



Research article

Moisture content and mycorrhizal fungi in maternal environment influence performance and composition of *Lallemantia* species offspring

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ABSTRACT

The availability of soil water content and nutrition in the maternal plant environment plays pivotal roles in shaping the performance, physio-biochemical properties, and chemical composition of the produced seed. This study aimed to investigate the effects of water and arbuscular mycorrhizal fungi (AMF) of maternal plant environment on performance, physio-biochemical properties, and chemical compositions of *Lallemantia* species offspring. A split-factorial experiment was performed using a randomized complete block design (RCBD) with three replications. The main plot consisted of three drought stress (30 %, 60 % and 90 % of soil available water depletion). The subplots were the factorial combination of arbuscular mycorrhizal fungi (AMF⁻ and AMF⁺) and *Lallemantia* species (*L. iberica* and *L. royleana*). The offspring of both *Lallemantia* species experienced a decrease in seed performance, superoxide dismutase, catalase, ascorbate peroxidase enzyme activities, proline, and chemical composition as well as a rise in hydrogen peroxide and lipid peroxidation due to the limited availability of water in the maternal plant environment. On the other hand, providing adequate nutrition in the maternal plant environment resulted in improved germination index, increased starch, and oil content, as well as higher levels of nitrogen and phosphorus in the offspring of both *Lallemantia* species. Compared to the offspring of *L. royleana*, the offspring of *L. iberica* had a higher number of achenes, seeds, seed weight, larger seed size, greater germination index, and higher levels of starch, oil, nitrogen, phosphorus, potassium, and calcium. In contrast, the offspring of *L. royleana* exhibited higher longevity, enhanced germination under osmotic and salinity stress, increased proline levels, and higher activities of antioxidant enzymes such as superoxide dismutase, catalase, and ascorbic peroxidase as well as sucrose and total soluble sugar. The study concludes that the best seed performance, antioxidant enzyme activities, and carbohydrate levels were observed in the offspring of both *Lallemantia* species produced under 60 % soil available water depletion with AMF inoculation in the maternal plant environment. These findings highlight the significant impact of the soil

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available water depletion and AMF inoculation on the seed performance, physio-biochemical properties, and chemical composition of the offspring, providing valuable insights for optimizing seed production and performance.

1. Introduction

Dragon's head (*Lallemantia iberica* Fisch. & C.A.Mey.) and Lady's mantle (*L. royleana* Benth.), are annual herbs from the *Lamiaceae* family and are cultivated in Southwestern Asia and Europe [1]. The seeds of the above crops are widely used in the food and pharmaceutical industries due to their high mucilage and oil contents. Of note is the high linolenic acid (LA) contents, constituting 67–74 % of the oil, which has been associated with significant health benefits [2,3].

Seed performance pertains to the ability of seeds to sprout in different environmental situations and is a crucial aspect of the plant life cycle that holds significant ecological and agricultural value [4]. It has been noted that alterations in nutrient availability or exposure to drought stress during seed development and maturation can greatly influence seed performance [5]. Seeds, integral to plant propagation, directly influence germination rates, crop establishment, growth, and agronomic yield based on their inherent performance [6]. The performance and composition of seeds are influenced by a myriad of factors operating during plants developmental stages, including flowering and seed maturation. Among these factors, the maternal plant environment significantly contributes to seed attributes by shaping the conditions in which seeds develop. Previously, it has been demonstrated that the maternal plant environment plays a pivotal role in the performance and chemical compositions of offspring, especially during seed filling [7]. In addition, the sink-source interaction between maternal plants and their offspring (seeds) permits the seeds to accumulate reserves required for growth and germination [8]. Thus, variation in the maternal environment can greatly alter the performance of offspring produced [9]. Moisture availability and the presence of beneficial microorganisms, such as arbuscular mycorrhizal fungi, are key components of the maternal environment that can profoundly influence seed development, performance, and composition.

Water deficit is one of the major limiting factors affecting crop production worldwide [10]. It limits root development, resulting in the reduction of water and nutrient absorption [11]. These limitations exert a wide range of impacts on plant growth, seed development and chemical compositions of seeds [12]. Several studies have demonstrated that low soil available water during seed maturation reduces the seed performance of plants such as *L. iberica*, *L. royleana* [12] and *Glycine max* [13]. Loss of seed weight due to low soil available water during seed maturation has been related to a decline in carbohydrate synthesis and translocation of assimilates to the developing seeds as a result of reduced photosynthetic activities [14,15]. It has been reported that a decline in the moisture content of the maternal plant environment not only caused a reduction in seed weight and seed size but also a decrease in the germination of offspring under osmotic and salinity stress [16]. Insufficient soil moisture content can lead to poor pollination, higher rates of flower abortion, impaired cell division, and results in fewer and smaller seed production [17].

Drought induces the overproduction of reactive oxygen species (ROS), such as superoxide anion (O_2^-), hydroxyl radical (OH^\cdot), and hydrogen peroxide (H_2O_2) during seed development, [12]. These ROS provoke damage to lipids, proteins, and nucleic acid, causing lipid peroxidation, protein denaturation, and DNA mutation [18]. Previous studies reported that germination and longevity of alfalfa (*Medicago sativa* L.) [19], manduirana (*Senna macranthera* (Collad.) H.S.Irwin & Barneby) [20] and mung bean (*Vigna radiata* (L.) R. Wilczek) [21] seeds decreased due to the accumulation of ROS and lipid peroxidation. However, the expanding enzymatic and non-enzymatic detoxification systems during seed development can protect offspring against the deleterious effects of ROS [22].

The use arbuscular of mycorrhizal fungi (AMF) has been found effective in improving the plant drought tolerance and performance of produced seeds [13]. The inoculation of AMF can mitigate the detrimental effects of drought stress by strengthening the root systems [23]. The symbiosis relationship between AMF and the roots of maternal plants can promote nutrient and water uptake, and photosynthetic efficiency [3]. The role of AMF in enhancing stored resources such as carbohydrates and lipids in seeds, presumably through enhancement of photosynthesis in maternal plant leaves has been reported [24]. Accumulation of essential nutrients such as nitrogen and phosphorus in seeds produced under AMF inoculation has been linked to improved seed germination, weight, and chemical composition in various plant species [25].

Although previous studies have evaluated the impact of AMF on the growth productivity of *Lallemantia* species under drought, studies on the performance of produced seeds in the next generation are lacking. This study was, therefore, conducted to assess the influence of AMF inoculation in the maternal plant environment on the subsequent germination, growth, and physiological and biochemical responses of Dragon's head and Lady's mantle seeds under osmotic and salinity stress conditions. It was hypothesized that increasing drought stress in the maternal plant environment decreases the germination, growth, and physio-biochemical properties in offspring of *Lallemantia* species, while AMF inoculation in the maternal plant environment improves the germination and growth of *Lallemantia* offspring.

2. Materials and methods

2.1. Experimental design and treatments

This experiment was conducted in a randomized complete block design (RCBD) with split-factorial arrangement with three replications at the Research farm of the Agricultural College of Shahed University (35.34 E, 51.8 N, altitude: 1190 m above the sea level), Tehran, Iran in 2019 and 2020. The main plot consisted of three drought stress levels: 30 % (Ir1; without stress), 60 % (Ir2; mild stress),

and 90 % (Ir₃; severe stress) of soil available water depletion. The subplots were a factorial combination of arbuscular mycorrhizal fungi (AMF⁺ (inoculated) and AMF⁻ (non-inoculated)) and plant species of *Lallemantia* (*L. iberica* and *L. royleana*) [12].

2.1.1. Drought stress

To water the surrounding environment of the maternal plants, the soil moisture in the field was assessed utilizing a pressure plate device. The measurements encompassed determining the field capacity (FC) at 20.86 % and the permanent wilting point (PWP) at 10.81 %. An equation was employed to compute the maximum potential soil water depletion within the 0–20 cm depth range [26]:

$$\text{MAD} = \frac{Fc - \theta}{Fc - \text{PWP}} \quad (1)$$

The symbols MAD, θ , FC, and PWP stand for the maximum allowable depletion, soil volumetric moisture, soil volumetric moisture at field capacity, and the permanent wilting point, in that order. The following equation was utilized to quantify the allocated water volume [27]:

$$\text{In} = \frac{(Fc - \theta) \times D \times A}{100} \quad (2)$$

FC, θ , D, and A stand for the amount of water allocated, field capacity, soil moisture content, effective rooting depth, and the surface area of the plot (4 m²), respectively.

