the soil. Over the 11-month experimental period, nutrient depletion was more pronounced in manure-amended substrates under HR, especially for K, P, Mg, Cu, B and S, as well as for the parameters SB and T, reflecting greater nutrient demand for plant growth.

Foliar N content decreased with increasing light intensity in both control and fertilized plants, consistent with findings in *Sinarundinaria nitida*, where shaded plants maintained higher N and chlorophyll levels (Yang et al. 2014b). In the control group, P, K, Ca, Mg, B, and Mn remained relatively stable across light environments, while in the manure-treated group, nutrient levels fluctuated without a clear pattern. Fertilized plants accumulated, under high radiation, more P, Mg, Cu, B, and Zn, whereas K, Ca, and S decreased. These variable responses align with reports of light-dependent nutrient allocation in other tropical tree species, such as *Swietenia macrophylla* and *Dipteryx odorata* (Gonçalves et al. 2005), and with studies noting inconsistent effects of light intensity on macronutrient composition (Ronquim et al. 2009; Dalmolin et al. 2012).

These patterns in nutrient dynamics also help explain the observed physiological responses. Plants under HR exhibited higher total protein content than those under VLR and LR, regardless of fertilization. Interestingly, despite lower foliar N levels under HR, protein content was higher. This apparent discrepancy reflects the complex distribution of nitrogen within leaf tissues, which can shift between photosynthetic and structural pools depending on environmental conditions (Wang et al. 2021). According to these authors, foliar nitrogen is allocated among several functional compartments, including photosynthetic proteins such as RuBisCo and components of the light-harvesting complexes, as well as non-photosynthetic proteins in cell walls, mitochondria, and cytosol. *S. jambos* also exhibited higher chlorophyll concentrations under VLR, as confirmed by spectrophotometric analysis and by non-destructive analyses with SPAD-502 (Resende et al. unpublished data), suggesting a greater investment in light-harvesting structures under low-light conditions. This allocation pattern likely explains the higher

foliar N levels observed under VLR despite lower total protein content, as more nitrogen was directed to chlorophyll and associated proteins rather than to bulk protein synthesis. Positive correlations between foliar N and chlorophyll content have also been reported in other species (Mizusaki et al. 2013; Yang et al. 2014a; Schlichting et al. 2015).

Proline levels exhibited divergent responses: they increased under HR in the control group but decreased under LR and HR in organic fertilizer plants. Proline accumulation differs with fertilization and light, suggesting that its role in osmoprotection or stress mitigation varies depending on nutrient status. Although proline stabilizes subcellular structures and acts as a redox buffer (Reddy et al. 2004; Molinari et al. 2007; Verslues and Sharma 2010), its primary role is to facilitate osmotic adjustment under water stress (Hong et al. 2000; Carvalho et al. 2013).

SOD serves as the first enzymatic barrier against ROS, converting $O_2^{\cdot -}$ to H_2O_2 (Alscher et al. 2002), which is then scavenged by CAT and various PODs to prevent the formation of highly reactive species, such as OH. (Kibinza et al. 2011; Shivashankara et al. 2016). PPO, abundant in plants, oxidizes phenolics into quinones and may act synergistically with POD (Krishna et al. 2008). Overall, SOD and PPO activities were significantly lower under HR, as were H_2O_2 and superoxide levels. Such reductions in SOD and PPO under HR may reflect enzyme inhibition or a strategic shift in antioxidant defense, with other enzymes (POD, CAT) compensating depending on light intensity. CAT and POD showed complementary activity: CAT was more active under VLR and HR, while POD peaked under LR. Lipid peroxidation (TBARs index) was highest under HR.

These patterns indicate that high radiation may trigger protein synthesis and lipid peroxidation as part of a protective response to light stress, while simultaneously reducing ROS accumulation through efficient scavenging mechanisms. This finding aligns with the observed increase in lipid peroxidation but lower ROS levels under HR, suggesting a dynamic regulation of defense pathways. These results also indicate increased ROS production in shaded environments (LR) and an effective response to oxidative stress under higher radiation. Interestingly, lower H_2O_2 and superoxide levels under HR may reflect alternative antioxidant defenses, such as carotenoids, which deactivate singlet oxygen and other ROS. Indeed, *S. jambos* under HR exhibited significantly lower chlorophyll/carotenoid ratios (Resende et al. unpublished), highlighting the photoprotective role of these pigments in full sunlight conditions. Moreover, fertilization modulates these stress responses, likely by influencing nutrient-dependent metabolic pathways and antioxidant capacity.

