Fatty Acid Composition and Eco-agronomical Traits of *Lallemantia* Species Modulated upon Exposed to Arbuscular Mycorrhizal Fungi and Nano-iron Chelate Fertilizers under Water Deficit Conditions

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Abstract

The main objectives of the current study were to investigate the effect of arbuscular mycorrhizal fungi (AMF) and nano-iron chelate fertilizer under water deficit conditions on grain yield, root colonization, leaf chlorophyll concentration, oil percentage, and fatty acid profile of *Lallemantia* species. The experiment was carried out as a factorial based on a complete randomized block design consisting of three factors of irrigation levels of 30, 60, and 90% depletion of available soil water (ASW), fertilizer levels of control (without fertilizer), AMF inoculation, and nano-iron chelate, and plant species of *Lallemantia* (*L. iberica* and *L. royleana*). The results showed that increasing water deficit stress significantly decreased the above traits, while applying nano-iron and AMF fertilizers significantly increased them across water treatments. AMF fertilizer inoculation significantly improved yield of both *Lallemantia* species. Higher root colonization by AMF inoculation enhanced seed oil production with all major fatty acid moieties improved. In contrast, applying nano-iron chelate by increasing chlorophyll concentration in any irrigation regime could enhance seed oil of *L. royleana* and some fatty acids such as palmitoleic acid. Water deficit stress and application of fertilizers had different effects on both species. *L. iberica*, compared with *L. royleana*, had the most tolerance to water deficit stress and the highest dependence on AMF inoculation. Overall, these results demonstrated that the application of AMF could improve major features of *Lallemantia* species under irrigation deficit conditions, especially at the 60% depletion of ASW.

Keywords Fatty acid component · *Lallemantia iberica* · *Lallemantia royleana* · Oil content · Root colonization

1 Introduction

Plants belonging to the genus *Lallemantia* sp. are known because of their economic features. These plants can be either served as food, industrial crop, or medicinal plant. The genus *Lallemantia* sp. (Balangu) belongs to the Lamiaceae family and comprises five species. Of these, *Lallemantia iberica* L. (dragon head) and *Lallemantia royleana* L. (lady’s mantle) are mainly noticeable because of their high concentration of oilseed (approximately 30–45%) (Al-Snafi 2019a, b). The oil of *L. iberica* seeds is known as Iberian oil. Therefore, the economic value of *Lallemantia* seeds may be due to the high concentration of oil and fatty acids (Zlatanov et al. 2012). The application of *Lallemantia* oil in the pharmaceutical and food industries is due to its richness of ω-3 unsaturated fatty acids (PUFAs, approximately 67–74%) (Al-Snafi 2019a, b; Heydari and Pirzad 2021). Furthermore, it has been reported that because of the high concentration of PUFAs in *Lallemantia* seeds, their epoxidized oil has potential industrial applications in the fields of adhesives, coatings, and resins (Sharma et al. 2021). The most critical production input is water that significantly affects plant growth and crop production (Hossein-zadeh et al. 2020; Zhao et al. 2020). On the other hand, a decrease in soil-available water makes drought stress in plants during growth (Paravar et al. 2021). The most common effect of drought stress is decreased plant growth, which is caused by decreased cell inflammation (Pashang et al. 2021). Indeed, limited plant availability to water and CO₂ during drought stress causes a reduction in allocated...
photosynthates to the growing plant parts (Wang et al. 2021). In other words, the production and transport of photosynthates decrease from leaf to seed (Khan et al. 2020; Zhang et al. 2020). As a result, a decrease in photosynthesis during drought stress can lead to a decline in many processes, including chlorophyll content, NADPH/NADP⁺ ratios, ribulose 1,5-bisphosphate carboxylase/oxygenase activity, and NADP-dependent malate dehydrogens, all of which play important roles in the biosynthesis of oil and fatty acids (Shahzad et al. 2018). It has been reported that the decrement of grain yield and oil content in Lallemantia iberica L. (Paravar et al. 2021), Oenothera biennis L. (Mohammadi et al. 2019), Carthamus tinctorius L., Sesamum indicum L., Helianthus annuus L. (Ebrahimian et al. 2019), and Portulaca oleracea L. (Celik Altunoglu et al. 2018) was due to the degradation of photosynthesis pigments and reduction of assimilates. It is accordingly critical to develop methods for improving plant yield and biochemical properties under drought stress, and the application of fertilizers is among such methods (Zafari et al. 2020).