Before implementing the Ir₂ soil available water depletion on *Lallemantia* species, the required irrigation water amount for Ir₁ was determined by monitoring soil water level changes. This process involved extracting soil samples from the root development depth (0–30 cm) of the experimental plots, 24 h post-irrigation. The moisture content of these soil samples was then assessed by drying them in an oven at 105 °C for 24 h. The water content of each experimental plot was assessed through daily soil sampling [28,29].

The water demand for stress level I60 was calculated in a similar manner to I1. The irrigation volume for the Ir₂ treatment was regulated using volumetric water meters installed at the irrigation system's outlet. The field underwent irrigation once every five days. These irrigation procedures were initiated at the onset of plant establishment, particularly at the 8–12 leaf stage, occurring between February 2–8, 2019 and 2020. Following the harvesting process on June 14–22, 2019 and 2020, the seed batches of *L. iberica* and *L. royleana* with their initial seed moisture content were packed in aluminum foil bags (20 cm × 10 cm L × W) and stored at –28 °C until they were utilized in aging experiments conducted on November 1, 2020 and 2021.

2.1.2. Arbuscular mycorrhizal fungi

The arbuscular mycorrhizal fungi consisted of spores from three AMF species (*Funneliformis mosseae* (TH Nicolson & Gerd.) C. Walker & A. Schüssler, *Claroideoglossum etunicatum* (W.N. Becker & Gerd.) C. Walker & A. Schüssler, and *Rhizophagus intraradices* (NC Schenck & GS Sm.), which were obtained from the Soil Biology Laboratory at the Soil and Water Research Institute in Tehran, Iran. This Soil Biology Laboratory had cultivated the arbuscular mycorrhizal fungi on *Medicago sativa* L. and *Sorghum bicolor* L. as host plants [30]. In this research, about 20 g of mycorrhizal fungi was applied, which contained a rate of 1000 spores/10 g soil and were carefully blended with the soil (up to a depth of 20 cm) in each row [31].

Seeds were sown on November 14th in both years at a depth of 1–2 cm. Each plot consisted of four rows that were 2 m long, with a spacing of 50 cm between rows and a spacing of 5 cm between plants within each row. The spaces between the subplots, main plots, and replicates were 1.5, 2, and 3 m, respectively.

Seeds of *L. iberica* and *L. royleana* were harvested (on 14–22 June 2019 and 2020) from maternal plants which were grown under varied soil available water depletion and mycorrhizal fungi inoculations. After harvesting, the seeds (5 % moisture content) of both *Lallemantia* species were stored in a dark, cool room at a constant temperature of 10 °C with 30 % relative humidity for two months [12].

2.2. Measurements

2.2.1. Seed performance assessment

2.2.1.1. Characterization of seed development. The number of achenes, the number of seeds, seed weight, and seed size were determined. To obtain the mean seed weight, a batch of dry seeds was weighed and divided by the number of the weighed seeds [32].

2.2.1.2. Germination assays. A germination study was carried out at the Seed Science Laboratory of Shahed University in Tehran (in 2020 and 2021) to assess the germination index, longevity, seedling growth of offspring, germination under osmotic and salinity stress along with seedling length and seedling dry weight. The study was carried out as a factorial experiment utilizing a complete randomized design (CRD) comprising three variables: soil available water depletion, AMF inoculation, and plant species, each with three replicates. The experimental treatments consisted of soil available water depletion levels (Ir₁ (30 %), Ir₂ (60 %) and Ir₃ (90 %)), mycorrhizal inoculation (AMF⁻ and AMF⁺), and plant species (*L. iberica* and *L. royleana*).

Seed germination was recorded following the methods of the International Seed Testing Association [33]. Seeds (50) were placed on moist filter papers in 9 cm Petri dishes, and 10 mL water was added to them. The germination test was carried out under a 16/8 h fluorescent-white light/dark photoperiod at room temperature and 85 % relative humidity for 14 days. Seeds with radicle protrusions of at least 2 mm were considered germinated. The seedling length was measured, then dried for 24 h at 70 °C, and the dry matter of the

seedlings was weighed. Seed germination counts were conducted every day. Afterwards, the seed germination percentage and mean germination time (MGT) were calculated using the following equations [34]:

$$\text{Germination (\%)} = (\text{germinated seeds number} / \text{total number of sown seeds}) \times 100 \quad (3)$$

$$\text{MGT} = \Sigma(f \times i) / \Sigma f \quad (4)$$

where f is the number of newly germinated seeds on day i .

2.2.1.3. Seed longevity test. To assess seed longevity, an artificial ageing test was performed by incubating seeds at 40 °C and 100 % relative humidity in a closed tank for 1 day [35].

2.2.1.4. Germination under osmotic and salinity stress. Seed germination under stress conditions of salt (–6 bar NaCl), and osmotic (–6 bar PEG) stress was performed as previously reported [36].

2.2.2. Physio-biochemical properties

2.2.2.1. Proline content. Seeds weighing 0.2g were crushed in 3 mL sulfosalicylic acid (3.0 % w/v) and then the mixture was centrifuged at 180000 rpm for 20 min. Subsequently, a mixture of 3 mL of filtrate, 2 mL of glacial acetic acid, and 2 mL of ninhydrin reagent was placed in a separate test tube and left to incubate at 100 °C for 1 h. The process was halted by cooling the test tubes in an ice bucket. Following this, 4 mL of toluene was introduced and the solution was vigorously agitated for 1 min. The aqueous layer of toluene was then separated and left to settle at room temperature, after which the absorbance was measured at 520 nm using toluene as a reference [37].

2.2.2.2. Antioxidant enzyme extraction and activity assays. Seeds (0.2 g) were homogenized in ice-cold condition with 2 mL of 50 mM sodium phosphate buffer (pH 7.0), 1 % (w/v) polyvinyl pyrrolidone, 2 mL of ethylene diamine tetra acetic acid (EDTA) (2 mM). The mixture was centrifuged at 15000 rpm for 10 min at 4 °C. The supernatant obtained was used to analyze the antioxidant enzyme activities, such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX). The SOD activity was determined using 835 μ L of sodium phosphate buffer 50 mM (pH7), 33 mL of *p*-nitroblue tetrazolium chloride (NBT) (0.75 mM), 33 μ L of riboflavin, and 33 μ L enzyme extract [38]. To assay CAT activity, the enzyme extract (200 μ L) was mixed with 10 mM H₂O₂ and 5 mL of 50 mM phosphate buffer (pH 7.0). Afterwards, the CAT activity was analyzed spectrophotometrically following H₂O₂ consumption at 240 nm for 3 min after the addition of enzyme extract to the reaction mixture [39]. The reaction of APX included 50 mL of enzyme extract, 2 mL of ascorbic acid (5 mM), 5 mL of 50 mM phosphate buffer (pH 7.0), and 10 μ L of H₂O₂ (0.5 mM). The reaction was analyzed at 290 nm for 3 min [40].

2.2.2.3. Hydrogen peroxide. Seeds (250 mg) were mixed with 5 mL of 10 % (w/v) trichloroacetic acid and centrifuged at 13000 rpm for 20 min at 4 °C. Then 0.2 mL of supernatant was collected and added to 0.5 mL of 5 mM phosphate buffer (pH 7.0) and 1 mL of 1 M potassium iodide. The absorbance was measured at 390 nm. Hydrogen peroxide was measured using a standard curve of H₂O₂ [41].

2.2.2.4. Lipid peroxidation. About 250 mg seeds were mixed with 10 mL of 0.1 % trichloroacetic acid (TCA) acid (TCA). The mixture was centrifuged at 15000 rpm for 20 min at 4 °C, and then 1.0 mL of the supernatant was added to 1 mL of 0.5 % thiobarbituric acid (TBA). The samples were heated at 95 °C for 30 min and placed in an ice bath. The absorbance was analyzed at 532 nm and 600 nm. Malondialdehyde concentration was measured using the extinction coefficient of malondialdehyde at 532 nm (155 mM⁻¹ cm⁻¹) [42].

2.2.2.5. Electrical conductivity. Firstly, seeds were washed with deionized water to get rid of any surface-adhered electrolytes. The seeds were soaked with 10 mL of distilled water and placed on a shaker (100 rpm) for 6 h at 25 °C. The initial electrical conductivity was determined using a conductivity meter. Afterwards, the samples were incubated at 95 °C for 15 min, and then the final electrical conductivity was measured [43].

2.2.3. Seed chemical compositions

2.2.3.1. Total soluble sugars. For the measurement of total soluble sugars, 0.3 g of seeds were powdered in 10 mL of ethanol (80 % v/v), and then incubated at 80 °C for 40 min. The obtained mixtures were centrifuged at 12000 rpm for 15 min at 100 °C. Total soluble sugars were analyzed at 490 nm [44].

