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Memory or Reset? Transgenerational Water Stress in an Herbaceous Species from the Semiarid Region

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Abstract

Annual plants native to seasonally dry environments are exposed to fluctuating water availability across successive generations. Environmental conditions experienced by parental plants can influence offspring performance through a phenomenon known as transgenerational memory. This study examined drought-induced transgenerational memory in *Macroptilium lathyroides*, an annual Fabaceae native to the Caatinga, the largest tropical semiarid region in South America. Seeds from natural populations were cultivated over three consecutive generations under well-watered (FC100%; No Stress) and water-limited (FC40%; Stress) conditions. From third-generation (3G) progenies, germination was evaluated under different osmotic potentials, and plant performance was assessed under both FC100% and FC40% soil moisture regimes. Physiological responses in seeds and plants were analyzed using oxidative stress markers and hormonal profiling. No significant transgenerational effects were detected on germination or plant growth. However, changes in antioxidant and hormonal components were observed in the 3G-Stress progeny. Seeds from this group exhibited higher cytokinin and gibberellin concentrations, reflecting metabolic adjustments likely associated with the establishment of vigorous seedlings. In contrast, plants derived from the 3G-Stress progeny showed increased γ-tocopherol levels and reduced cytokinin and gibberellin concentrations. The absence of transgenerational effects on phenotypic traits of *M. lathyroides* indicates a high species resistance to transgenerational water stress, a key adaptive feature supporting survival under the irregular water availability characteristic of the Caatinga. The results underscore the remarkable adaptive capacity of species from the Brazilian semiarid region to marked hydric irregularity and highlight physiological adjustments in the progeny that may be triggered by parental drought history.

Keywords Caatinga · *Macroptilium lathyroides* · Maternal effect · Plant hormones · Seed germination

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Introduction

Seasonality affects the distribution and resilience of diverse plant groups (Huang et al., 2021; Manrique-Ascencio et al. 2024). Plants from environments subject to high water seasonality exhibit a set of adaptations to cope with water limitation caused by low and irregular rainfall patterns (Dodd and Ryan 2016; Bandurska 2022). Brazil harbors a vast semiarid region characterized by one of the largest and richest tropical dry forests in the world, the Caatinga (Silva et al. 2018). This ecosystem is marked by high rainfall irregularity, distinguished by low annual precipitation, elevated temperatures, and high evapotranspiration rates (Moro et al. 2016; Dexter et al. 2018). Due to the high level of adaptation of Caatinga plant species and the predicted vulnerability to climate change, the flora of this ecosystem has become a model for studies aimed at understanding plant responses to low and irregular water availability (Marengo et al. 2017; Manrique-Ascencio et al. 2024; Moura et al., 2023).

In environments with pronounced water unpredictability, high interannual variability in rainfall patterns is observed (Sala et al. 2015; Almeida and Garcia in prep.). Variability in precipitation regimes can directly influence plant phenology, growth, and productivity (Sun et al. 2022; Liu et al. 2023). Annual herbaceous plants occurring in environments with interannual precipitation variability face different levels of water availability across successive generations. The transmission of information across generations can influence offspring performance, a phenomenon known as transgenerational memory (Bruce et al. 2007; Walter et al. 2011). However, little is currently known about how this phenomenon operates in species from natural ecosystems that experience differing water availability across successive generations.

Individuals derived from parents that experienced water stress have demonstrated a series of improvements enabling greater resistance to water limitation. It was observed that seeds produced by parents subjected to water stress exhibited higher mass and volume, as well as faster germination rates under water-limited conditions compared to those from well-irrigated plants (Matzrafi et al. 2021). Seeds from plants grown under stress produced seedlings with increased vigor and rapid development, which optimized the chances of establishment and survival (Hatzig et al. 2018; Racette et al. 2020). Positive effects of transgenerational drought memory on physiological resistance and productivity were also observed in adult plants, which showed increased biomass accumulation (Nosalewicz et al. 2016; Hatzig et al. 2018; Racette et al. 2020; Kambona et al. 2023). However, all these studies focused on cultivated plants, with few investigations addressing the transgenerational effects of drought on native species (Gonzalez et al., 2016; Lukić et al. 2023). Knowledge of native species' responses to water limitation is fundamental to understanding adaptive mechanisms developed in semiarid environments characterized by unpredictable water availability.

Improvements in the performance and productivity of offspring from parents exposed to water limitation generally arise from metabolic alterations that enhance the capacity to respond to stress. Different transgenerational effects of water deficit on the photosynthetic process have been observed, with some species exhibiting a reduction in photosynthesis associated with photoprotection (Walter et al. 2011), while others show an increase in net photosynthesis (Racette et al. 2020). Resistance and protection strategies may be closely associated with modifications in antioxidant defense capacity or alterations in hormonal metabolism. In certain species, transgenerational memory has been demonstrated to directly influence the activity of antioxidant systems and the concentration of photosynthetic pigments (Lukić et al. 2023). Fleta-Soriano et al. (2015) reported lower gibberellin and higher abscisic acid (ABA) concentrations in plants exposed to stress twice compared to those that had experienced a single stress event during their life cycle. According these authors, the hormonal changes found were positively associated with shifts in the cellular redox state, playing a signaling role rather than causing oxidative damage. Thus, it can be inferred that the positive transgenerational effects of water stress on the performance of plant species may be related to adjustments in hormonal balance and antioxidant defense.

Drought tolerance and the maintenance of photosynthetic activity and plant productivity are directly related to the coordinated interaction of various hormones and antioxidant defense mechanisms (Peleg and Blumwald 2011; Ullah et al. 2018; Mesa and Munné-Bosch 2023). Abscisic acid (ABA), salicylic acid (SA), and jasmonates (JAs) have been shown to act directly in response to water stress, particularly by optimizing water uptake and use (Verma et al. 2016; Ullah et al. 2018; Andrade et al. 2017; Villadangos and Munné-Bosch 2023). Conversely, auxin (IAA), cytokinins (CKs), and gibberellins (GAs) are recognized for their roles in developmental processes such as germination, vigor, growth, and reproduction (Ullah et al. 2018; Li et al. 2021; Castro-Camba et al. 2022). Cytokinins have been demonstrated to play an important role not only in early seedling development but also in the vigor and stress resistance of plants under water limitation, by maintaining photosynthetic activity and growth (Xu et al. 2016; Beznec et al. 2021; Alsubaie et al. 2025). Coupled with hormonal signaling, the antioxidant actions of tocopherols and melatonin stand out, as they have been recognized as central regulators of various physiological processes in plants (Mesa and Munné-Bosch 2023; Sandoval et al. 2024). In this context,

plants present a network of metabolic mechanisms that act in concert to maintain tissue homeostasis under water deficit conditions. However, little is known about the influence of transgenerational memory of water deficit on these mechanisms, as well as its effects on plant performance, especially in native species from semiarid environments.

Various ecosystems around the world are characterized by a semiarid climate and intense climatic seasonality, including tropical savannas, transitional zones between deserts and more humid areas, temperate steppes, and Mediterranean ecosystems (Scholes 2020). Among these ecosystems, the Caatinga stands out as the most extensive semiarid tropical region in South America (Allen et al. 2017; Silva et al. 2018, 2020). Although transgenerational effects have been reported in several cultivated species and in some wild species, it remains unclear whether plants native to semiarid environments exhibit comparable levels of plasticity or whether long-term adaptation attenuates such responses. To address this gap, the annual herbaceous species *Macroptilium lathyroides* (Fabaceae), which naturally occurs in the Caatinga, was used to investigate the transgenerational effects of water deficit on offspring responses to water limitation during the seed stage, throughout germination, and during adult plant growth. It was hypothesized that individuals produced from successive generations under water stress develop an adaptive memory, which is expressed through metabolic adjustments resulting in greater resistance to water stress during seed germination and plant growth. To test this hypothesis, seed germination, plant growth, and their responses to water limitation were analyzed through a set of traits related to germination, growth, photosynthesis, antioxidant system, and hormonal profile.

Materials and Methods

Studied Species and Cultivation of Generations

M. lathyroides (Fabaceae) is an ephemeral herbaceous species commonly found in Caatinga areas. It has a short life cycle, lasting approximately three months. Due to these characteristics, this taxon was selected to investigate the transgenerational effect of water stress on seed germination traits and plant growth attributes. Seeds of *M. lathyroides* were collected from a population in a Caatinga area in northeastern Brazil (7°23’40.36"S; 36°26’43.54"W).

In this study, priority was given to establishing a consistent environmental history through strict control of cultivation conditions, which ensured that each progeny cohort reflected the collective response of the parental plants, focusing on process-level understanding rather than on estimating genetic variance among parents. From this perspective, for each generation, five plants were cultivated, one plant per pot (8 L capacity), under two distinct water availability regimes. Thus, over three consecutive generations (G1, G2, and G3), two groups of plants were subjected to different irrigation regimes: (I) cultivation throughout the entire life cycle with water availability maintained at 100% of field capacity (FC100%), and (II) cultivation under 100% field capacity until the onset of flowering, after which soil moisture was reduced to 40% of field capacity (FC40%; Fig. 1). This treatment imposed a moderate yet biologically meaningful drought stress, previously shown to significantly reduce growth and biomass accumulation in Caatinga species (Ferreira et al. 2015; Aguiar et al. 2020) as well as in species from other ecosystems (Singh et al. 2022), while avoiding severe impairment of survival and reproductive capacity, a condition essential for evaluating transgenerational responses. At the end of each generation, seeds produced were harvested and sown under the same irrigation conditions as the parent plants. By the end of the experiment, seeds were obtained from plants grown over three consecutive generations under abundant water availability (3G-No stress) and from individuals developed over three consecutive generations under water stress conditions (3G-Stress; Fig. 1).

Transgenerational Memory in Seeds

Germination Tests

The germination of seeds from the 3G-No stress and 3G-Stress progenies was evaluated under different water potentials: 0, -0.3, -0.6, -0.9, and −1.2 MPa, which were generated using polyethylene glycol (PEG) 6000. For each generation and water potential level, five replicates of 20 seeds were used, with the seeds maintained at 25 °C under a 12-hour photoperiod. Due to the presence of physical dormancy, all seeds were mechanically scarified using a scalpel.