Contrasting results are reported in the literature regarding these enzymes activities. Yang et al. (2008) found increased SOD and CAT activities, and reduced POD activity in *Picea asperata* under high light conditions. The role of CAT in H_2O_2 detoxification under intense radiation was demonstrated in *Arabidopsis thaliana* mutants, which exhibited elevated H_2O_2 levels and cell death (Vandenabeele et al. 2004; Vanderauwera et al. 2005). Liu et al. (2016) observed significantly higher levels of hydrogen peroxide and superoxide radicals, along with increased activities of CAT, SOD, and APX, in *Alnus* species grown under full sunlight, with no significant changes in lipid peroxidation. In *Torreya grandis*, SOD

activity was light-dependent, peaking at both the extremes of light levels, indicating that both excessive and insufficient light can impair plant metabolism (Tang et al. 2015).

In the present study, gas exchange measurements were conducted under a standardized light intensity (1,000 µmol photons m^{-2} s^{-1}) using the IRGA LED light chamber. The higher values of *A*, E, *gs*, and *A*/Ci observed in plants from shaded environments indicate an enhanced capacity for light utilization under limited irradiance. Furthermore, these results demonstrate the absence of photoinhibition, enabling shade-adapted plants to efficiently exploit the available light in environments where this resource is scarce. Shade plants in forest understories often experience brief, high-intensity sunflecks throughout the day, which contribute substantially to their daily carbon gain. These species are able to utilize sunflecks for positive net photosynthesis without suffering significant photoinhibition, due to rapid activation of energy dissipation mechanisms and other physiological adaptations (Way and Pearcy 2012, Zhang et al. 2021).

In contrast, elevated WUE in plants exposed to HR reflects efficient carbon assimilation relative to transpiration, indicating reduced water loss. Different patterns were reported for *Piper aduncum*, a pioneer species, which showed increased *A* and *E* and reduced WUE under higher light (Pacheco et al. 2013). Similarly, *Alnus formosana*, an invasive species, exhibited higher *A*, *E*, and g_s under high radiation (Liu et al. 2016). Compared to the native species *Alnus cremastogyne*, *A. formosana* demonstrated superior photosynthetic and stomatal performance, highlighting functional advantages linked to invasiveness. In our study, high irradiance led to reduced net photosynthesis and increased stomatal limitation, reducing CO_2 assimilation and carboxylation efficiency.

In contrast to our work, Silva et al. (2016) reported increased RuBisCo carboxylation efficiency (A/C_i) under high light, suggesting species-specific responses to irradiance. These findings underscore the complexity of light-mediated physiological responses and the importance of ecological strategy in shaping gas exchange dynamics. Photosynthetic traits of plants from different successional stages were compared under contrasting light conditions (Zhang et al. 2015). Pioneer species showed greater reductions in photosynthetic rates under shade compared to mid- and late-successional species. This reflects the generally lower shade tolerance of early successional species and their reliance on open (under high light) environments for optimal carbon gain. Additional traits – such as lower light compensation points, reduced respiration rates, and higher apparent quantum yield – suggest that late-successional species are better adapted to low-light conditions. This response aligns with our findings, considering that light levels in the understory of mature forests, where these species grow and *S. jambos* is commonly found, can drop below 2% of full daylight (Chazdon and Fetcher 1984). Such environments favor species with enhanced light-use efficiency and physiological plasticity.

The ΦPSII represents the fraction of absorbed light energy allocated to photochemical processes and typically shows higher values in plants exposed to low irradiance (Yang et al. 2025). Species adapted to high light intensities tend to exhibit lower effective quantum yield of PSII, as a larger portion of absorbed light is dissipated through non-photochemical pathways. This strategy helps to protect the

photosynthetic apparatus from excess energy, minimizing photoinhibition (Yang et al. 2025). This pattern was confirmed in our study, where measured fluorescence parameters were generally higher in plants grown under VLR compared to those under HR. Previous studies support these findings. Zhang et al. (2015), for example, reported increased ΦPSII in response to reduced light intensity in five tree species; for *Quercus aliena*, shaded plants exhibited higher ΦPSII and ETR values (Xu et al. 2015). Enhanced photochemical efficiency under low light likely contributes to maintaining positive carbon balance in shaded environments, reinforcing the ecological advantage of high shade tolerance in *S. jambos*.