2.2.3.2. Sucrose and starch contents. To analyze the sucrose content, 0.3 g of seeds were ground with 5 mL of 80 % ethanol (v/v) for half an hour. The resulting mixture was centrifuged at 10000 rpm for 10 min. The residue underwent two additional extractions with 80 % ethanol. The combined supernatants from the three extractions were then mixed with more 80 % ethanol to reach a total volume of 5 mL. The sucrose content was measured at 480 nm. Following the removal of ethanol through evaporation, 2 mL of distilled water was added to the samples, which were subsequently incubated at 100 °C for 15 min. Starch hydrolysis was carried out using 9.2 M and

4.6 M HClO₄. The starch content was quantified by measuring the absorbance with anthrone reagent at 620 nm [45].

2.2.3.3. Mucilage. To collect mucilage, 10 g of seeds were placed in boiling water at 100 °C for 30 min, and then left to cool down to room temperature (20 °C) for 3 h. The mucilage was precipitated by adding ethanol to obtain a final concentration of 80 % (v/v). Seeds were removed from mucilage by centrifugation (4500 rpm for 30 min at 5 °C) and the precipitate dried in an oven (50 °C). The weight of the dried precipitate was taken to represent the total mucilage content [46].

2.2.3.4. Oil. The oil content was obtained using a Soxhlet apparatus. First, 10 g of seed was soaked in 150 mL hexane solution (ACS grade, Reag. Ph. Eur., ≥99 %; obtained from Merck Chemical Co., Germany) for 10 h. After solvent removal, oil was extracted from powdered seed [47].

2.2.3.5. Mineral concentration. To measure seed minerals such as nitrogen (N) and phosphorus (P), 25 g of seed samples were ashed (500–600 °C) and then dissolved in 2.0 M HCl. Nitrogen concentrations were measured by the Kjeldahl method [48]. Seed phosphorous was measured using a spectrophotometer (Lambda 25, PerkinElmer, USA) at 700 nm [49].

2.3. Statistical analyze

Data were analyzed using SAS (SAS version 9.2, SAS Institute, Cary, NC, USA). A combined analysis of variance (ANOVA) was performed to analyze the data. The mean comparisons were carried out using Tukey's honestly significant difference test (0.05 %). Heatmap and Pearson correlation were carried out using the R packages 'FactoMinerR' and 'factoextra' [50].

3. Results

The combined analysis of variance showed that the three-way interaction of drought stress, mycorrhizal inoculation and plant species was significant in seed performance (Table 1S), seed physio-biochemical properties (Table 2S), and seed chemical composition (Table 3S) of both *Lallemantia* species.

Table 1

Seed performance in *L. iberica* and *L. royleana* offspring produced under varied soil available water depletion with or without arbuscular mycorrhizal fungi inoculation of maternal plant environment.

Treatments			Number of achenes in plant	Number of seed in plant	Seed size (mm)	Seed weight (g)	Seedling length (cm)	Seedling dry weight (g)
Soil available water depletion	Plant Species	Mycorrhizal fungi						
Ir1	<i>L. iberica</i>	AMF ⁻	417.38 ± 1.82h	0.06 ± 0.0007c	0.06±0c	0.04 ± 0.00005e	7.67 ± 0.07e	0.03±0d
		AMF ⁺	557.71 ± 6.03ef	0.06 ± 0.0004b	0.06±0b	0.05 ± 0.00099b	9.95 ± 0.1b	0.04±0b
	<i>L. royleana</i>	AMF ⁻	665.48 ± 8.27c	0.05 ± 0.0004f	0.05±0f	0.02 ± 0.00011i	6.58 ± 0.09g	0.03±0ef
		AMF ⁺	959.15 ± 8.15b	0.05 ± 0.0004e	0.05±0e	0.02 ± 0.00012g	8.5 ± 0.06d	0.03±0c
Ir2	<i>L. iberica</i>	AMF ⁻	376.7 ± 7.72i	0.06 ± 0.0007d	0.06±0d	0.04 ± 0.00006d	7.28 ± 0.09f	0.03±0e
		AMF ⁺	683.94 ± 1.7c	0.07 ± 0.0006a	0.07±0a	0.05 ± 0.00017a	10.6 ± 0.08a	0.05±0a
	<i>L. royleana</i>	AMF ⁻	564.68 ± 9.4e	0.05 ± 0.0003f	0.05±0f	0.02 ± 0.00004h	5.83 ± 0.05h	0.02±0g
		AMF ⁺	1145.53 ± 16.23a	0.06 ± 0.0004d	0.06±0d	0.03 ± 0.00016f	9.35 ± 0.08c	0.04±0c
Ir3	<i>L. iberica</i>	AMF ⁻	256.25 ± 8.66j	0.05 ± 0.0007e	0.05±0e	0.04 ± 0.00008e	6.62 ± 0.08g	0.02±0 fg
		AMF ⁺	530.48 ± 7.65f	0.06 ± 0.0005d	0.06±0d	0.04 ± 0.00009c	8.4 ± 0.09d	0.04±0c
	<i>L. royleana</i>	AMF ⁻	475.35 ± 3.47g	0.04 ± 0.0006g	0.04±0g	0.02 ± 0.0001i	5.28 ± 0.09i	0.02±0h
		AMF ⁺	618.29 ± 3.5d	0.05 ± 0.0004e	0.05±0e	0.02 ± 0.00015g	7.95 ± 0.08e	0.03±0ef

Diverse letters over the bars indicate significant differences ($p < 0.05$) among treatments using Tukey's test. Ir1: 30 %, Ir2: 60 %, and Ir3: 90 % of soil available water depletion. AMF⁺: inoculated, AMF⁻: non-inoculated.

Table 2

Proline and antioxidant enzyme activities in *L. iberica* and *L. royleana* offspring produced under varied soil available water depletion with or without arbuscular mycorrhizal fungi inoculation of maternal plant environment.

Treatments			Proline ($\mu\text{M g}^{-1}$)	SOD (Unit mg^{-1} protein min^{-1})	CAT (Unit mg^{-1} protein min^{-1})	APX (Unit mg^{-1} protein min^{-1})
Soil available water depletion	Plant Species	Mycorrhizal fungi				
Ir1	<i>L. iberica</i>	AMF ⁻	9.72 ± 0.05g	8.96 ± 0.21g	12.57 ± 0.14g	3.23 ± 0.13e
		AMF ⁺	12.85 ± 0.03e	12.01 ± 0.09d	16.35 ± 0.13d	5.07 ± 0.09c
	<i>L. royleana</i>	AMF ⁻	10.82 ± 0.07fg	10.27 ± 0.05f	13.92 ± 0.05e	4.05 ± 0.04d
		AMF ⁺	17.76 ± 0.03c	13.15 ± 0.05c	16.91 ± 0.04bc	6.17 ± 0.06b
Ir2	<i>L. iberica</i>	AMF ⁻	9.51 ± 0.04g	7.87 ± 0.14h	11.25 ± 0.24h	2.31 ± 0.06f
		AMF ⁺	19.79 ± 0.01b	14.24 ± 0.09b	17 ± 0.04b	5.87 ± 0.07b
	<i>L. royleana</i>	AMF ⁻	10.02 ± 0.07g	9.19 ± 0.07g	13.3 ± 0.08f	4.01 ± 0.05d
		AMF ⁺	22.92 ± 0.05a	16.04 ± 0.1a	17.67 ± 0.03a	7.03 ± 0.12a
Ir3	<i>L. iberica</i>	AMF ⁻	7.35 ± 0.94h	6.02 ± 0.09i	11.23 ± 0.24h	1.97 ± 0.04f
		AMF ⁺	11.73 ± 0.07ef	10 ± 0.09f	15.97 ± 0.06d	4.88 ± 0.05c
	<i>L. royleana</i>	AMF ⁻	9.52 ± 0.02g	8.32 ± 0.11h	13.15 ± 0.14f	3.37 ± 0.03e
		AMF ⁺	14.79 ± 0.05d	11.06 ± 0.1e	16.47 ± 0.12cd	6.02 ± 0.04b

Diverse letters over the bars indicate significant differences ($p < 0.05$) among treatments using Tukey's test. Ir1: 30 %, Ir2: 60 %, and Ir3: 90 % of soil available water depletion. AMF⁺: inoculated, AMF⁻: non-inoculated. SOD: superoxide dismutase; CAT: catalase, APX: ascorbate peroxidase.

Table 3

Seed chemical compositions in *L. iberica* and *L. royleana* offspring produced under varied soil available water depletion with or without arbuscular mycorrhizal fungi inoculation of maternal plant environment.