Collection of Material for Biochemical Analyses

Based on germination responses, two water potentials — 0 MPa and −0.9 MPa (the lowest potential at which germination occurred) — were selected to evaluate seed tocopherol concentrations and hormonal profiles. To determine the sampling time points for biochemical analyses, an imbibition curve was previously established for each applied water potential. From the imbibition curve, samples were collected halfway between the start of imbibition and the emergence of the primary root (visible germination), which corresponded to Phase II of the germination process. Thus, for the water potential of 0 MPa, samples were collected 5 h after the start of imbibition, while for the

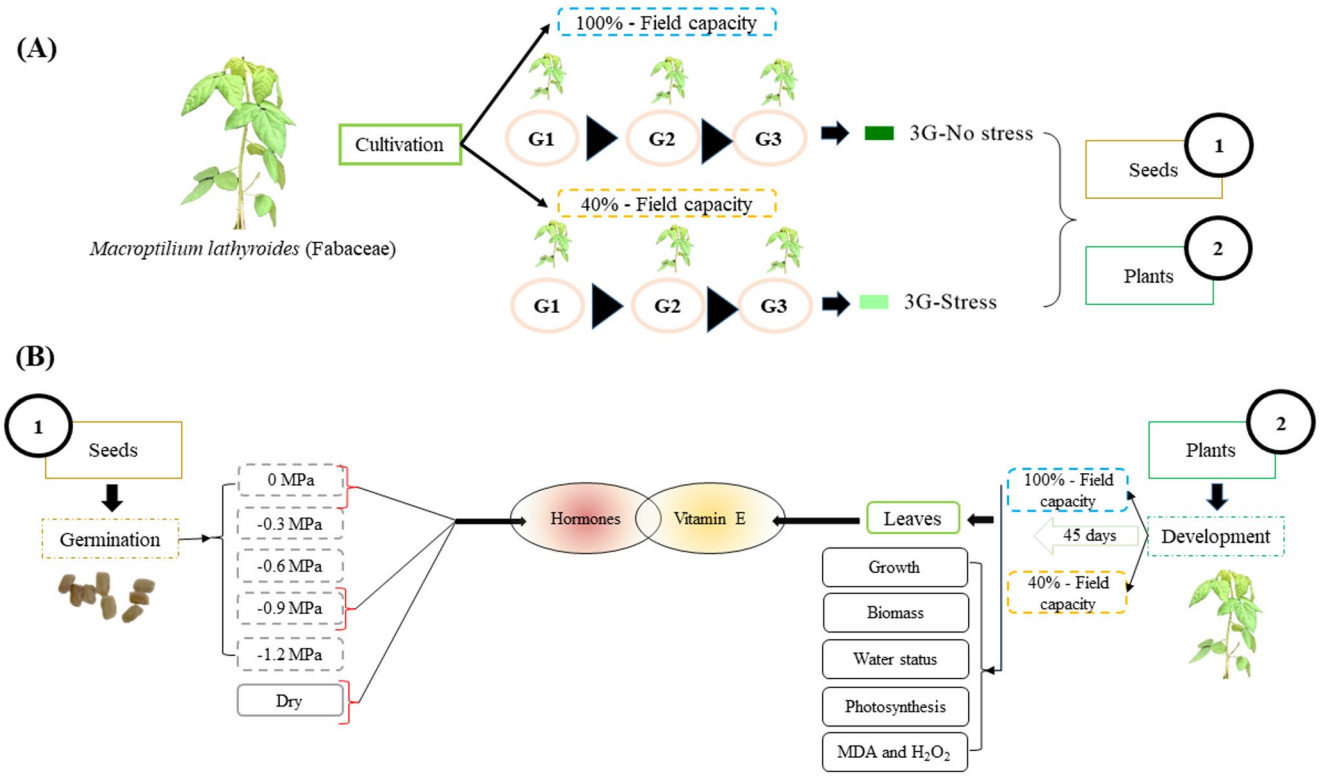


Fig. 1 Experimental approach used to assess the occurrence of transgenerational memory in *Macroptilium lathyroides*. (A) Schematic representation of the cultivation of successive generations (G) to obtain progenies derived from three generations grown under 100% field capacity (3G–No stress) and from three generations grown under 40% field capacity (3G–Stress). (B) Diagram of the experimental setup used to evaluate the physiological and biochemical responses of seeds and plants originating from the seed lots described in (A)

−0.9 MPa potential, collection occurred 18 h after imbibition began. As a comparative parameter, non-imbibed (dry) seeds were also analyzed. At each sampling point, 100 mg of plant material was collected, lyophilized, and stored in a desiccator with silica gel.

Tocopherols Analyses

The tocopherols were analyzed by high-performance liquid chromatography (HPLC) according to Amaral et al. (2005). For sample preparation, 30 mg of freeze-dried seeds was ground in liquid nitrogen and homogenized in a final extraction volume of 0.9 mL cold methanol. In the first extraction round, 0.3 mL of methanol was added in each sample and sonicated in an ultrasonic bath for 30 min. The extract was centrifuged at 4 °C for 10 min at 15.980 g, and the supernatant was collected. The process was repeated twice until achieving final extraction volume. Supernatants were then centrifuged and filtered into vials through 0.45 µm PTFE filters (Phenomenex, Torrance, CA, USA) and injected into the HPLC system, consisting of a Waters 600 controller pump, a Waters 717 plus auto-sampler, and a Jasco FP-1520 fluorescence detector. Tocochromanols were separated by using a normal-phase column (Inertsil 100 A, 5 µm, 30 × 250 mm, GL Sciences Inc., Tokyo, Japan) by using a mobile phase of n-hexane and 1,4-dioxane (95.5:4.5) and detected by fluorescence emission. Pure standards for tocopherols and tocotrienols (Extrasynthese, Genay, France) were used for calibration.

Hormonal Profiling

The endogenous concentrations of stress-related phytohormones, including abscisic acid (ABA), jasmonates [12-*oxo*-phytodienoic acid (OPDA), jasmonic acid (JA), and jasmonoyl-isoleucine (JA-Ile)], and salicylic acid (SA), along with growth- and development-associated hormones such as cytokinins (CKs) [*trans*-zeatin (tZ), 2-isopentenyl adenine (2iP), and their ribosides, *trans*-zeatin riboside (tZR) and isopentenyl adenosine (IPA)], auxin [indole-3-acetic acid (IAA)], and gibberellins (GA_1, GA_3, GA_4, and GA_7), were quantified using ultra high-performance liquid chromatography coupled with tandem mass spectrometry (UHPLC-MS/MS) following the methodology described by Müller and Munné-Bosch (2011). The hormonal profile was assessed using the same methanolic extraction method described previously but supplemented with deuterium-labelled internal standards (Olchemim, Olomouc, Czech

Republic). Briefly, 20 mg of freeze-dried seeds was ground and extracted in 0.4 mL of cold methanol with deuterium-labelled standards, by cold ultrasonication for 30 min, vortexing and centrifugating for 10 min at 4 °C and 15,980 *g*. After collecting supernatants, the pellet was re-extracted. Then, supernatants were filtered through hydrophobic 0.22 µm PTFE filters (Phenomenex, Torrance, CA, USA) and transferred to vials for analysis via UHPLC-MS/MS system (QTRAP 6500, AB Sciex, Concord, Ontario, Canada). Hormones were quantified in either the negative or the positive ion mode considering the recovery rate for each sample with the deuterium-labelled internal standard and by using calibration curves for each analyte in the MultiQuant TM 3.0.1. software.

Transgenerational Memory in Plants

Plant Cultivation

Plants progenies 3G-No stress and 3G-Stress treatments were grown in pots (5 L capacity) for 45 days under two water availability conditions: A - cultivation for 45 days with soil moisture maintained at 100% of field capacity; B - cultivation with soil moisture at 100% of field capacity for the first 30 days, followed by a reduction to 40% of field capacity for the final 15 days. Plants from both treatments were entering the reproductive stage at 45 days, when they were collected. Ten replicates were used for each progenies (3G-No stress and 3G-Stress) under each water availability regime.

Growth Parameters and Biomass

To analyze plant growth, height, stem diameter at soil level, and the number of leaves were measured for each plant at two time points: after 30 days of cultivation (when some plants were subjected to water stress under condition – B) and at the end of the experiment (45 days). From the measurements of stem diameter and height, the relative growth rate (RGR) was calculated using the following equation: $RGR = \ln (d_f^2 \times H_f) - \ln (d_i^2 \times Hi)/t$, where ln is the natural logarithm, D_f and D_i are the final and initial stem diameters, respectively, H_f and H_i denote the final and initial heights, respectively, and t is the time in days between the initial and final growth measurements (Baltzer and Thomas 2007).

At the end of the experiment, the plants were separated into roots, stems, and leaves. These fractions were dried in a forced-air circulation oven at 65 °C to determine the dry biomass.

Chlorophyll a Fluorescence and Photosynthetic Pigments

Parameters related to chlorophyll a fluorescence were measured at the end of the experiment (45 days) in fully expanded leaves using a portable modulated fluorometer (model PAM-2500, Walz, Effeltrich, Germany). To assess the potential quantum yield (Fv/Fm), leaves were dark-acclimated for 30 min. After this period, the minimum fluorescence (F0) was measured under weak modulated light (0.5 µmol m^{-2} s^{-1}), and the maximum fluorescence (Fm) was determined using a saturating light pulse (3000 µmol m^{-2} s^{-1}) lasting 0.8 s. The maximum quantum yield of PSII was calculated as Fv/Fm, where Fv is the difference between Fm and F0.

To determine the photosynthetic response to different light intensities, leaves were exposed to increasing actinic light intensities (0–2000 µmol m^{-2} s^{-1}) across 12 intervals. During these measurements, the following parameters were recorded: steady-state fluorescence (Fs) and light-adapted maximum fluorescence (Fm'). From these values, the following variables were calculated: Non-photochemical quenching (NPQ): NPQ = (Fm − Fm') / Fm' (Bilger and Bjorkman, 1990); Quantum yield of PSII (φII): φII = (Fm' − Fs) / Fm' (Genty et al., 1989); Electron transport rate (ETR): ETR = φII × PAR × 0.84 × 0.5, where PAR = photosynthetically active radiation, 0.84 = fraction of light absorbed by the leaves, and 0.5 = fraction of excitation energy distributed to PSII (Melis et al. 1987).

Photosynthetic pigments were extracted using 80% acetone from 100 mg of leaf tissue. Chlorophyll a (Chl a), chlorophyll b (Chl b), and carotenoids (Car) were quantified using a microplate reader (Multiskan FC Microplate Photometer, Thermo Fisher Scientific, Inc., Finland) at 470 nm (Chl a), 647 nm (Chl b), and 663 nm (Car), following Lichtenthaler and Buschmann (2001). Additionally, the chlorophyll a/b ratio (Chl a/b) and the total chlorophyll concentration (sum of Chl a and Chl b) were calculated.

Water Status and Gas Exchange

The relative water content (RWC) of the leaves from plants exposed to different water availability conditions was measured after 45 days of growth. To estimate RWC, the terminal leaflet of the fourth fully expanded leaf from each plant was collected. This leaflet was initially weighed to obtain the fresh weight (FW), then hydrated for 24 h at 4 °C in darkness to determine the turgid weight (TW), and finally dried in a forced-air oven at 65 °C until a constant dry weight (DW) was reached. RWC was calculated using the following equation: RWC= [(FW - DW)/ (TW - DW) x 100].