Variations in gas exchange parameters across dehydration durations and light environments reveal a nuanced interaction between water availability and irradiance. Under HR, sharper declines in A, E, and g_s after 20 days of dehydration reflect intensified physiological stress. Stomatal closure under drought is a primary adaptive response to minimize transpirational water loss. However, this response also restricts CO_2 uptake, thereby limiting photosynthetic carbon assimilation (Flexas et al. 2004, 2006, Oguz et al. 2022). Despite these reductions, the stability of WUE suggests a proportional decline in both CO_2 assimilation and water loss, reflecting balanced stomatal regulation. While stomatal closure explains the initial reductions in gas exchange, the observed drop in A/C_i after 20 days of dehydration under HR points to additional non-stomatal limitations, likely linked to biochemical constraints on photosynthesis (Flexas and Medrano 2002). Moreover, the overall stability of A/C_i suggests that such biochemical limitations only emerged under more severe stress, highlighting the species' resilience to combined environmental pressures. Under high irradiance, the compounded effects of water deficit and excess energy intensify photoprotective demands, leading to increased non-photochemical energy dissipation and further constraining carbon assimilation (Nosalewicz et al. 2022).

Our findings align with recent work by He et al. (2024), who reported similar patterns in tropical perennial trees: g_s, A, and E d ropped significantly under drought, followed by strong recovery after rehydration. In our study, the substantial recovery of A, E, g_s, and A/C_i – especially under HR – along with the rapid restoration of gas exchange and water potential after rehydration, reveals the strong desiccation tolerance and hydraulic recovery mechanisms of *S. jambos*. The rebound in plant water potential, particularly under HR, further supports the species' resilience to episodic drought, provided rehydration occurs. Such resilience and plasticity under fluctuating environmental conditions may help explain the invasive potential of *S. jambos*, especially in regions prone to intermittent drought and high irradiance.

The results of our study allow us to conclude that *S. jambos* exhibits remarkable physiological and biochemical plasticity, enabling it to thrive under varying light intensities, fertilization regimes, and water availability. Light intensity strongly influenced nitrogen allocation, protein synthesis, antioxidant activity, and gas exchange. The species maintains photosynthetic efficiency and photochemical performance across contrasting light environments, deploys effective antioxidant and osmotic stress responses, and recovers rapidly from dehydration. Its flexible allocation of nitrogen and pigments, combined with tolerance to both shade and high irradiance, underpins its ecological versatility and likely contributes to

its invasive potential. Understanding these adaptive mechanisms is essential for predicting their behavior under climate change and informing environmental management strategies.

Declarations

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Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

Both authors contributed to the conception and design of the study. Material preparation, data collection, and analysis were performed by Cristiano Ferrara de Resende. The first draft of the manuscript was written by Cristiano Ferrara de Resende and both authors commented on previous versions. Both authors read and approved the final manuscript.

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Data Availability Statement

Data will be made available from the corresponding author on request.