Treatments			Total soluble sugar (mg g^{-1})	Sucrose (mg g^{-1})	Starch (mg g^{-1})	Mucilage (%)	Oil (%)
Soil available water depletion	Plant Species	Mycorrhizal fungi					
Ir1	<i>L. iberica</i>	AMF ⁻	35.25 ± 0.07hi	4.31 ± 0h	18.32 ± 0.05d	3.2 ± 0.04i	27.12 ± 0.19c
		AMF ⁺	38.3 ± 0.08 fg	4.52 ± 0.01g	20.46 ± 0.03b	7.44 ± 0.11g	32.58 ± 0.1a
	<i>L. royleana</i>	AMF ⁻	44.48 ± 0.06cd	5.81 ± 0.01c	15.29 ± 0.05g	13.16 ± 0.26f	18.22 ± 0.17f
		AMF ⁺	48.45 ± 0.09b	6.02 ± 0.01b	17.5 ± 0.05e	18.34 ± 0.17e	20.09 ± 0.24de
Ir2	<i>L. iberica</i>	AMF ⁻	37.29 ± 0.07gh	4.1 ± 0.01i	16.52 ± 0.05f	6.51 ± 0.06gh	30.62 ± 0.26b
		AMF ⁺	41.39 ± 0.08e	5.52 ± 0.01e	25.52 ± 0.08a	13.04 ± 0.19f	32.62 ± 0.12a
	<i>L. royleana</i>	AMF ⁻	42.5 ± 0.07de	5.56 ± 0.01de	13.43 ± 0.1h	31.3 ± 0.3b	19.26 ± 0.07ef
		AMF ⁺	53.08 ± 1.65a	7.2 ± 0.1a	20.35 ± 0.02b	49.45 ± 1.25a	21.29 ± 0.18d
Ir3	<i>L. iberica</i>	AMF ⁻	33.22 ± 0.07i	3.81 ± 0.01j	13.2 ± 0.2h	1.55 ± 0.09i	28.35 ± 0.91c
		AMF ⁺	35.4 ± 0.09hi	4.24 ± 0.02h	19.3 ± 0.05c	5.52 ± 0.11h	31.39 ± 0.47b
	<i>L. royleana</i>	AMF ⁻	40.27 ± 0.07ef	5.3 ± 0.01f	10.37 ± 0.07i	20.64 ± 0.23d	17.88 ± 0.19f
		AMF ⁺	45.43 ± 0.1c	5.68 ± 0.02d	15.02 ± 0.23g	23.91 ± 0.15c	19.61 ± 0.33e

Diverse letters over the bars indicate significant differences ($p < 0.05$) among treatments using Tukey's test. Ir1: 30 %, Ir2: 60 %, and Ir3: 90 % of soil available water depletion. AMF⁺: inoculated, AMF⁻: non-inoculated.

3.1. Effects of drought stress and AMF inoculation of maternal plant environment on seed performance of *L. iberica* and *L. royleana* offspring

An increase in the drought stress in the maternal plant environment remarkably decreased the number of achenes, number of seeds,

seed weight, and seed size in both species. In contrast, improving maternal plant environment with mycorrhizal fungi inoculation increased the aforementioned traits. There was a greater rise in the number of achenes, number of seeds, seed weight, and seed size of *L. iberica* compared to *L. royleana* (Table 1).

The highest germination percentage (Fig. 1a), seedling length (Table 1), and seedling dry weight (Table 1) were observed in seeds of both *Lallelantia* species that matured under the Ir₂ and +AMF inoculation conditions. A reduction in mean germination time (Fig. 1b) was obtained in seeds produced under Ir₂ and arbuscular mycorrhizal fungi inoculation of the maternal plants. Compared with seeds of *L. royleana*, germination and seedling growth were higher in seeds of *L. iberica*. In contrast, the mean germination time in seeds of *L. royleana* was greater than that in *L. iberica* (Fig. 1).

The highest and least seed longevity was observed in seeds produced under Ir₂ and Ir₃, respectively. The longevity of seeds produced by AMF-inoculated plants was greater compared to seeds produced by non-inoculated plants. Notably, when comparing the two species, the longevity in the seeds of *L. royleana* was higher than that of *L. iberica* (Fig. 2a).

The germination percentage under osmotic (Fig. 2b) and salinity (Fig. 2c) stress was higher in seeds produced under Ir₂ of the maternal plant relative to those produced under Ir₃ of the maternal plant. Besides, inoculation of AMF in maternal plant environment significantly improved germination of produced seed subjected to osmotic and salinity stress. An increase in germination percentage under salinity and drought stress was observed in seeds of *L. royleana* compared with *L. iberica* (Fig. 2).

3.2. Effects of drought stress and AMF inoculation of maternal plant environment on physio-biochemical properties of *L. iberica* and *L. royleana* offspring

The activities of antioxidant enzymes such as SOD, CAT, and APX were higher in seeds produced by both *Lallelantia* species under Ir₂. The inoculation of the maternal plant environment with arbuscular mycorrhizal fungi was beneficial, significantly increasing the antioxidant enzyme activities of produced seeds subjected to drought stress. The seeds of *L. royleana* exhibited higher antioxidant enzyme activity compared to those of *L. iberica* (Table 2).

The highest levels of hydrogen peroxide (Fig. 3a), MDA (Fig. 3b), and membrane stability index (Fig. 3c) were recorded in seeds produced by mother plants grown under Ir₃. Conversely, seeds produced under the inoculation of arbuscular mycorrhizal fungi exhibited lower levels of hydrogen peroxide, MDA, and membrane stability index. Compared with *L. royleana*, the highest levels of hydrogen peroxide, MDA, and membrane stability index were observed in the seeds of *L. iberica* (Fig. 3).

3.3. Effects of drought stress and AMF inoculation of maternal plant environment on seed chemical compositions of *L. iberica* and *L. royleana* offspring

The reduction in available soil water resulted in lower levels of total soluble sugar, sucrose, and starch in seeds produced by *L. iberica* and *L. royleana*. However, inoculation of the maternal plant environment with arbuscular mycorrhizal fungi increased the contents of these compounds in the seeds of both species. There was a significant rise in total soluble sugar and sucrose levels in *L. royleana* relative to *L. iberica*. Additionally, higher starch content was observed in *L. iberica* compared with *L. royleana* (Table 3).

The mucilage content increased in seeds produced under Ir₂ of the maternal plant environment. Also, the mucilage content in seeds from AMF-inoculated plants was more than that in non-inoculated plants. Compared with *L. iberica* seeds, mucilage content was higher in *L. royleana* seeds (Table 3).

A reduction in soil available water depletion of the maternal plant environment resulted in decreased nitrogen (Fig. 4a), phosphorus (Fig. 4b), potassium (Fig. 4c), and calcium (Fig. 4d) levels in the offspring. On the contrary, arbuscular mycorrhizal fungi symbiosis with maternal plant roots increased the nutrient concentrations in the offspring. Compared with *L. royleana* seeds, the highest concentrations of nitrogen, phosphorus, potassium, and calcium were obtained in *L. iberica* seeds (Fig. 4).

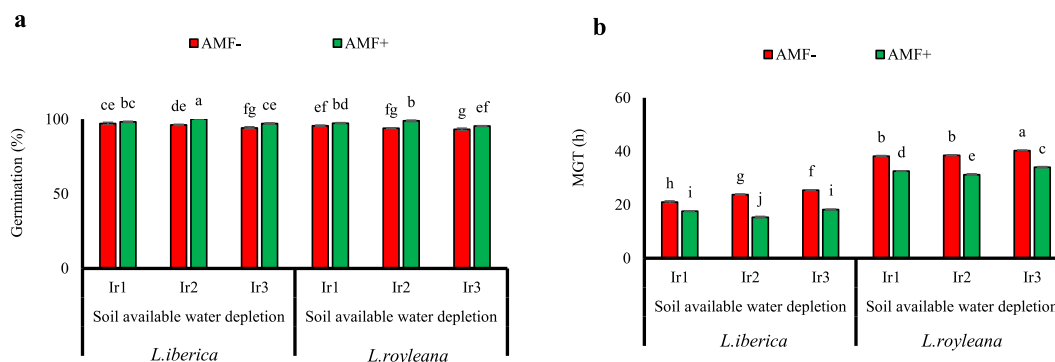


Fig. 1. Germination (a) and mean germination time (b) in *L. iberica* and *L. royleana* offspring produced under varied soil available water depletion with or without arbuscular mycorrhizal fungi inoculation of maternal plant environment. Diverse letters over the bars indicate significant differences ($p < 0.05$) among treatments using Tukey's test. The bars indicate the standard error of the means (\pm SE). Ir1: 30 %, Ir2: 60 %, and Ir3: 90 % of soil available water depletion. MGT: mean germination time. AMF⁺: inoculated, AMF⁻: non-inoculated.