Gas exchange measurements were performed on fully expanded leaves using an infrared gas analyzer model

LI-6400XT (Li-Cor Inc., Lincoln, NE, USA) equipped with the chamber 6400-40 with LED source. All measurements were conducted under a photosynthetic photon flux density (PPFD) of 1000 µmol m^{-2} s^{-1}, ambient CO2 concentration (420–450 µmol mol^{-1}), and temperature of chamber adjusted for 25 °C. The sampling was made between 8 and 11 A.M. with the following parameters evaluated: net photosynthesis rate (*A*, µmol m^{-2} s^{-1}); stomatal conductance (*gs*, mol m^{-2} s^{-1}), transpiration (*E*, mmol m^{-2} s^{-1}); internal and external CO2 concentration ratio (*Ci/Ca*, µmol mol^{-1}); and instantaneous water-use efficiency (WUE = A/E).

Hydrogen Peroxide (H_2O_2) and Malondialdehyde (MDA)

The H_2O_2 content was determined according to the methodology described by Velikova et al. (2000). Leaves samples of the 100 mg were cryogenically ground and homogenized with 0.1% trichloroacetic acid (TCA). The samples were then centrifuged, and an aliquot of the supernatant was added to a microplate well containing 75 µL of 10 mM potassium phosphate buffer (pH 7) and 150 µL of potassium iodide. The samples, along with the standard curve, were read in a spectrophotometer at a wavelength of 390 nm. Lipid peroxidation levels were estimated by quantifying malondialdehyde (MDA) equivalents in the leaves following the method described by Hodges et al. (1999), which accounts for potential interference from compounds in the thiobarbituric acid reactive substances (TBARS) assay. Leaf samples (100 mg) underwent multiple extractions with 80% ethanol, followed by ultrasonication in an ice bath. After centrifugation and supernatant recovery, 1 mL of the extracted sample was mixed with a solution containing 0.65% thiobarbituric acid (TBA) and 20% trichloroacetic acid (TCA). The reaction was conducted by heating the samples at 95 °C for 25 min. Absorbance was measured at 440 nm, 532 nm, and 600 nm using a microplate reader (Multiskan FC Microplate Photometer, Thermo Fisher Scientific, Finland).

Tocopherols and Phytohormones

After 45 days of cultivation, leaves from plants of the 3G-No stress and 3G-Stress progenies, grown under contrasting water availability regimes, were analyzed for tocopherol concentration and hormonal profiles. For each replicate, 100 mg of leaves was collected, lyophilized, and stored in a desiccator containing silica gel. A single extract was used for both tocopherol and hormone analyses, prepared from 15 mg of freeze-dried material homogenized in 0.6 mL of cold methanol. These analyses were performed according to the methodologies described in Sect. 2.2.3 and 2.2.4.

Statistical Analyses

Data obtained from seeds and plants were tested for normality and homoscedasticity using the Shapiro–Wilk and Bartlett tests, respectively. Among the analyzed variables, those related to GA_3, GA_4, Mel, 2iP, and Z concentrations in seeds, as well as Mel, Ci/Ca, chlorophyll a, and H_2O_2 in leaves, did not show a normal distribution. For these variables, logarithmic transformation was applied, allowing the assumptions of normality and homoscedasticity required for ANOVA to be met. Once these assumptions were met, the data were subjected to a two-way ANOVA to assess the effects of progeny origin (3G-No stress and 3G-Stress), seed imbibition conditions (dry, 0, and −0.9 MPa), and soil water availability during plant growth (FC100% and FC40%). When a significant interaction between the factors was detected by the two-way ANOVA, means were compared using Tukey's test ($p < 0.05$). All statistical analyses and graph generation were performed using GraphPad Prism software version 8.0.2 (San Diego, CA, USA).

Results

Transgenerational Effects on Seed Germination under Different Water Potentials

The origin of the seeds, as well as their imbibition conditions, influenced several of the evaluated traits, particularly the concentrations of tocopherols and phytohormones. Seed germination was affected solely by water potential, with no effect of seed origin on either germination percentage or germination speed (Fig. 2). Germination percentages remained close to 100% under water potentials ranging from 0 to −0.6 MPa, followed by a ~ 35% reduction at −0.9 MPa ($P < 0.0001$), and no germination was observed at −1.2 MPa. For seeds from both origins, germination speed decreased progressively as water potential declined (Fig. 2).

The levels of α- and γ-tocopherol differed between dry seeds and those imbibed under 0 and −0.9 MPa water potentials (Fig. 3). A significant interaction between seed origin and imbibition condition was observed for α-tocopherol ($P = 0.0138$), with the highest concentrations detected in dry seeds from the 3G-No stress progeny. α-Tocopherol levels decreased upon imbibition, particularly in seeds subjected to −0.9 MPa, compared to dry seeds (Fig. 3). In contrast, γ-tocopherol concentrations were higher in imbibed seeds ($P = 0.0006$), regardless of water potential, and were not influenced by seed origin.

The levels of stress-related hormones differed between dry and imbibed seeds (Fig. 4). ABA concentration was higher in dry seeds compared to imbibed seeds, with the

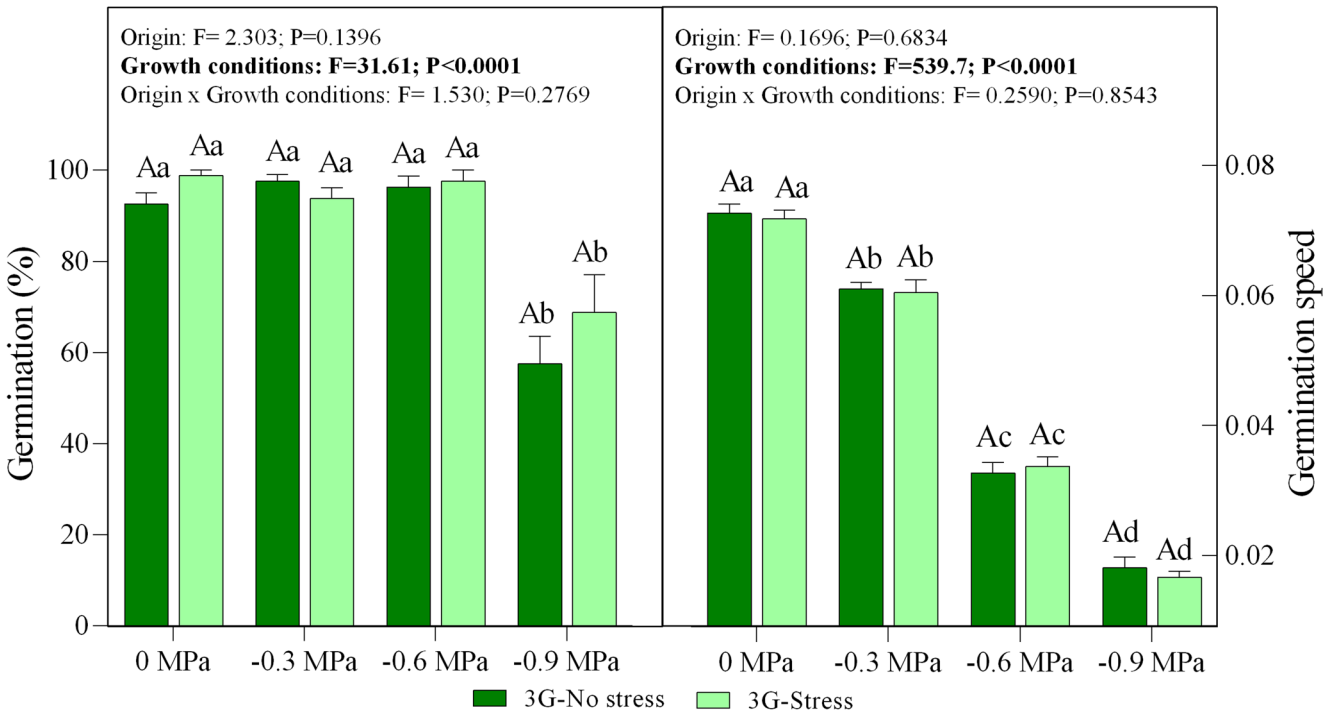


Fig. 2 Germination percentage and germination speed (means ± S.E.) of *Macroptilium lathyroides* seeds from 3G-No stress and 3G-Stress progenies subjected to different water potential levels. 3G–No stress: seeds produced by parent plants grown for three generations under 100% field capacity; 3G–Stress: seeds produced by parent plants grown for three generations under 40% field capacity. Uppercase letters denote significant differences between progenies under the same water potential while lowercase letters indicate significant differences among water potentials within the same progeny ($P<0.05$ Tukey's test)

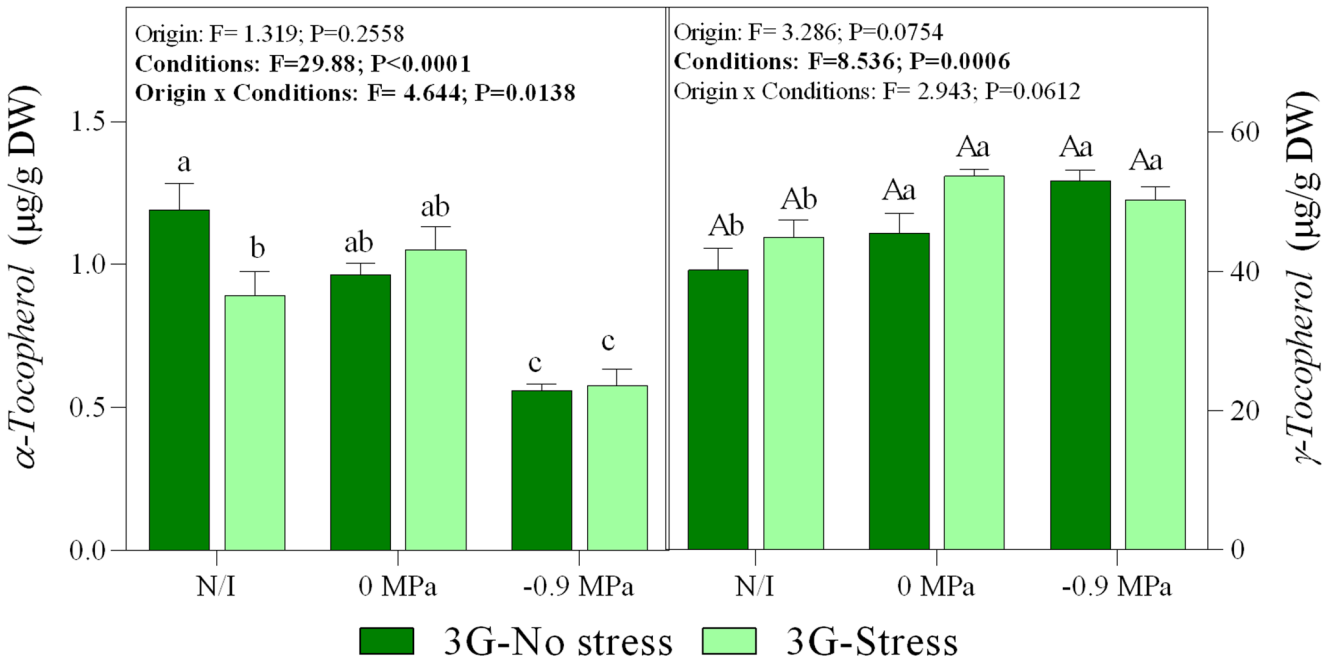


Fig. 3 Endogenous concentrations of α-tocopherol and γ-tocopherol in *Macroptilium lathyroides* seeds from different origins (3G-No stress and 3G-Stress progenies) under distinct imbibition conditions: dry; and imbibed up to Phase II at 0 MPa and −0.9 MPa. 3G–No stress: seeds produced by parent plants grown for three generations under 100% field capacity; 3G–Stress: seeds produced by parent plants grown for three generations under 40% field capacity. Values are presented as means ± S.E. ($N=10$). Uppercase letters indicate significant differences between seed origins under the same condition while lowercase letters indicate differences among imbibition conditions within the same origin ($P<0.05$ Tukey's test). In cases of interaction only lowercase letters are shown