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Figures

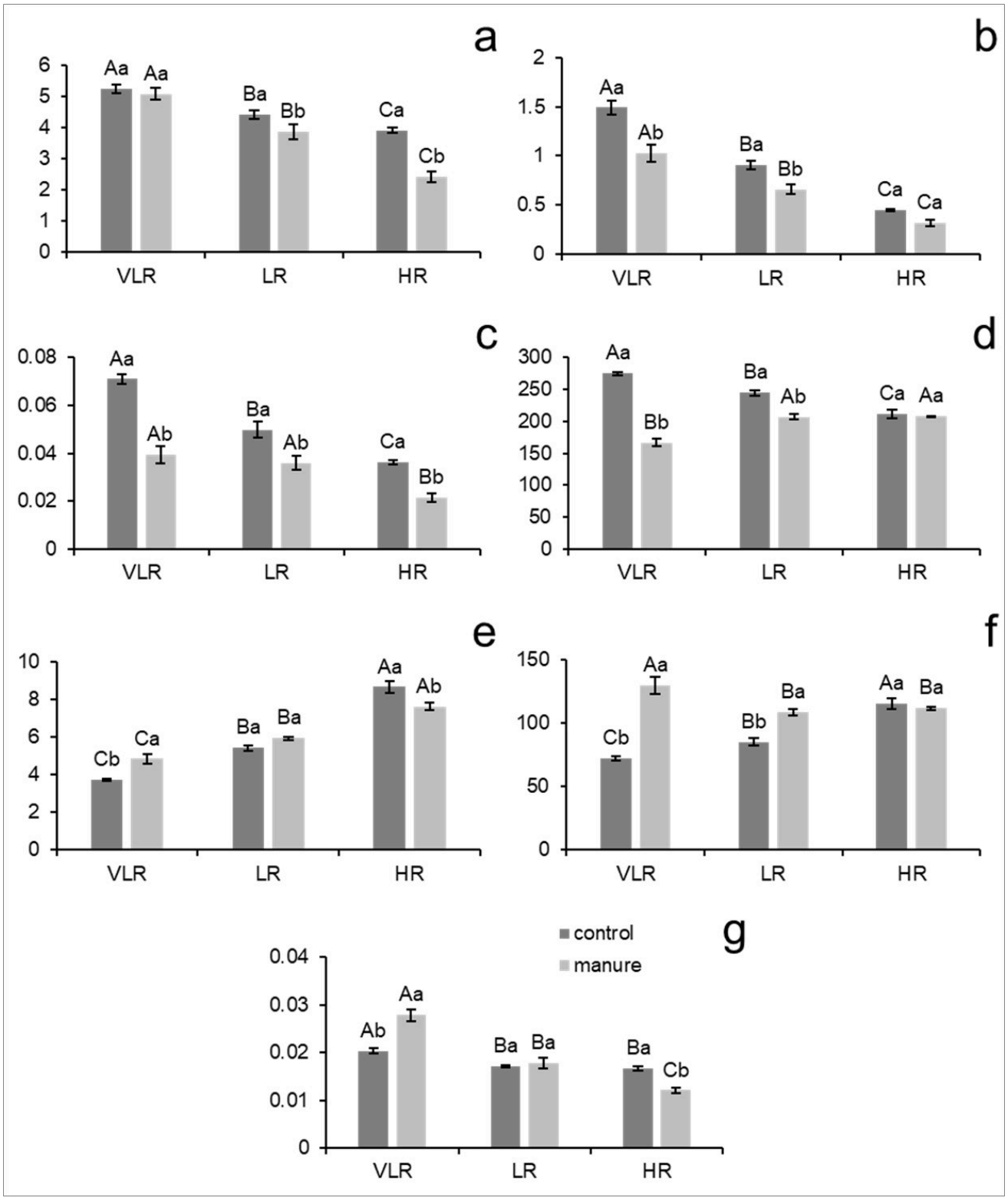

Figure 1

Gas exchange parameters in *Syzygium jambos* plants after 11 months of growth under three light environments (very low radiation – VLR, low radiation – LR, and high radiation – HR), subjected to two fertilization systems (control group and bovine manure-fertilized). **a)** CO_2 assimilation rate (A, μmol CO_2 m^{-2} s^{-1}); **b)** transpiration (E, mmol m^{-2} s^{-1}); **c)** stomatal conductance (g_s, mol H_2O m^{-2} s^{-1}); **d)** substomatal

CO_2 concentration (C_i, µmol mol^{-1}); **e)** water use efficiency (WUE, µmol CO_2 $mmol^{-1}$ H_2O); **f)** intrinsic water use efficiency (WUE_{int}, µmol CO_2 mol^{-1} H_2O); **g)** carboxylation efficiency (A/C_i, µmol m^{-2} s^{-1} Pa^{-1}). Uppercase letters compare the effect of light intensity within each fertilization system (control and bovine manure-fertilized), while lowercase letters compare the effect of fertilization within each light intensity. Means followed by the same letters do not differ from each other according to the Scott-Knott test at a 5% probability