A balanced nutrient concentration in the soil is another essential element for plant growth regulation (Taghizadeh et al. 2019). A balanced nutrient concentration can be supplied by applying chemical and biofertilizers, critical for the sustainability of soil fertility, photosynthetic reactions, assimilate transportation, photosynthesis, oil synthesis, and final performance (Rahimzadeh and Pirzad 2019). Biofertilizers are substance that contain living beneficial microorganisms which have the potential to improve soil fertility and crop productivity (Atieno et al. 2020; Srivastava et al. 2021). The application of biofertilizers such as arbuscular mycorrhizal fungi (AMF) as inoculants in soil not only is valuable to the environment healthy, but also declines dependency on chemical fertilizer (Bender et al. 2016; Hart et al. 2018). The AMF establishes a symbiotic relationship with the host plant roots to absorb carbon. Carbon enables the fungi to grow and complete their life cycle (Bonfante and Genre 2010). In return, AMF helps the host plants absorb water, macronutrients (e.g., nitrogen (N), phosphorus (P), potassium (K), and calcium (Ca)) and micronutrients (e.g., iron (Fe), manganese (Mn), zinc (Zn), and Copper (Cu)) (Ghanbarzadeh et al. 2020; Plouznikoff et al. 2019). Improvement of nutrients such as P in soil and increasing root colonization via AMF can maintain optimal growth and water relations and, in contrast, enhance host plant resistance under drought stress (Pirzad and Mohammadzadeh 2018). Root colonization by mycorrhizal fungus is an alternative strategy to improve plants’ drought tolerance and increase water balance in drought conditions (De Assis et al. 2020). It has been reported that adding AMF inoculum in soil not only enhances root colonization but also has an influence on increasing photosynthetic pigment and fatty acid synthesis under drought stress (Liu et al. 2020, 2018). Other studies have suggested that AMF inoculation can result in the highest oil percentage and oleic acid in flax (Linum usitatissimum L.) (Rahimzadeh and Pirzad 2019) and purslane (Portulaca oleracea L.) (Hosseinzadeh et al. 2020). Generally, in plant cell metabolism enhancing, the biosynthesis of beneficial host phytochemicals, stimulation of photosynthesis, and nutrient acquisition can be changed by AMF symbiosis (Pawar et al. 2018).

The third most limiting nutrient for the growth of plants is iron (Fe) (Zhang et al. 2019) that plays a vital role in plant growth and food production (Fang et al. 2008) and, as a cofactor for approximately 140 enzymes, can improve photosynthesis and assimilate transportation to sink and eventually amend grain yield and oil content under drought stress (Mohasseli et al. 2020). The nano-iron chelate fertilizer application is highly efficient due to excessive chemical fertilizers and the resulting contamination of groundwater and soil salinization (Mohammad Ghasemi et al. 2020). Applying nano-iron chelate over other Fe fertilizers is a significant step to reach sustainable agriculture due to improving plant mineral nutrition and decreasing conventional fertilizer consumption (Tavallali et al. 2020). Nano-iron, by reducing Fe availability in the rhizosphere, stimulates operation of the proton pump in plants and by activating plasma membrane H⁺-ATPase to secretion protons leads to acidification of the rhizosphere of plant roots (Kim et al. 2015) and eventually improves the solubility and dispersion of insoluble nutrients in the soil (Mohasseli et al. 2020). According to researchers, nano-iron chelate on Lallemantia iberica L. (Mohammad Ghasemi et al. 2020), Sesamum indicum L. (Ayoubizadeh et al. 2018), and AMF inoculation on Lallemantia iberica L. had a significant effect on the enhancement of grain yield. In addition, one study suggested that the application of AMF and nano-iron chelate increased the grain yield and oil content of Silybum marianum L. and found that the effect of AMF inoculation was greater than that of nano-iron chelate (Yadegari et al. 2021). An in-depth review of the literature suggests that the interaction between available soil water and different fertilizers on grain and oil yield in Lallemantia species is still limited. Thus, the current study’s goal was to evaluate AMF and nano-iron fertilizer’s effects on grain yield and fatty acid composition of L. iberica and L. royleana under irrigation deficit.

2 Material and Methods

2.1 Experimental Design and Plant Materials

The field trial was conducted at the research farm of the College of Agriculture, Shahed University, Tehran, Iran, (35°34’ E, 51°8’ N, altitude: 1190 m above sea level) on 14th November 2018 and 2019 (Fig. 1, Supplementary Fig. S1). In order
to determine some of the soil’s physical and chemical properties, a sample of farm soil was experimented (Table 1). The content of soil total nitrogen (N) content was measured using Kjeldahl methods (Bremener and Mulvaney 1982). We determined soil iron (Fe) by atomic absorption spectroscopy (AAS, NovaAA400, German) (Berry and Johnson 1966). As well as, soil-available phosphorus content was measured by colorimetric analysis (Stuffins 1967), and soil-available potassium (K) content was measured by a flame photometer (BWB Technologies, UK) (Hunter and Pratt 1957). Soil pH (Thomas 1996) and EC (Rhoades 1996) were determined with a soil–water extraction ration of 1:2.5 using pH meter (HI 9017, Hanna Instruments Inc., USA) and conductivity meter (YK 2001CT, Lutron, Taiwan), respectively. Figure 2 represents total rainfall and average monthly air temperature during the growing season.