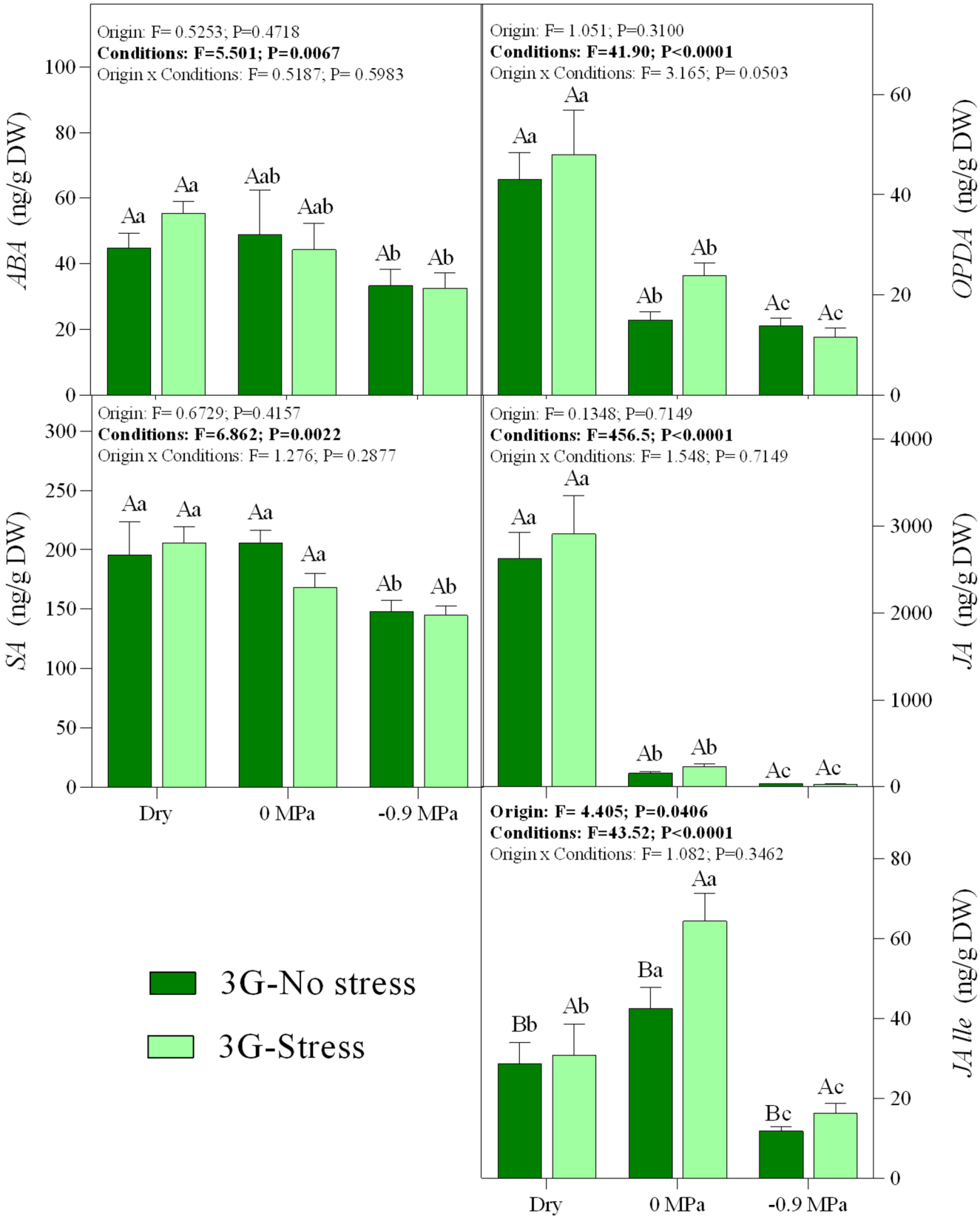

Origin: F= 0.5253; P=0.4718
Conditions: F=5.501; P=0.0067
Origin x Conditions: F= 0.5187; P= 0.5983
ABA (ng/g DW)
Origin: F= 1.051; P=0.3100
Conditions: F=41.90; P<0.0001
Origin x Conditions: F= 3.165; P= 0.0503
OPDA (ng/g DW)
Origin: F= 0.6729; P=0.4157
Conditions: F=6.862; P=0.0022
Origin x Conditions: F= 1.276; P= 0.2877
SA (ng/g DW)
Origin: F= 0.1348; P=0.7149
Conditions: F=456.5; P<0.0001
Origin x Conditions: F= 1.548; P= 0.7149
JA (ng/g DW)
Origin: F= 4.405; P=0.0406
Conditions: F=43.52; P<0.0001
Origin x Conditions: F= 1.082; P=0.3462
JA Ile (ng/g DW)
Dry
0 MPa
-0.9 MPa
3G-No stress
3G-Stress

Fig. 4 Endogenous concentrations of stress-related hormones—abscisic acid (ABA) salicylic acid (SA) 12-oxo-phytodienoic acid (OPDA) jasmonic acid (JA) and JA-isoleucine (JA-Ile)—in *Macroptilium lathyroides* seeds from different origins (3G-No stress and 3G-Stress progenies) under distinct imbibition conditions: dry; and imbibed up to Phase II at 0 MPa and −0.9 MPa. 3G–No stress: seeds produced by parent plants grown for three generations at 100% field capacity; 3G–Stress: seeds produced by parent plants grown for three generations at 40% field capacity. Values are expressed as means ± S.E. ($N=10$). Uppercase letters indicate significant differences between seed origins under the same condition while lowercase letters indicate differences among imbibition conditions within the same origin ($P<0.05$ Tukey's test)

lowest levels observed in seeds subjected to −0.9 MPa ($P=0.0067$). SA concentration decreased only in seeds incubated at −0.9 MPa (Fig. 4). Dry seeds exhibited higher concentrations of OPDA compared to imbibed seeds, with the lowest values found in seeds incubated at −0.9 MPa ($P<0.0001$), a response similar to that observed for JA (Fig. 4). Only JA-Ile concentration was influenced by both imbibition ($P<0.0001$) and seed origin ($P=0.0406$), with the highest levels found in seeds imbibed at 0 MPa compared to dry seeds and those exposed to −0.9 MPa. Regardless of imbibition condition, seeds from the 3G-Stress progeny showed higher JA-Ile concentrations compared to the 3G-No stress progeny (Fig. 4).

Distinct responses were observed among different types of GAs (Fig. 5). Concentrations of GA_1 and GA_7 did not differ between dry and imbibed seeds, nor were they influenced by seed origin ($P>0.05$). GA_3 levels were directly affected by imbibition ($P<0.0001$), and a significant interaction was found between imbibition and seed origin ($P<0.0001$). Dry seeds, regardless of origin, exhibited the highest GA_3 concentrations compared to imbibed seeds, while the lowest value was observed in seeds from the 3G-No stress progeny incubated at −0.9 MPa (Fig. 5). GA_4 concentration was influenced by both imbibition ($P<0.0001$) and seed origin ($P=0.0002$), with a significant interaction between these factors ($P=0.0058$). GA_4 concentration was higher in dry seeds of both progenies, similar to that observed in seeds from the 3G-Stress progeny exposed to −0.9 MPa. Imbibed seeds from the 3G-No stress progeny showed the lowest GA_4 levels (Fig. 5).

Among cytokinins, IPA concentration varied only according to imbibition, while ZR and Z levels were also influenced by seed origin (Fig. 5). IPA levels were higher in imbibed seeds ($P<0.0001$), regardless of osmotic potential, whereas 2iP levels did not vary among treatments. ZR levels increased after imbibition ($P<0.0001$), independent of water potential, with seeds from the 3G-Stress progeny exhibiting higher ZR concentrations than those from the 3G-No stress progeny ($P=0.0494$). For Z concentration, in addition to the individual effects of imbibition and origin, a significant interaction between these factors was observed ($P<0.0001$). Seeds from the 3G-Stress progeny showed higher Z concentrations than the 3G-No stress progeny, regardless of imbibition condition (Fig. 5).

Neither imbibition nor seed origin alone affected IAA concentration; however, a significant interaction between these factors was detected ($P=0.0042$). Seeds from the 3G-No stress progeny contained higher IAA levels than those from the 3G-Stress progeny when dry and imbibed in water (Fig. 5). No variation in melatonin levels was observed among seeds, regardless of origin or imbibition condition.

Transgenerational Effects on Plant Responses to Water Stress

Biomass accumulation, growth, and physiological responses of the plants were influenced solely by water availability during the experiment ($P<0.0001$), with no effect of plant origin observed on these traits ($P>0.05$). Plants grown under 100% field capacity (FC100%) exhibited greater biomass and higher relative growth rate (RGR) compared to those grown under 40% field capacity (FC40%) (Fig. 6). The RWC was higher in plants subjected to FC100%, remaining around 85%, approximately 10% greater than that observed in plants grown under water deficit (Table 1). Net CO_2 assimilation (A) was also higher in plants of both origins when cultivated without water restriction ($P<0.0001$). Transpiration (E) and stomatal conductance (gs), however, did not vary in response to any treatments. The ratio of intercellular to ambient CO_2 concentration (Ci/Ca), as well as water use efficiency (WUE), were influenced by cultivation conditions, both being higher in plants grown without water limitation (Table 1). Fv/Fm differed statistically between the two cultivation conditions ($P=0.0466$), with slightly higher values in plants grown under FC40% (Table 1). Plants subjected to water deficit also presented higher concentrations of photosynthetic pigments (Chl a, Chl b, and total Chl a + b) compared to those grown under FC100%. However, a higher Chl a/b ratio was observed in plants grown under FC100%, while carotenoid levels were not affected by any of the factors analyzed (Table 1).

Relationships between biochemical parameters related to oxidative stress and plant origin were observed (Fig. 7). Oxidative stress markers, malondialdehyde (MDA) and hydrogen peroxide (H_2O_2), were not influenced by plant origin or growth conditions ($P>0.05$). Tocopherol concentration, however, was affected by plant origin (Fig. 7). Although neither origin nor water availability alone influenced α-tocopherol concentration, a significant interaction between these two factors was detected ($P=0.0363$). α-Tocopherol levels in the 3G-Stress progeny grown under FC40% were higher compared to those grown under

FC100%. γ-Tocopherol concentration was influenced by plant origin ($P=0.0002$), with the 3G-Stress progeny exhibiting higher concentrations of this compound than the 3G-No stress progeny under both growth conditions (Fig. 7).