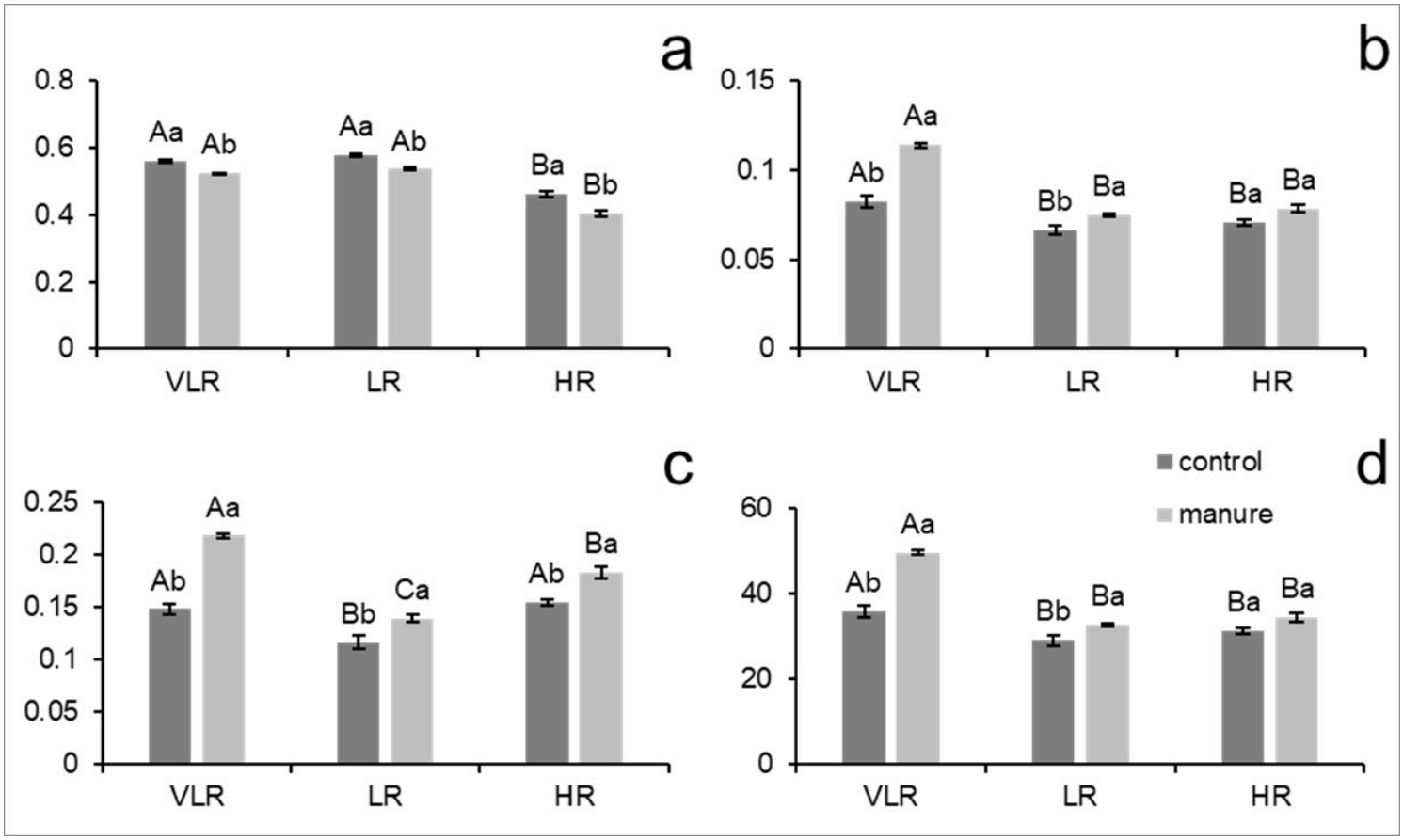

Figure 2

Fluorescence parameters in *S. jambos* plants after 11 months of development under three light environments (very low radiation – VLR, low radiation – LR, and high radiation – HR), subjected to two fertilization systems (control group and bovine manure-fertilized). **a)** Energy capture efficiency of excitation by the open reaction centers of PSII (Fv'/Fm'); **b)** effective quantum yield of PSII electron transport (ΦPSII); **c)** photochemical quenching coefficient (q_P); **d)** apparent electron transport rate (ETR). Uppercase letters compare the effect of light intensity within each fertilization system (control and bovine manure-fertilized), and lowercase letters compare the effect of fertilization within each light intensity. Means followed by the same letters do not differ statistically according to the Scott-Knott test at a 5% probability