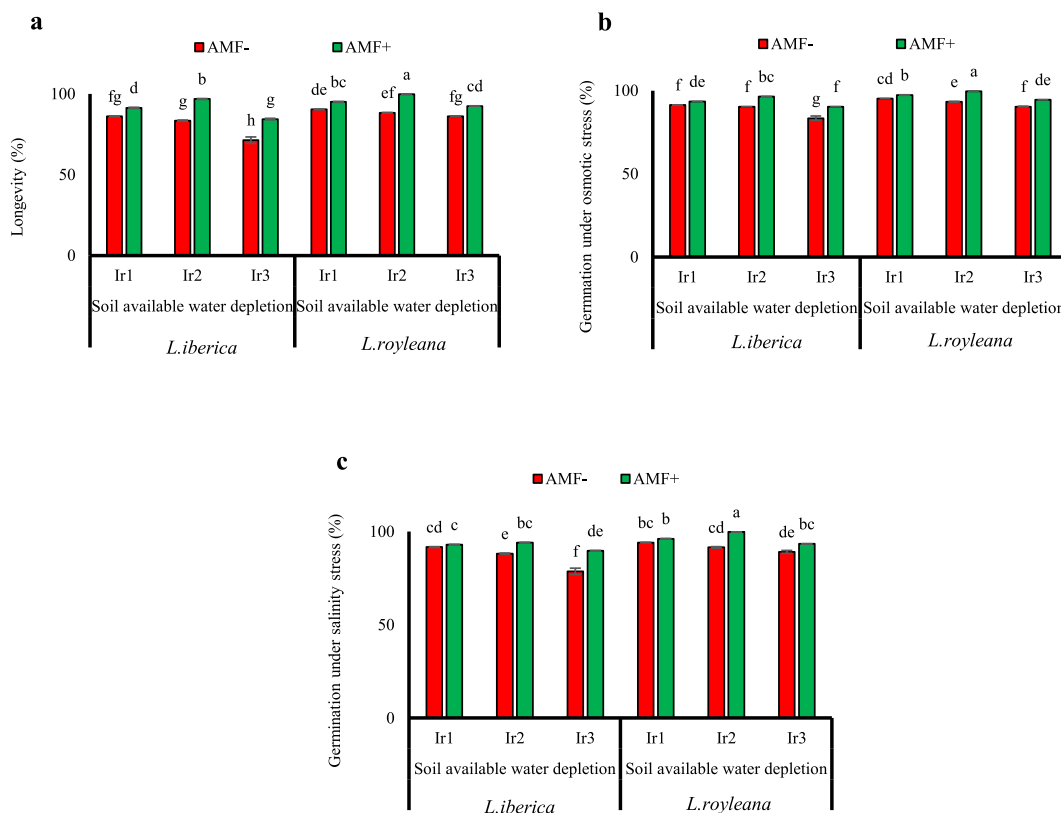


Fig. 2. Longevity (a), germination under osmotic stress (b) and germination under salinity stress (c) in *L. iberica* and *L. royleana* offspring produced under varied soil available water depletion with or without arbuscular mycorrhizal fungi inoculation of maternal plant environment. Diverse letters over the bars indicate significant differences ($p < 0.05$) among treatments using Tukey's test. The bars indicate the standard error of the means (\pm SE). Ir₁: 30 %, Ir₂: 60 %, and Ir₃: 90 % of soil available water depletion. AMF⁺: inoculated, AMF⁻: non-inoculated.

3.3.1. Pearson correlations

The Pearson correlation for *L. iberica* (Fig. 5a) and *L. royleana* (Fig. 5b) indicated that the germination percentage showed a correlation with starch content, superoxide dismutase activity, longevity, seedling length and seedling dry weight. Also, it showed that total soluble sugar had a positive correlation with seed mucilage. Additionally, the strongest correlation was observed between seed size, seed weight and starch content. On the other hand, malondialdehyde, hydrogen peroxide, electrical conductivity and mean germination time were negatively correlated with the number of achenes in plant, number of seeds in plant, Gp, Gp under osmotic stress, Gp under salinity stress, seedling length, seedling dry weight, longevity, sucrose, starch, total soluble sugar, mucilage, seed oil, nitrogen, phosphorus, proline, and antioxidant enzyme activities (Fig. 5).

3.3.2. Heatmap analysis

A correlation heatmap was generated to provide a comprehensive overview of the effects of soil available water depletion and arbuscular mycorrhizal fungi of maternal plant environment on seed performance, physio-biochemical attributes and seed chemical composition in seeds produced by *L. iberica* (Fig. 6a) and *L. royleana* (Fig. 6b). The heatmap indicated that Ir₂ and AMF were the most beneficial treatments in increasing the Gp, seedling length, seedling dry weight, seed longevity, Gp under osmotic stress, Gp under salinity stress, proline content, antioxidant enzyme activities, and seed chemical compositions. Additionally, these treatments were effective in reducing MGT, MDA, H₂O₂, and EC levels. In the dendrogram clustering heatmap analysis, it was observed that soil available water depletion and arbuscular mycorrhizal fungi inoculation treatments manifested four groups. The first group included offspring produced under Ir₂ AMF⁺. The second group contained the seeds matured under Ir₁ AMF⁺ and Ir₃ AMF⁺. The third group has seeds which were matured under Ir₃ AMF⁻. The last group included the offspring which were grown under Ir₁ AMF⁻ and Ir₂ AMF⁻. Furthermore, the traits were split into two clusters. The first cluster contained MDA, H₂O₂, EC, and MGT. The second cluster included the Gp, seedling length, seedling dry weight, seed longevity, Gp under osmotic stress, Gp under salinity, proline content, antioxidant enzyme activities, and seed chemical compositions, which confirmed the Pearson correlation.

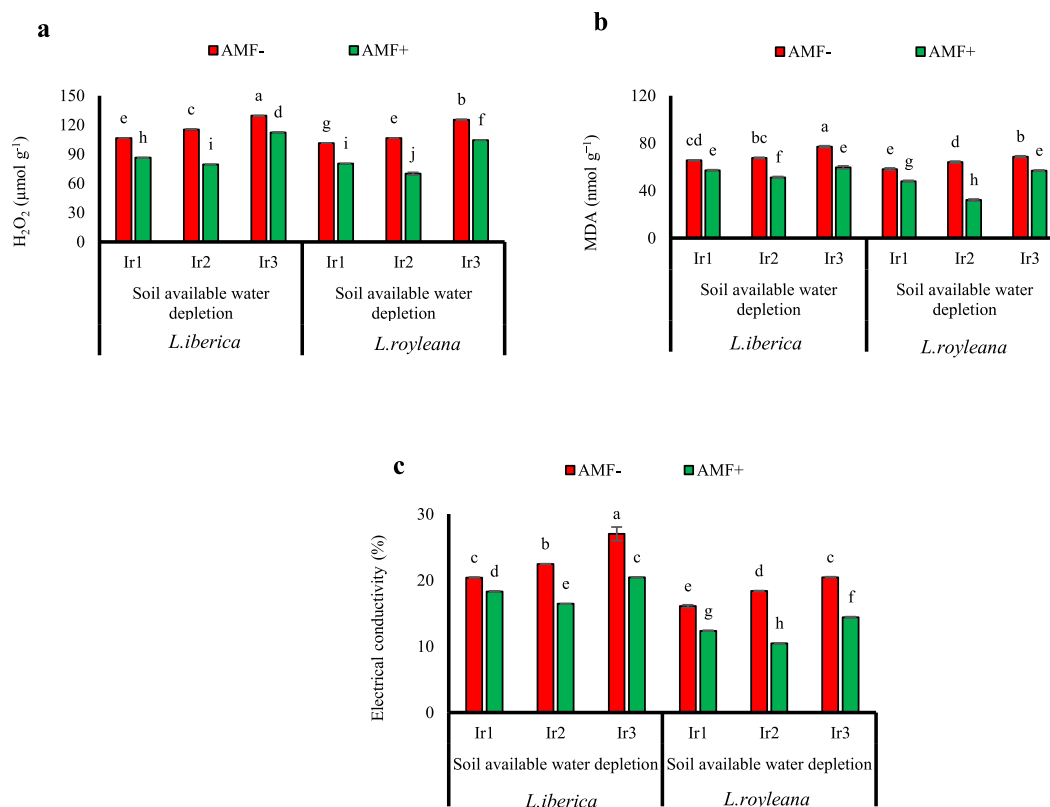


Fig. 3. Hydrogen prooxide (a), lipid peroxidation (b) and electrical conductivity (c) in *L. iberica* and *L. royleana* offspring produced under varied soil available water depletion with or without arbuscular mycorrhizal fungi inoculation of maternal plant environment. Diverse letters over the bars indicate significant differences ($p < 0.05$) among treatments using Tukey's test. The bars indicate the standard error of the means (\pm SE). H₂O₂: hydrogen peroxide; MDA: malondialdehyde. Ir1: 30 %, Ir2: 60 %, and Ir3: 90 % of soil available water depletion. AMF⁺: inoculated, AMF⁻: non-inoculated.