The concentrations of stress-related hormones were primarily influenced by the water availability during growth. Plants from both origins grown under water deficit conditions exhibited higher levels of ABA ($P<0.0001$) compared to those grown under FC100% (Fig. 8). Plant origin significantly affected SA levels ($P=0.0308$), with the 3G-No stress progeny presenting higher SA concentrations regardless of the growth condition (Fig. 8). Jasmonate concentrations were not influenced by origin but were affected by the growth condition (Fig. 8). Higher concentrations of OPDA, JA, and JA-Ile were detected in plants cultivated under water deficit compared to those grown under FC100% ($P<0.05$).

GA levels were mainly influenced by plant origin (Fig. 9). For GA_3, no individual effect of origin or growth condition was observed; however, a significant interaction between these two factors was detected ($P<0.0001$). The lowest GA_3 concentrations were found in the 3G-No stress progeny grown under FC40%, compared to other combinations of origin and growth condition (Fig. 9). Conversely, GA_4 concentration was affected solely by plant origin, with individuals from the 3G-No stress progeny exhibiting higher GA_4 levels under both growth conditions ($P=0.0470$).

Among the cytokinins, the concentrations of IPA, ZR, and Z remained unaffected by the analyzed factors, whereas the concentration of 2iP was significantly influenced by both plant origin ($P<0.0001$) and growth conditions ($P<0.0001$) (Fig. 9). Higher concentrations of 2iP were observed in the 3G-No stress progeny. However, regardless of origin, individuals grown under FC40% exhibited higher 2iP levels compared to those grown under FC100% (Fig. 9).

The IAA concentration was influenced by growth conditions but not by plant origin (Fig. 9). Plants from both origins grown under FC100% showed higher IAA concentrations compared to those cultivated under FC40% ($P=0.0001$). The Mel concentration was influenced by both origin ($P<0.0001$) and growth conditions ($P=0.0007$). The 3G-No stress progeny cultivated under water deficit exhibited nearly twice the Mel concentration compared to individuals grown under FC100% and to those from the 3G-Stress progeny subjected to both water regimes (Fig. 9).

Discussion

The species *M. lathyroides* exhibited remarkable stability when exposed to transgenerational water deficit. Regardless of parental water history, individuals maintained essential physiological processes under limited water availability and showed no detectable transgenerational effects on germination, growth, or photosynthetic performance. These findings contrast with the initial hypothesis of this study, which predicted that individuals derived from plants exposed to water deficit over three successive generations (3G-Stress progeny) would outperform those originating from non-stressed lineages (3G-No Stress progeny) under limited water conditions. Despite the absence of functional changes, parental water history induced metabolic adjustments in hormonal and antioxidant components, which may become advantageous during seedling establishment or under more severe water stress conditions. This pattern of stability is consistent with the species' ecology, as plants in semiarid regions such as the Caatinga experience pronounced climatic unpredictability due to irregular rainfall (Marengo et al. 2017; Moura et al., 2023). Over time, such conditions have selected for robust drought-tolerance mechanisms that are maintained across generations, largely independent of interannual variation in water availability (Almeida and Garcia, in prep.). In this context, experimental cultivation over three generations under contrasting water regimes was insufficient to change these deeply established mechanisms. Overall, our results highlight the strong ecological resilience of *M. lathyroides*, a semiarid native species capable of maintaining adaptive stability even under transgenerational water stress.

The reduction in osmotic potential negatively affected seed germination in both progenies, indicating that transgenerational water stress did not influence the germinative response of *M. lathyroides*. Seeds require a minimum water potential threshold to allow imbibition and the completion of the germination process (Maleki et al. 2024; del Alba et al. 2025). The water potential gradient affected *M. lathyroides* seeds from both lineages in a similar manner, with no observed effect of parental water stress on germinative performance. Previous studies have reported null or negative transgenerational effects of the parental environment on seed germination (Wijewardana et al. 2019; Hatzig et al. 2018). Seeds of *M. lathyroides* derived from plants exposed to water stress or well-watered conditions over three generations originated from natural populations occurring in the Caatinga, a biome characterized by pronounced rainfall irregularity. The drought conditions characteristic of the Brazilian semiarid region, to which this species has been exposed throughout its life history, have likely promoted the development of an robust and efficient adaptive response to water deficit, which could not be altered by three generations grown under contrasting water regimes (FC 40% and 100%).

Tocopherol concentration was influenced by the imbibition conditions, irrespective of seeds origin. The compounds α-tocopherol and γ-tocopherol are key antioxidants involved in the protection of plant tissues against oxidative

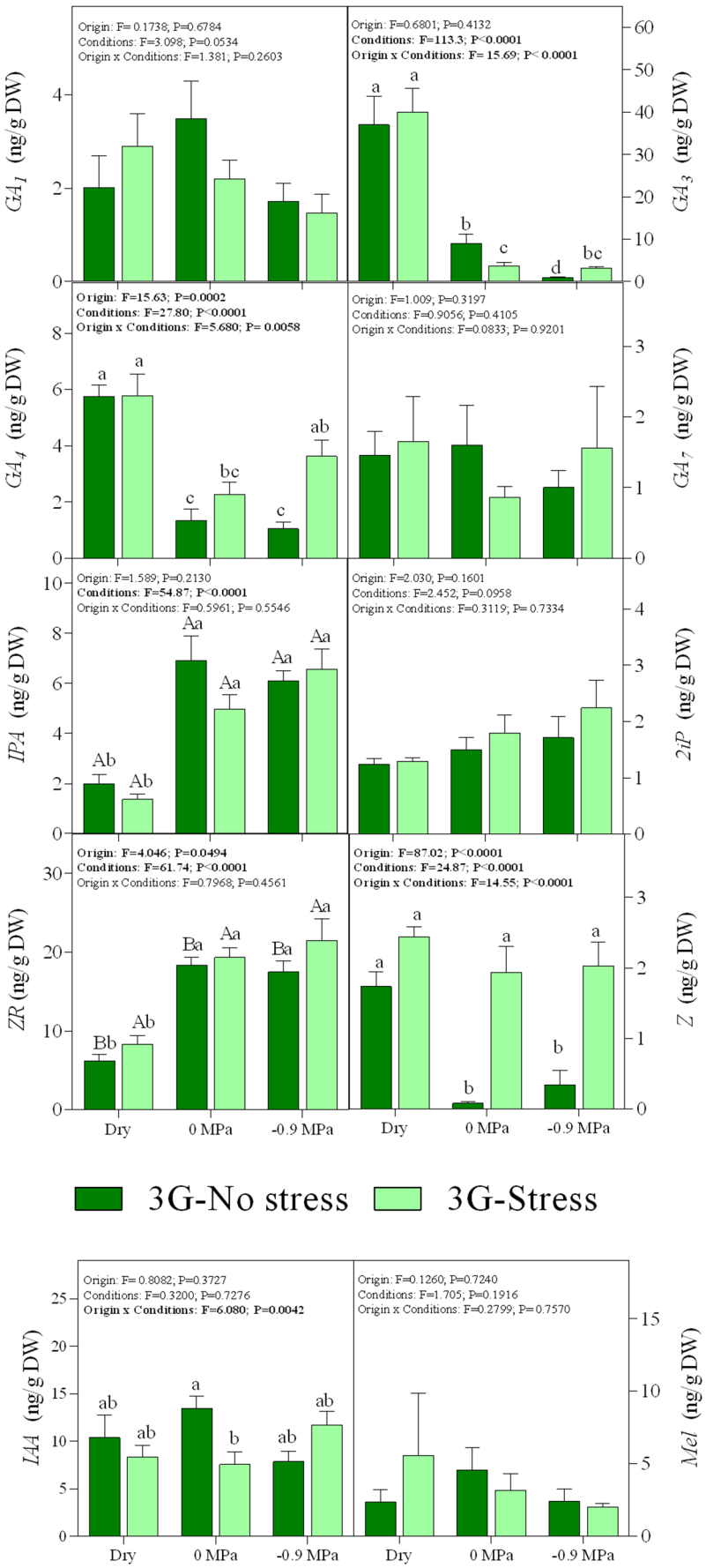


Fig. 5 Endogenous concentrations of growth-related hormones gibberellins (GA_1 GA_3 GA_4 and GA_7) and cytokinins (IPA-isopentenyl adenosine 2iP – 2-isopentenyl adenine Z – *trans*-zeatin and ZR – *trans*-zeatin riboside) auxin indole-3-acetic acid (IAA) and melatonin (Mel) in *Macroptilium lathyroides* seeds from different origins (3G-No stress and 3G-Stress progenies) under distinct imbibition conditions: dry; and imbibed up to Phase II at 0 MPa and −0.9 MPa. 3G–No stress: seeds produced by parent plants grown for three generations at 100% field capacity; 3G–Stress: seeds produced by parent plants grown for three generations at 40% field capacity. Values are presented as means ± S.E. ($N = 10$). Uppercase letters indicate significant differences between seed origins under the same condition while lowercase letters indicate differences among imbibition conditions within the same origin ($P < 0.05$ Tukey's test). In cases of interaction only lowercase letters are shown