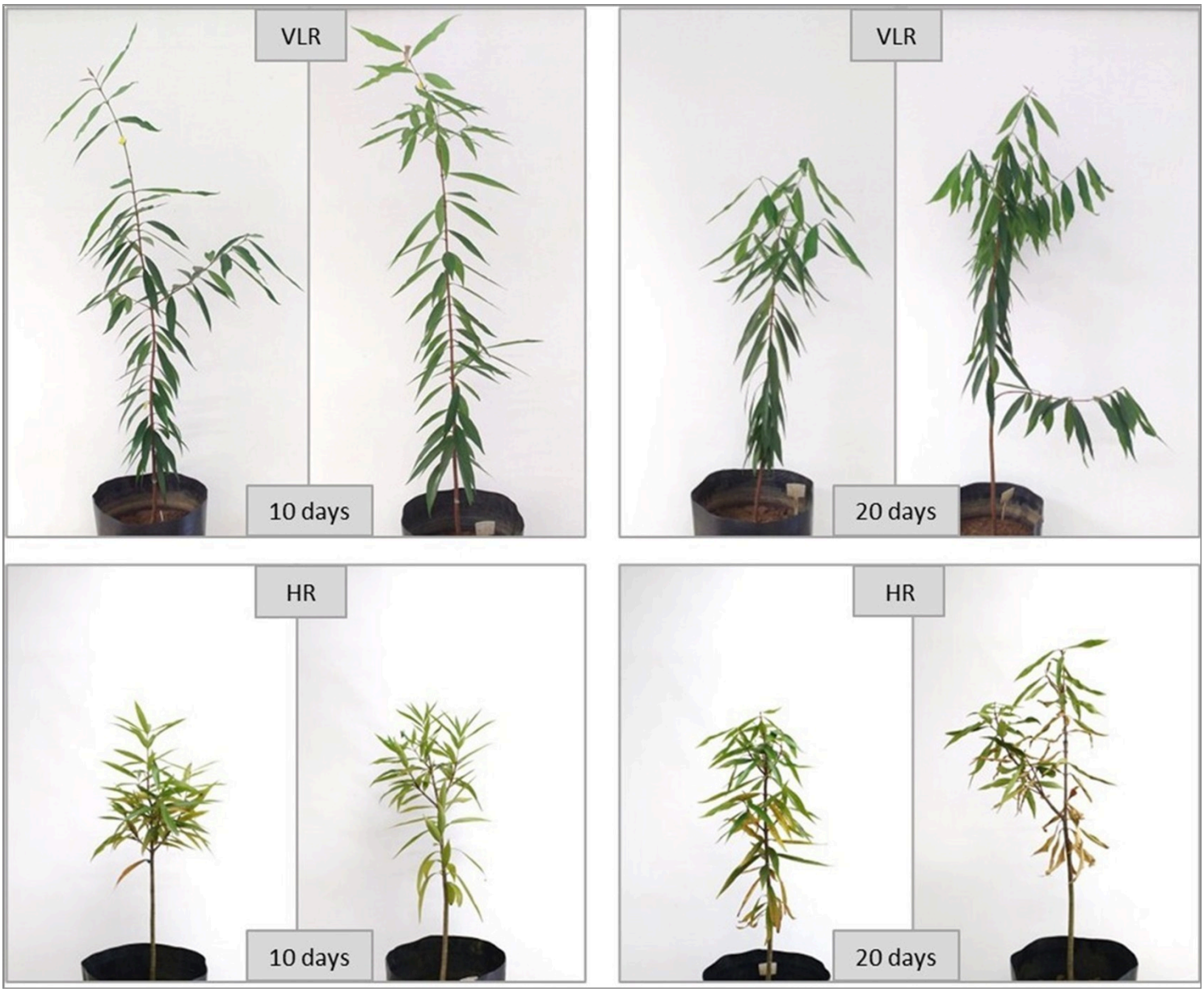

Figure 3

Visual appearance of *Syzigium jambos* plants subjected to 10 and 20 days of dehydration under very low radiation (VLR) and high radiation (HR). Progressive leaf wilting and stem curvature are more pronounced under VLR after 20 days, indicating greater physiological stress compared to HR conditions