4. Discussion

In the present study, water and the presence of arbuscular mycorrhizal fungi in the maternal plant environment played a significant role in intricately shaping the seed performance, physio-biochemical characteristics, and chemical composition of the next generation [1,51].

It's noteworthy that the moisture levels in the maternal plant environment may be linked to the impact of photosynthetic activities [52]. As a consequence of reduced water availability during seed filling, there is a decrease in the distribution of macronutrients such as carbohydrates. This decline, in turn, has implications for the number of seeds produced, as well as their weight and size [53]. Conversely, when the maternal plant environment was enriched through inoculation with arbuscular mycorrhizal fungi, seeds exhibited increased resistance to water deficit. This enhancement was reflected in a higher number of achenes, seeds, greater seed weight, and larger seed size. These findings align with other studies that have demonstrated the benefits of growing mother plants under the influence of mycorrhizal fungi, resulting in higher seed yield and weight [54]. In the present study, better performance of *L. iberica* seeds in terms of higher number of achenes, number of seeds, seed weight, and seed size compared to *L. royleana* can be attributed to the higher nutrient uptake such as phosphorus and nitrogen in *L. iberica* maternal plant [51].

A decline in the germination index can be attributed to a reduction in sucrose levels, which are essential for providing energy during seed development and germination [48]. Additionally, an increase in mean germination time has been observed under drought stress conditions in various plant species such as *Oryza sativa* [55] and *Lavandula stoechas* [56]. A rise in germination index and seedling growth as well as a decrease in mean germination time in produced seeds under arbuscular mycorrhizal inoculation can be related to the expansion of mother plants' roots in the soil and uptake of more nutrients, particularly nitrogen, and phosphorus [57]. The absorbed nitrogen and phosphorus appear to play an important role in the structure of free amino acids and nucleic acids, ultimately contributing to improved seed development and germination [58,59]. Compared with *L. royleana*, higher germination index and seedling growth observed in *L. iberica* may be related to its greater seed weight. In contrast, more mean germination time in seeds of *L. royleana* may be due to higher mucilage in seeds of *L. royleana* [60]. Mucilage may limit the energy needed for germination, potentially delaying the germination process and increasing the mean germination time [61].

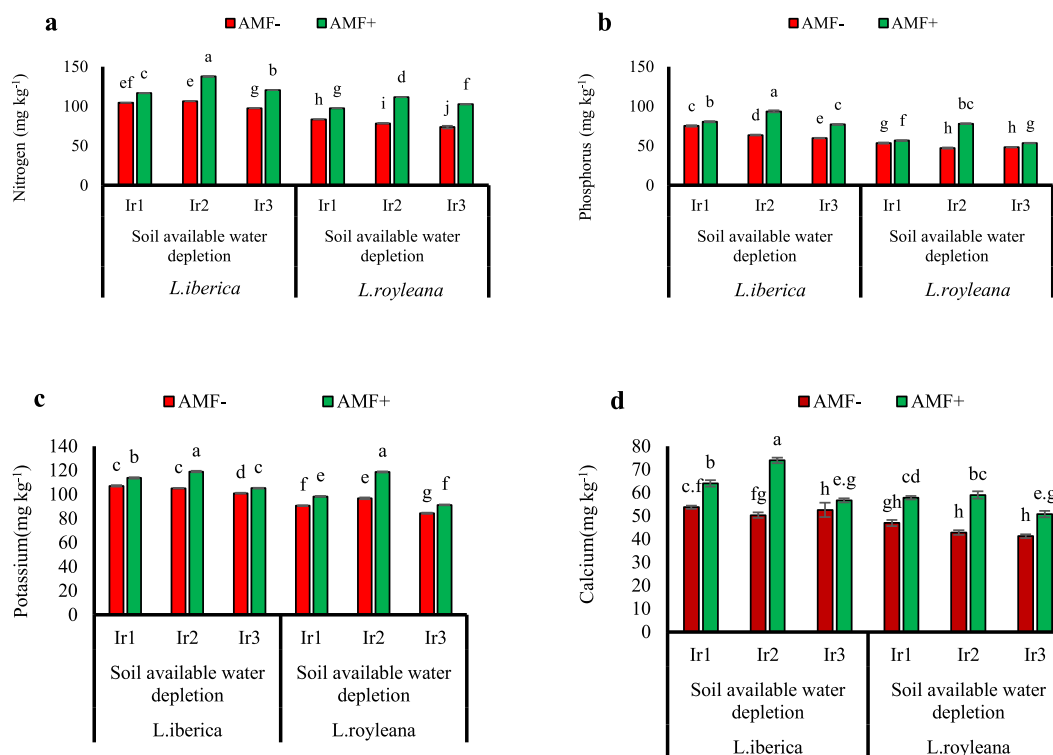


Fig. 4. Nitrogen (a) and phosphorus (b), potassium (c), and calcium (d) levels in *L. iberica* and *L. royleana* offspring produced under varied soil available water depletion with or without arbuscular mycorrhizal fungi inoculation of maternal plant environment. Diverse letters over the bars indicate significant differences ($p < 0.05$) among treatments using Tukey's test. The bars indicate the standard error of the means (\pm SE). Ir1: 30 %, Ir2: 60 %, and Ir3: 90 % of soil available water depletion. AMF⁺: inoculated, AMF⁻: non-inoculated.

A decline in the longevity of *Lallemantia* offspring under drought stress may be owing to the reduction of chlorophyll content in the maternal plants [62]. However, inoculation of AMF caused increasing the photosynthesis activity, leading to greater production of carbohydrates, especially starch and sucrose [63]. Hence, the accumulation of these carbohydrates can play a role in reducing seed deterioration, thereby contributing to seed longevity [64]. These results are consistent with those reported in *Paubrasilia echinata* [65] and *Glycine max* [66]. Higher longevity in *L. royleana* seeds compared to *L. iberica* seeds was probably due to lower oil content in *L. royleana* seeds [1]. Thus, higher lipid content in *L. iberica* seeds may make them more susceptible to increased lipid oxidation reactions and aging-related damage via reactive oxygen species (ROS) activities [67].

The decreased germination of *Lallemantia* offspring under osmotic and salinity stress resulting from water stress during their production can be attributed to factors such as limited water availability, osmotic stress, toxicity from ions, inhibition of enzymes, tissue damage, limited oxygen supply, imbalances in nutrients, physiological and biochemical alterations, and genetic variation [68]. On the other hand, inoculation of arbuscular mycorrhizal fungi in maternal plant environment improved the germination of the produced offspring under osmotic and salinity stress due to the enhancement of seed carbohydrates via photosynthetic activities and the assimilation of CO₂ [24]. Compared with *L. iberica*, greater germination in seeds of *L. royleana* under osmotic and salinity stress was probably related to the higher mucilage in *L. royleana* seeds [1]. Seed mucilage plays a crucial role in enhancing germination during osmotic and salinity stress conditions [69]. The presence of mucilage likely aids moisture retention around the seeds and facilitates germination in water deficit and salinity conditions [70].

The reduction in proline as well as activities of SOD, CAT, and APX in produced offspring under water stress, may be linked to increased oxidative damage to cellular membranes, primarily driven by increasing accumulation of H₂O₂ [71]. The heightened presence of H₂O₂ within various organelles of stressed seeds can lead to lipid peroxidation and loss of membrane integrity [72]. However, it can be inferred that inoculation of mycorrhizal fungi in maternal plant environment could improve proline levels and maintain the antioxidant enzyme system against drought stress while also mitigating excessive ROS accumulation [73,74], as reported in other species such as *Zea Mays* [71] and *Oryza sativa* [75]. Our findings showed that in comparison to *L. iberica* offspring, *L. royleana* offspring exhibited increased proline contents, higher activities of antioxidant enzymes such as SOD, CAT, and APX, and decreased H₂O₂ accumulation, MDA, and EC. These differences can likely be attributed to the higher carbohydrate content in *L. royleana* seeds [76,77]. Higher sugar levels can contribute to maintaining the formation of a glassy state of the cytoplasm under drought stress conditions, limiting biochemical activities such as H₂O₂ accumulation and lipid peroxidation [78].