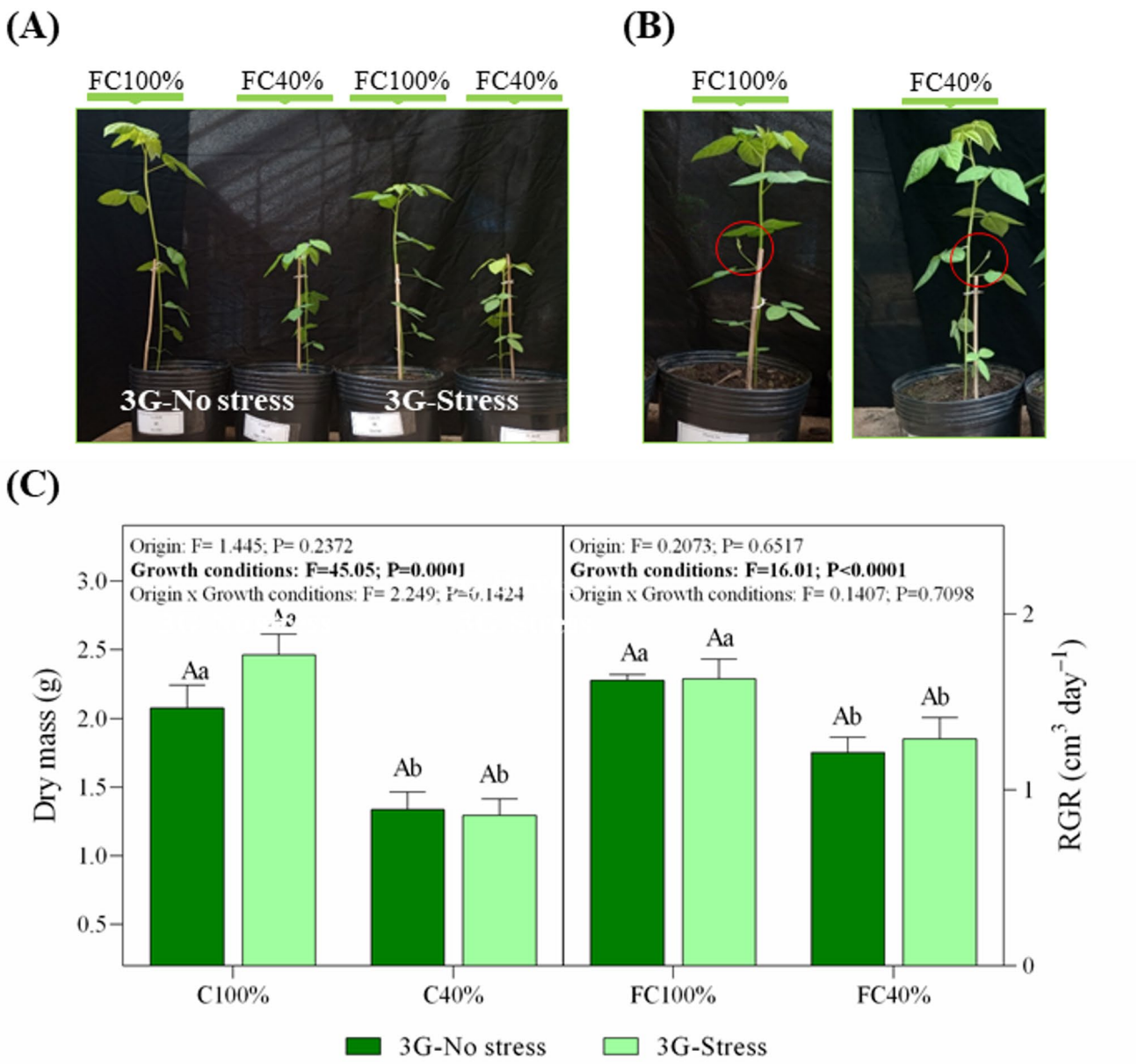


Fig. 6 Growth and biomass accumulation in *Macroptilium lathyroides*. (A) Individuals from different progenies (3G–No stress and 3G–Stress) grown under contrasting water availability regimes; (B) Plants at the end of the experimental period cultivated under distinct irrigation conditions initiating flowering synchronously; (C) Whole-plant dry mass and relative growth rate (RGR) of the 3G-No stress and 3G-Stress progenies after 45 days of cultivation under 100% field capacity (FC100%) and 40% field capacity (FC40%). 3G–No stress: plants produced from seeds obtained from parent plants grown for three generations at 100% field capacity; 3G–Stress: plants produced from seeds obtained from parent plants grown for three generations at 40% field capacity. Values are expressed as means ± S.E. ($N = 10$). Uppercase letters indicate significant differences between progenies under the same condition while lowercase letters indicate differences within progenies across conditions ($P < 0.05$ Tukey's test)

damage (Voll and Abbasi 2007; Mesa and Munné-Bosch 2023). α-Tocopherol plays a particularly important role in leaves, especially in protecting against photodamage, whereas γ-tocopherol, its precursor, acts mainly in seeds by mitigating potential damage associated with aging and stress during germination (Voll and Abbasi 2007; Mesa and Munné-Bosch 2023). The −0.9 MPa condition during seed imbibition in *M. lathyroides* may have reduced the conversion of γ-tocopherol to α-tocopherol. Given the prominent role of γ-tocopherol during germination, its conversion to α-tocopherol may further delay germination speed under osmotic stress conditions (Ma et al. 2020). Imbibed seeds, regardless of the osmotic potential, showed higher concentrations of γ-tocopherol compared to dry seeds, which may

Table 1 Relative water content (RWC), gas exchange parameters, maximum photochemical efficiency of photosystem II (Fv/Fm) and photosynthetic pigment concentrations in *Macroptilium lathyroides* plants derived from 3G-No stress and 3G-Stress progenies after 45 days of cultivation under 40% field capacity (FC40%) and 100% field capacity (FC100%)

Attributes	FC100%		FC40%	
	3G-No stress	3G-Stress	3G-No stress	3G-Stress
RWC	83.45 ± 1.72 Aa	69.29 ± 1.61 Aa	69.29 ± 1.61 Ab	82.53 ± 1.37 Ab
A ($\mu mol\ m^{-2}s^{-1}$)	23.65 ± 0.56 Aa	21.17 ± 0.36 Aa	21.17 ± 0.36 Ab	24.16 ± 0.75 Ab
E ($mmol\ m^{-2}s^{-1}$)	5.77 ± 0.25	5.58 ± 0.21	5.58 ± 0.21	5.90 ± 0.19
g_s($mmol\ m^{-2}s^{-1}$)	0.55 ± 0.02	0.53 ± 0.03	0.53 ± 0.03	0.48 ± 0.05
Ci/Ca	0.79 ± 0.009 Aa	0.77 ± 0.007 Aa	0.77 ± 0.007 Ab	0.81 ± 0.007 Ab
WUE	4.07 ± 0.16 Aa	3.82 ± 0.12 Aa	3.82 ± 0.12 Ab	4.22 ± 0.19 Ab
Fv/Fm	0.790 ± 0.004 Ab	0.796 ± 0.004 Ab	0.796 ± 0.004 Aa	0.789 ± 0.005 Aa
φPSII	0.32 ± 0.01	0.32 ± 0.09	0.32 ± 0.09	0.31 ± 0.01
NPQ	0.78 ± 0.07	0.77 ± 0.06	0.77 ± 0.06	0.80 ± 0.19
ETR ($\mu mol\ m\ -^{2}s^{-1}$)	115.5 ± 3.91	116.5 ± 6.47	116.5 ± 6.47	112 ± 4.45
Chl a($\mu g\ g^{-1}$)	25.82 ± 0.34 Ab	26.84 ± 0.22 Ab	26.84 ± 0.22 Aa	25.46 ± 0.46 Aa
Chl b ($\mu g\ g^{-1}$)	12.54 ± 0.57 Ab	15.34 ± 0.83 Ab	15.34 ± 0.83 Aa	12.85 ± 0.65 Aa
Chl a + b ($\mu g\ g^{-1}$)	38.37 ± 0.84 Ab	42.18 ± 1.00 Ab	42.18 ± 1.00 Aa	38.32 ± 0.93 Aa
Chl a/b ($\mu g^{g\ -1}$)	2.08 ± 0.09 Aa	1.79 ± 0.09 Aa	1.79 ± 0.09 Ab	2.01 ± 0.09 Ab
Carotenoids ($\mu g\ g^{-1}$)	4.68 ± 0.33	3.81 ± 0.46	3.81 ± 0.46	4.79 ± 0.23

3G–No stress: plants produced from seeds obtained from parent plants grown for three generations at 100% field capacity; 3G–Stress: plants produced from seeds obtained from parent plants grown for three generations at 40% field capacity. Gas exchange parameters include net CO_2 assimilation (A), leaf transpiration (E), stomatal conductance (gs), intercellular to ambient CO_2 ratio (Ci/Ca) and water use efficiency (WUE). Pigment concentrations include chlorophyll a (Chl a), chlorophyll b (Chl b), total chlorophyll (Chl a + b), carotenoids and the Chl a/b ratio. Values for effective quantum yield of PSII (φPSII), non-photochemical quenching (NPQ) and electron transport rate (ETR) refer to measurements taken at a light intensity of 1000 µmol m^{-2} s^{-1} on the light response curve. Data are presented as means ± S.E. ($N = 10$). Uppercase letters indicate significant differences between progenies under the same water condition; lowercase letters indicate significant differences within progenies across water conditions ($P < 0.05$ Tukey's test)

be associated with its role in protecting against the increase in reactive oxygen species resulting from the resumption of metabolic activity during imbibition (Bewley et al. 2013).

Although previous studies have shown that water stress experienced by parental plants influences the concentrations of stress-related hormones in seeds (Vigliocco et al. 2007; Andrade et al. 2009), the present study observed an increase only in JA-Ile concentrations. Seeds of *M. lathyroides* derived from the 3G–Stress progeny exhibited higher levels of JA-Ile compared to those from the 3G–No Stress progeny. Sheteiwy et al. (2018) found that in rice seeds, priming combined with jasmonates improved germination response under water stress conditions. However, the elevated JA-Ile concentration—the bioactive form of JA—did not affect seed germination, even when seeds were subjected to -0.9 MPa. This result suggests that the increased JA-Ile concentration in seeds from the 3G-Stress progeny may represent a metabolic adjustment potentially associated with enhanced seedling resistance to water deficit, as pointed out previously (Andrade et al. 2017; Sheteiwy et al. 2018).

The levels of ABA, SA, OPDA, and JA decreased during seed imbibition in *M. lathyroides* compared to dry seeds. It is well documented that under water stress, concentrations of ABA, SA, and jasmonates tend to increase in plant tissues as a tolerance mechanism to such conditions (Peleg and Blumwald 2011; Ullah et al. 2018; Ahmad et al. 2023; Villadangos and Munné-Bosch 2024). The reduction in these hormone levels after seed imbibition in *M. lathyroides* may be associated with leaching that occurs during the imbibition process (Andrade et al. 2005). Under water stress conditions, ABA can inhibit germination, acting as a defense mechanism by delaying this process until conditions are favorable for seedling establishment (Jia et al. 2020). Considering the high seasonal variability in water availability in the Caatinga (Silva et al. 2019, 2020), it can be suggested that the ability of *M. lathyroides* seeds to germinate even at low water potentials allows the exploitation of short rainfall pulses. This strategy, combined with the species' high drought resistance during adulthood, optimizes the chances of utilizing scarce water resources and enhances species survival.

The main metabolic adjustments associated with parental cultivation conditions were observed in gibberellin and cytokinin concentrations, which were higher in the 3G-Stress progeny. The increase in these hormone levels did not influence seed germination responses, suggesting that this enhancement may prepare the seedlings for initial development. GAs and CKs are well recognized for their roles in plant development, including cell division, elongation and differentiation, leaf expansion, bud formation, and root development (Ullah et al. 2018; Li et al. 2021; Martínez et al. 2016; Castro-Camba et al. 2022; Alsubaie et al.

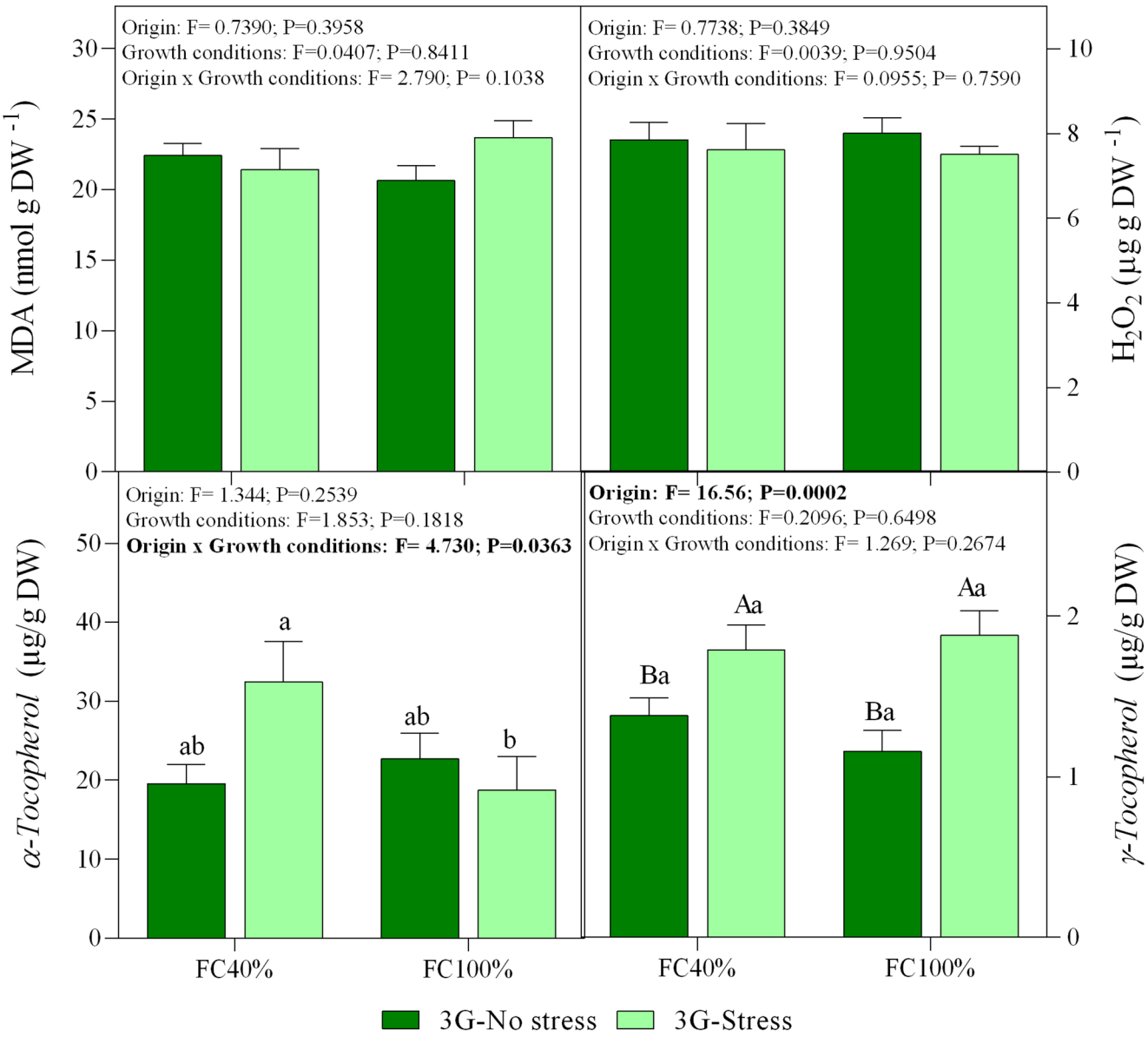


Fig. 7 Endogenous concentrations of hydrogen peroxide (H_2O_2) malondialdehyde (MDA) α-tocopherol and γ-tocopherol in leaves of *Macroptilium lathyroides* plants from 3G-No stress and 3G-Stress progenies after 45 days of cultivation at 100% field capacity (FC100%) and 40% field capacity (FC40%). 3G–No stress: plants produced from seeds obtained from parent plants grown for three generations at 100% field capacity; 3G–Stress: plants produced from seeds obtained from parent plants grown for three generations at 40% field capacity. Values are expressed as means ± S.E. ($N = 10$). Uppercase letters indicate significant differences between progenies under the same condition while lowercase letters indicate differences within progenies across conditions ($P < 0.05$ Tukey's test). In cases of significant interaction only lowercase letters are shown

2025). Previous studies have shown that plants derived from parents grown under water stress were able to produce seedlings with greater vigor than those derived from individuals cultivated without water stress (Hatzig et al. 2018; Racette et al. 2020). In this context, the higher concentrations of GA_3 and GA_4, as well as ZR and Z, in seeds of the 3G-Stress progeny compared to the 3G-No stress progeny suggest a physiological response that promotes increased vigor in the offspring. Considering the high irregularity of rainfall in the Caatinga, greater vigor would result in faster growth, thereby increasing the chances of plant establishment within the window of water availability, representing an important adaptive strategy (Hatzig et al. 2018).

It is well established that stress memory involves the offspring's ability to store information acquired under stressful parental environmental conditions, which optimizes their performance and survival under stress (Bruce et al. 2007; Walter et al. 2011). In this study, no differences were

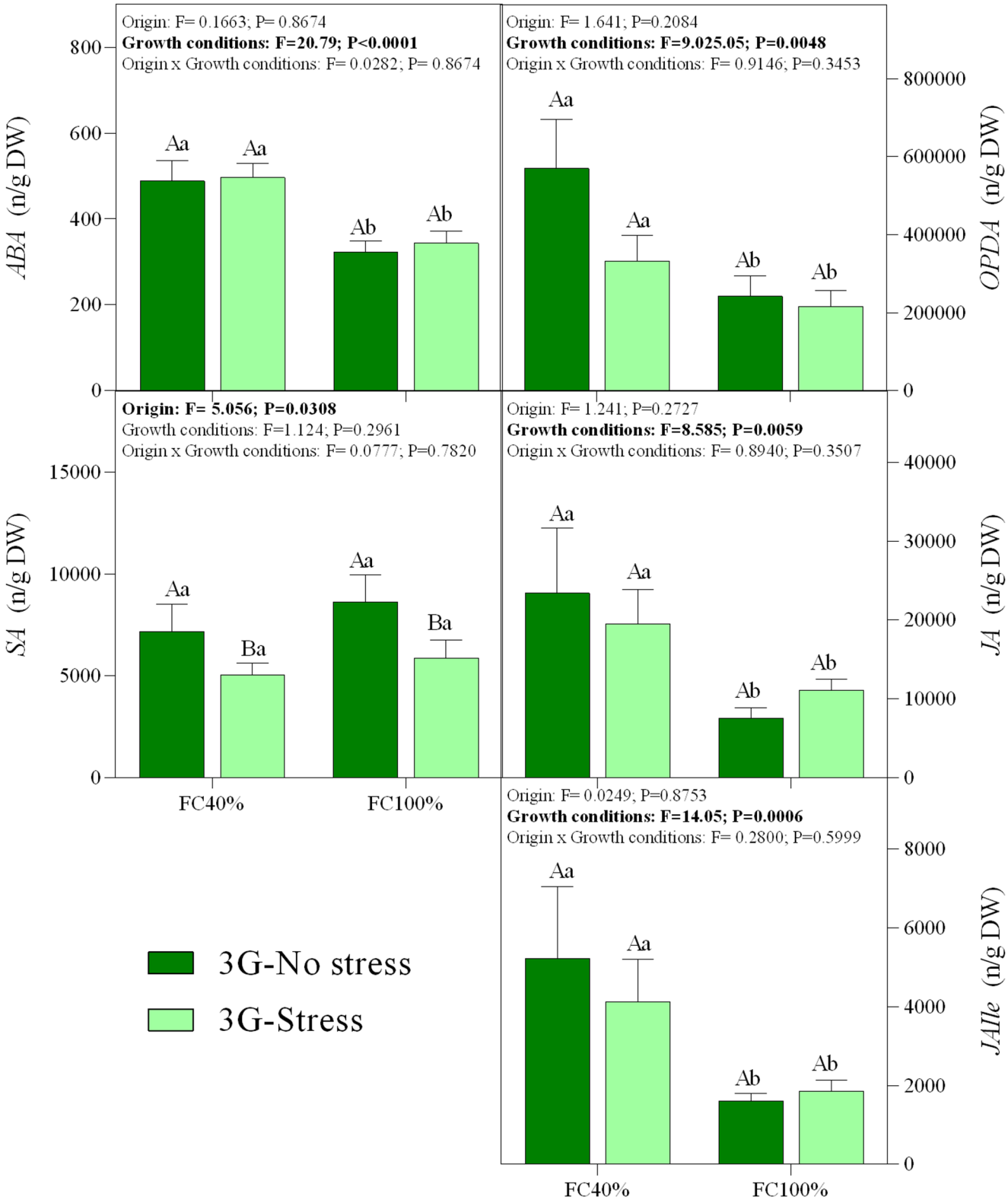


Fig. 8 Endogenous concentrations of stress-related hormones including abscisic acid (ABA) salicylic acid (SA) 12-oxo-phytodienoic acid (OPDA) jasmonic acid (JA) and JA-isoleucine (JA-Ile) in leaves of *Macroptilium lathyroides* plants from 3G-No stress and 3G-Stress progenies after 45 days of cultivation at 100% field capacity (FC100%) and 40% field capacity (FC40%). 3G–No stress: plants produced from seeds obtained from parent plants grown for three generations at 100% field capacity; 3G–Stress: plants produced from seeds obtained from parent plants grown for three generations at 40% field capacity. Values are presented as means ± S.E. ($N = 10$). Uppercase letters indicate significant differences between progenies under the same condition while lowercase letters indicate differences within progenies across conditions ($P < 0.05$ Tukey's test). In cases of significant interaction only lowercase letters are shown