A decrease in the chemical composition, such as total soluble sugar, sucrose, starch, and mucilage of offspring, may be due to a

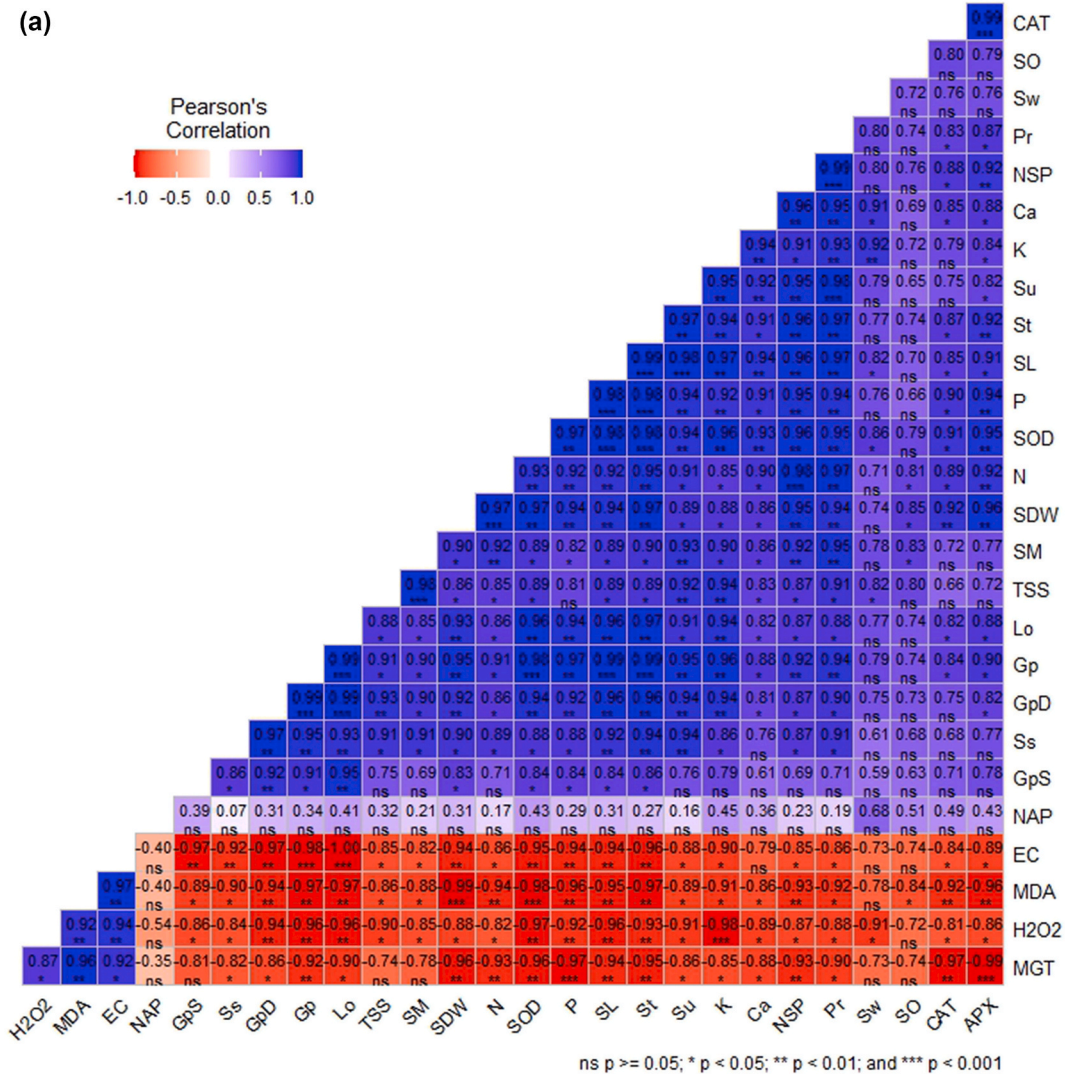


Fig. 5. Pearson correlation of seed performance, seed physio-biochemical properties and seed chemical compositions for *L. iberica* (Fig. 5a) and *L. royleana* (Fig. 5b). Significant correlations are indicated by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). Gp: germination percentage; MGT: mean germination time; NAP: number of achenes in plant; NSP: number of seed in plant; Ss: seed size; Sw: seed weight; SDW: seedling dry weight; SL: seedling length, Lo: longevity; GpD: germination percentage under osmotic stress; GpS: germination under salinity stress; Pr: proline; SOD: superoxide dismutase; CAT: catalase; APX: ascorbate peroxidase; H₂O₂: hydrogen peroxide; MDA: malondialdehyde; EC: electrical conductivity; St: starch; Su: sucrose; TSS: total soluble sugar; SM: seed mucilage; SO: seed oil; N: nitrogen; P: phosphorus; K: potassium; Ca: calcium.

reduction in the chlorophyll content of maternal plants [79]. The decline in chlorophyll can have cascading effects, including a decrease C: N (carbon-to-nitrogen) ratio and the activity of enzymes involved in carbohydrate metabolism [80]. However, the highest contents of total soluble sugar, starch, sucrose, and mucilage were observed in offspring produced under the inoculation of arbuscular mycorrhizal fungi. This could be attributed to the symbiotic relationship between arbuscular mycorrhizal fungi and host plant roots, which may stimulate the activity of enzymes such as rubisco and increase photosynthesis in the leaves of the mother plant [81]. Compared with *L. iberica* seeds, the highest total soluble sugar, and sucrose content was observed in *L. royleana* seeds, which was probably due to the higher mucilage content in *L. royleana* seeds. On the other hand, more starch content in seeds of *L. iberica* than that of *L. royleana* may be due to higher seed weight and seed size [82].

There was a decline in the contents of oil, nitrogen, phosphorus, potassium, and calcium of seeds produced under a Ir₃. The reduction of these chemical compositions may be related to the limitation of root length, which plays a major role in the uptake of soil moisture and nutrient [83]. In contrast, the highest oil, nitrogen, phosphorus, potassium, and calcium were observed in seeds produced under arbuscular mycorrhizal fungi inoculation. This can be attributed to the beneficial symbiotic relationship between arbuscular mycorrhizal fungi and the roots of the mother plants [84]. Mycorrhizal fungi symbiosis with the roots of mother plants can promote the