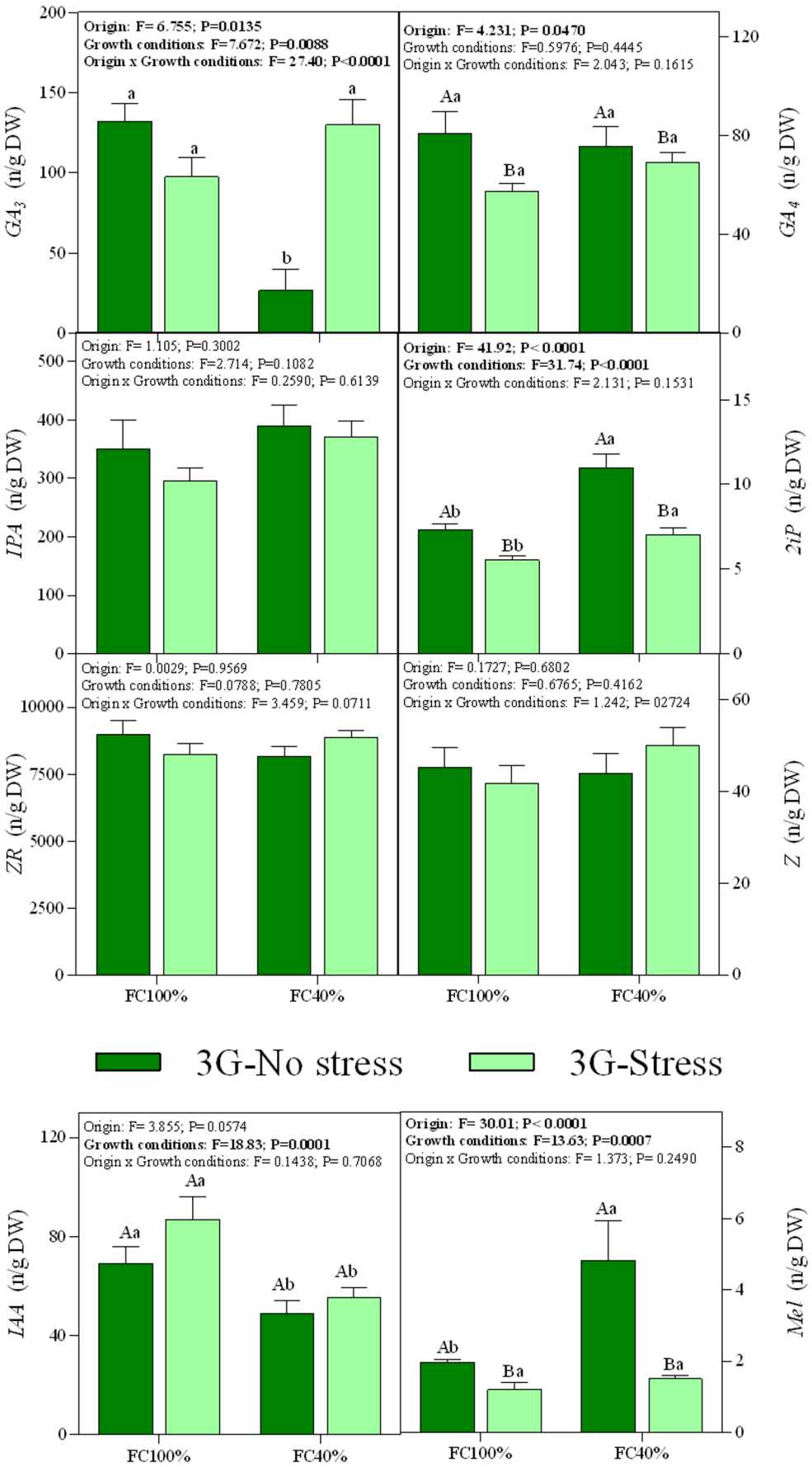


Fig. 9 Endogenous concentrations of growth-related hormones including gibberellins (GA_3 and GA_4) cytokinins (IPA – isopentenyl adenosine 2iP – 2-isopentenyl adenine Z – *trans*-zeatin and ZR – *trans*-zeatin riboside) auxin (indole-3-acetic acid IAA) and melatonin (Mel) in leaves of *Macroptilium lathyroides* plants from 3G-No stress and 3G-Stress progenies after 45 days of cultivation under 100% field capacity (FC100%) and 40% field capacity (FC40%). 3G–No stress: plants produced from seeds obtained from parent plants grown for three generations at 100% field capacity; 3G–Stress: plants produced from seeds obtained from parent plants grown for three generations at 40% field capacity. Values are presented as means ± S.E. ($N = 10$). Uppercase letters indicate significant differences between progenies under the same cultivation condition while lowercase letters denote significant differences within the same progeny under different cultivation conditions ($P < 0.05$ Tukey's test). In cases of significant interaction only lowercase letters are shown

observed in growth or photosynthetic attributes between plants derived from the 3G-Stress and 3G-No stress progenies. However, individuals from the 3G-Stress progeny exhibited biochemical adjustments that may represent adaptive signals to water deficit conditions, including higher γ-tocopherol concentrations and lower levels of 2iP and GA_4. In contrast, the 3G-No Stress progeny showed higher melatonin levels, particularly when exposed to water deficit, which may also reflect a response linked to parental environmental history.

Studies in soybean and wheat have reported developmental and productivity impairments in individuals whose parents were grown under water deficit compared with those not exposed to water limitation (Wijewardana et al. 2019; Becheran et al. 2023). In contrast, positive effects of transgenerational drought memory on physiological resistance and productivity have been demonstrated in barley, rapeseed, peanut, and wheat (Nosalewicz et al. 2016; Hatzig et al. 2018; Racette et al. 2020; Kambona et al. 2023). Transgenerational effects of water deficit have also been observed in non-domesticated plants, although mainly in species occurring in environments with more stable water availability than that characteristic of the Caatinga (Gonzalez et al., 2016; Lukić et al. 2023). The seeds of *M. lathyroides* used in the experimental generations originated from natural populations historically exposed to the intense fluctuations in water availability typical of the Caatinga. The stability of this species under transgenerational water deficit suggests that, unlike many crops shaped by artificial selection, native species with a long evolutionary history under water scarcity exhibit high resilience to hydric instability. However, transgenerational drought induced metabolic adjustments that, while not essential for plant resistance under the conditions evaluated here, may represent potentially important mechanisms under more severe stress or be amplified over a greater number of generations. Overall, the results presented here expand current knowledge by demonstrating the resilience of a species naturally adapted to the water stress characteristic of semiarid environments.

Individuals grown under FC40%, regardless of seeds origins, exhibited lower RWC and biomass. The reduction in growth and biomass accumulation may be related to the combined effect of decreased CO_2 assimilation (A), RWC, the Ci/Ca ratio, and water use efficiency (WUE) (Hatfield and Dold 2019; Haghpanah et al. 2024). These adjustments could be linked to the observed increase in ABA concentration and decrease in auxin levels in plants under water stress, a response typically evident under drought conditions (Peleg and Blumwald 2011; Ullah et al. 2018). Despite the reduced growth, plants grown under water limitation maintained development and phenological stages synchronized with those cultivated under FC100%, as evidenced by simultaneous flowering in both groups (Fig. 6). Plants cultivated at FC40% retained turgid leaves without any visible damage such as chlorosis or necrosis (Fig. 6), which may be associated with the absence of oxidative damage, as indicated by MDA and H_2O_2 levels. In this context, photosystem II appeared unaffected by water restriction, with Yield, NPQ, and ETR values remaining similar to those of plants under FC100%, and Fv/Fm values in stressed plants remaining around 0.8. The preservation of photosynthetic efficiency may be related to the maintenance of photosynthetic pigment concentrations, particularly chlorophyll, which was higher in plants grown at FC40%. The maintenance of plant vigor, photosynthetic performance, and pigment concentration may be attributed to the activity of antioxidant compounds and the coordinated regulation by multiple plant hormones (Peleg and Blumwald 2011; Verma et al. 2016).

M. lathyroides plants, regardless of seed origin, exhibited higher levels of ABA, OPDA, JA, and JA-Ile when grown under FC40%. ABA is recognized as the primary hormone responsible for drought tolerance in plants through various morphophysiological and molecular processes, notably including the regulation of stomatal activity and root development (Verma et al. 2016; Ullah et al. 2018). Jasmonates play a key role in mitigating the impacts of water deficit by modulating root hydraulic conductivity, thereby enhancing water uptake from the soil under drought conditions (Sánchez-Romera et al. 2014; Andrade et al. 2017). Among the different jasmonates, the bioactive form JA-Ile stands out and has been associated with ABA biosynthesis (de Ollas et al. 2015; Villadangos and Munné-Bosch 2023). Alongside increased concentrations of stress-related hormones in plants cultivated under FC40%, cytokinin levels of IPA, ZR, and Z remained similar to those observed in plants grown without water stress. Previous studies have indicated the role of cytokinins during drought in maintaining plant integrity by preserving antioxidant activity, delaying leaf senescence, conserving foliar pigments, and sustaining photosynthetic activity (Xu et al. 2016; Ullah et al. 2018; Beznec et al. 2021). Since drought responses are mediated by the combined action of multiple hormones (Ahmad et al. 2023), the results obtained for *M. lathyroides* suggest that drought resistance is linked to the coordinated action of ABA, jasmonates, and cytokinins, which collectively mitigate the impact of water deficit while maintaining plant performance under these conditions.

In the 3G–Stress progeny, changes in certain biochemical attributes were identified that may indicate transgenerational memory to water deficit. Plants derived from the 3G–Stress progeny exhibited higher γ-tocopherol concentrations than those from the 3G–No Stress progeny, regardless of the cultivation condition. This elevated γ-tocopherol may serve as a reserve compound, potentially converted

into α-tocopherol under more intense stress conditions, in line with findings from other species that demonstrated positive transgenerational effects on oxidative stress defense (Lukić et al. 2023). In addition to increased γ-tocopherol, plants from the 3G–Stress progeny also showed reduced levels of 2iP and GA_4. Although high cytokinin levels are commonly associated with improved stress tolerance, some studies have shown that both cytokinins and gibberellins can decrease under drought as part of an adaptive strategy (Jang et al. 2017; Li et al. 2019; Villadangos and Munné-Bosch 2024). Fleta-Soriano et al. (2015) reported lower gibberellin higher ABA concentrations in plants exposed to stress twice compared to those that had experienced a single stress event during their life cycle. In this context, the combination of elevated γ-tocopherol with reduced 2iP and GA4 in the 3G–Stress progeny suggests that these molecules may contribute to drought memory, enhancing plant responses under harsher conditions. Meanwhile, plants from the 3G–No Stress progeny accumulated more melatonin when cultivated under FC40%, which may represent a defense mechanism triggered in individuals with no prior exposure to drought over three generations. Melatonin has been recognized for its protective role under water stress, contributing to growth regulation, photosynthetic efficiency, and antioxidant defense (Ahmad et al. 2021; Sandoval et al. 2024). Therefore, the increase in melatonin in plants from non-stressed parental lines may reflect an induced response aimed at mitigating damage caused by the drought experienced during cultivation.

In conclusion, *M. lathyroides* demonstrated a remarkable ability to withstand water limitation, reflected in the physiological responses of plants grown under water restriction. Cultivation over three consecutive generations under contrasting water regimes did not alter the progeny's performance, both in the seed and plant stages, indicating a consolidated adaptive response to drought that does not change over a few generations. However, seeds and plants from the water-limited lineage exhibited consistent changes in cytokinin, gibberellin, and γ-tocopherol levels, showing that environmental information can be retained and transmitted at the biochemical level, even in the absence of visible phenotypic changes. The rigorous control of parental cultivation conditions in this study provides a solid basis for understanding how transgenerational water deficit influences progeny responses. Building on these findings, future research could benefit from examining multiple populations within the same ecosystem, thereby expanding insights into how intraspecific variability may modulate transgenerational responses to water deficit. Overall, the present results contribute to a broader understanding of how native species in semiarid ecosystems integrate and transmit stress signals across generations, offering valuable perspectives on the mechanisms underlying ecological resilience. Such knowledge may inform predictions of plant responses to increasingly frequent drought events and support the development of strategies to improve plant performance in water-limited environments.

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Data Availability Data will be made available on request.

Declarations

Competing interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence.

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