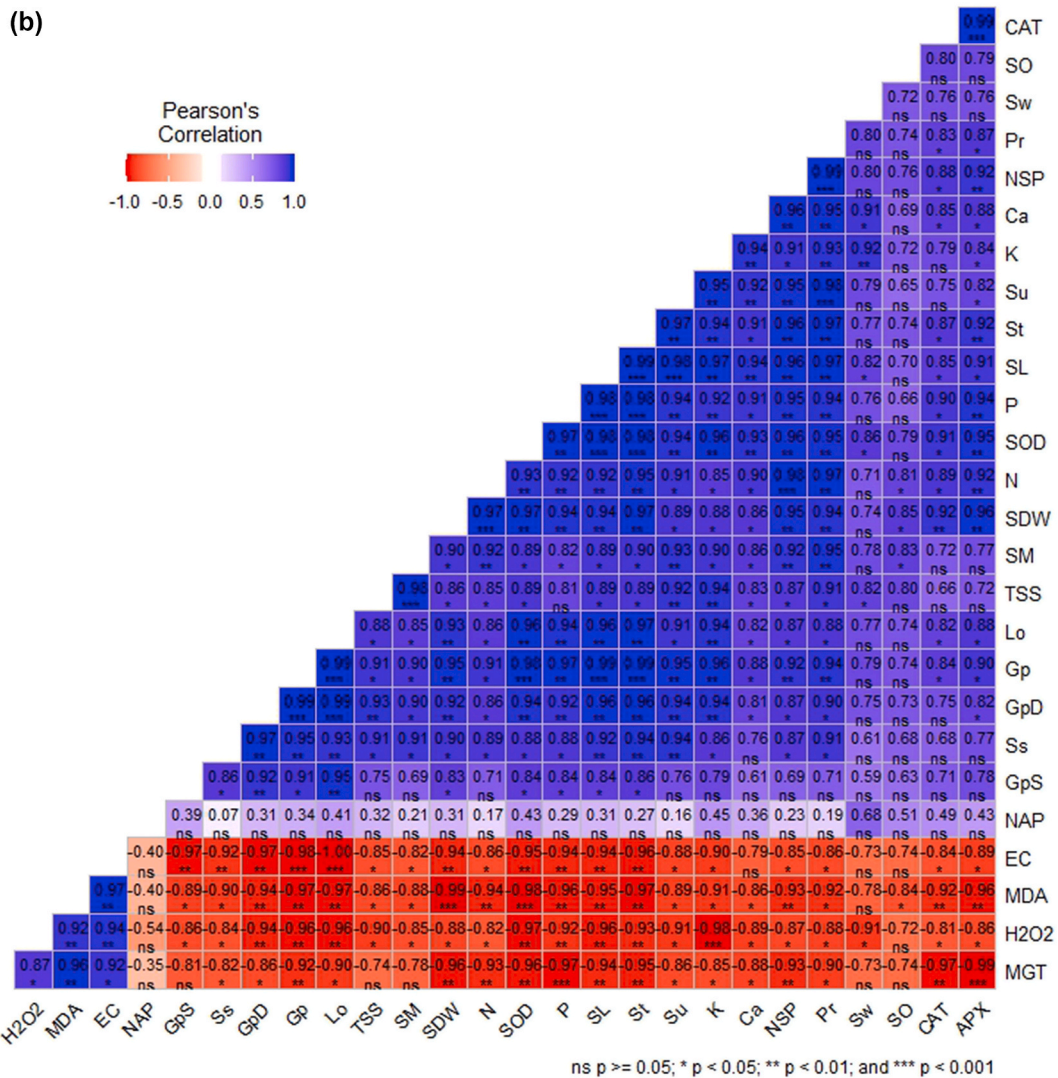


Fig. 5. (continued).

development of the root structures in soil, thus increasing the surface area for nutrient absorption. This extended root network can efficiently absorb and transport nutrients to the mother plant, ultimately benefiting seed composition [85]. The increased levels of oil, nitrogen, phosphorus, potassium, and calcium found in *L. iberica* in comparison to *L. royleana* may be attributed to the larger size of *L. iberica*'s offspring [86].

5. Conclusion

Water limitation in the maternal plant environment negatively affected the germination, physio-biochemical properties, and chemical composition of the offspring of *Lallemantia* species. Maintaining the soil moisture content of Ir₂ and inoculating the maternal environment with mycorrhizal fungi positively influenced the seed performance, including total soluble sugar, starch, sucrose, anti-oxidant enzyme activities, proline, mucilage, oil, nitrogen, phosphorus, potassium and calcium. *L. iberica* offspring exhibited higher chemical compositions, which contributed to a higher germination index and oil content compared to *L. royleana* offspring. On the other hand, *L. royleana* offspring showed increased longevity, higher antioxidant enzyme activities, and lower accumulation of H₂O₂ and MDA, which could be attributed to higher total soluble sugar, sucrose, and mucilage content. Although further studies are required, these preliminary results support the idea that maternal plant environmental effects such as moisture content and nutrition influence offspring performance and physio-biochemical. Therefore, based on these results, future research could investigate the potential for transgenerational changes in the performance, growth, and reproductive traits of offspring compared to their maternal plants under different conditions of moisture and nutrition.

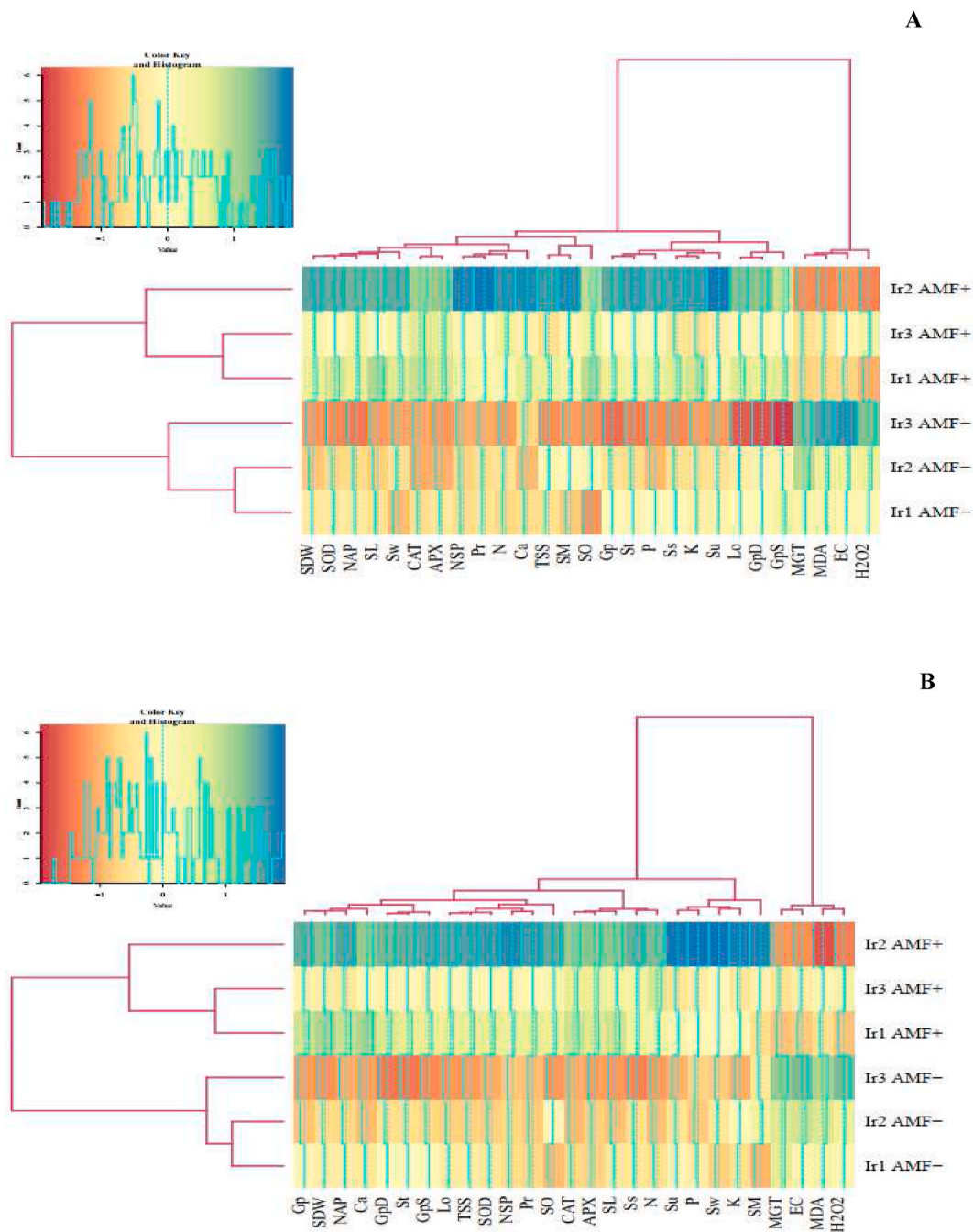


Fig. 6. Heatmap analysis indicating the level and type of connection between traits and treatments (soil available water depletion and arbuscular mycorrhizal fungi inoculation) in *L. iberica* (A) and *L. royleana* (B). Each square shows various treatments' effect on every trait using a false-color scale. Dark red and dark blue colors indicate the traits abundance. Gp: germination percentage; MGT: mean germination time; NAP: number of achenes in plant; NSP: number of seed in plant; SL: seedling length; SDW: seedling dry weight; Sw: seed weight; Ss: seed size; Lo: longevity; GpD: germination percentage under osmotic stress; GpS: germination under salinity stress; Pr: proline; SOD: superoxide dismutase; CAT: catalase, APX: ascorbate peroxidase; H₂O₂: hydrogen peroxide; MDA: malondialdehyde; EC: electrical conductivity; St: starch; Su: sucrose; TSS: total soluble sugar; SM: seed mucilage; SO: seed oil; N: nitrogen; P: phosphorus; K: potassium; Ca: calcium. Ir1: 30 %, Ir2: 60 %, and Ir3: 90 % of soil available water depletion. AMF⁺: inoculated, AMF⁻: non-inoculated.

Data availability statement

Data associated with this study are included in the article/supplementary material referenced in the article. No additional information is available for this paper.

CRediT authorship contribution statement

Arezo Paravar: Writing – original draft, Software, Resources, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Saeideh Maleki Farahani:** Supervision. **Alireza Rezazadeh:** Formal analysis. **Ademola Emmanuel Adetunji:** Writing – review & editing. **Muhammad Farooq:** Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. Arezo Paravar reports financial support was provided by Shahed University. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.heliyon.2024.e31334>.

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