A split-factorial layout based on randomized complete block design (RCBD) was employed to study three factors: irrigation regimes, irrigation after 30% (without stress), 60% (mild stress), and 90% (severe stress) of available soil water (ASW) depletion; fertilizer treatments, without fertilizer (control treatment), biofertilizers (arbuscular mycorrhizal fungi (AMF)), and nano-iron chelate; and Lallemantia species, Lallemantia royleana and Lallemantia iberica using three replications. Irrigation treatment was placed in the main plots, while a factorial combination of fertilizer treatments and plant species was allocated to the subplots. The experiment involved 54 plots (2 × 2 m²) with 2-m interval between main plots, 1-m interval between subplots, and 2-m interval between blocks that were assigned. Seeds were planted with spacing between 50 at a depth of 2 cm manually in four rows. The seeding rate for L. iberica and L. royleana was 0.6 and 0.2 kg ha⁻¹, respectively. After emergence, plants were thinned, and a final plant population of 40 plants m⁻² was maintained. Weeds were controlled by hand 20 and 45 days after planting. No fertilizer was applied according to the soil test results.

### Table 1 The physical and chemical properties of the experimental field

| Year      | Texture | N (%) | Fe (mg.kg⁻¹) | P (mg.kg⁻¹) | K (mg.kg⁻¹) | EC (dS.m⁻¹) | pH  |
|-----------|---------|-------|--------------|-------------|-------------|-------------|-----|
| 2018–2019 | Loamy   | 0.11  | 2.1          | 8.52        | 376         | 4.20        | 7.1 |
| 2019–2020 | Loamy   | 0.05  | 2.9          | 8.78        | 383         | 4.10        | 7.4 |

N, nitrogen; Fe, iron; P, phosphorus; K, potassium; EC, electrical conductivity; pH, potential of hydrogen
Lallemantia iberica and Lallemantia royleana seeds were kindly provided by the Agricultural Research Center of Urmia and Pakan Bazr Company, Iran, respectively. Seed viability and germination percentage (Table 2) were determined using the test of tetrazolium and germination (ISTA 2013). The arbuscular mycorrhizal fungi inocula (Funneliformis mosseae (T.H. Nicolson & Gerd.) C. Walker & A. Schübler; Claroideoglomus etunicatum (W.N. Becker & Gerd.) C. Walker & A. Schüßler; and Rhizophagus intraradices (N.C. Schenck & G.S. Sm.) C. Walker & A. Schübler) were a mixture of sterile sand, mycorrhizal hyphae, spores, and colonized roots which were propagated on the Medicago sativa L. and Sorghum bicolor L. as trap plants (Schenck and Perez 1990) by the Soil Biology Laboratory, Soil and Water Research Institute (Tehran, Iran). At sowing time, 20 g m⁻² of AMF inoculum (approximately 20 spores per g of soil) was poured and mixed with the soil to a depth of 2 cm in each planting row (Rahimzadeh and Pirzad 2019). The size of nano-iron particles was 40 nm and contained 9% water-soluble iron chelate. Nano-iron chelate fertilizer was applied as a solution in irrigation water after sowing (Gholinezhad 2017; Heidari et al. 2016) at a rate of 5 kg.ha⁻¹.

### 2.2 Irrigation Treatment

Drought stress was imposed via prolonging irrigation regimes, thus greater depletion of soil-available water before rewatering. The field capacity (FC: 20.9%) and permanent wilting point (PWP) (10.8%) were measured using a pressure plate apparatus, and plots were irrigated based on maximum allowable soil-available water depletion (30% (without stress), 60% (mild stress), and 90% (severe stress)). The maximum allowable depletion (MAD) in the 0–30 cm soil depth was measured using the following equation (Mohammadi et al. 2018):

\[
MAD(\%) = 100 \times \frac{FC - \theta}{FC - PWP}
\]

where $MAD$, $FC$, $\theta$, and $PWP$ represent maximum allowable depletion, soil volumetric moisture at field capacity, soil volumetric moisture, and soil volumetric moisture at the permanent wilting point, respectively.

The volume of allocated water was measured using the following equation (Abdollahi and Maleki Farahani 2019):

\[
In = \frac{(FC - \theta) \times D \times A}{100}
\]

where $In$, $FC$, $\theta$, $D$, and $A$ represent the volume of allocated water, field capacity, soil moisture, the effective rooting depth, and plot surface area (4 m²), respectively. Before applying irrigation treatments, the amount of water required for irrigation of Lallemantia species was calculated for 30% depletion of ASW by monitoring changes in soil water gravimetrically. According to this method, 24 h after irrigation, samples from an experimental plot were taken from the root development depth (0–30 cm), and the samples were immediately weighed and then dried in an oven at 105 °C for 24 h. Indeed, the percentage of soil water content (Xu et al. 2018) was registered according to sampling taken daily from an experimental plot. According to that measured amount (irrigation regime of 30% depletion of ASW), the water used in each level of drought stress (irrigation regime 60% and 90% depletion of ASW) was calculated. The irrigation volume was controlled using the meter that was installed at the beginning of the irrigation system (Fig. 3). Measured values with the help of a volumetric flow of water were performed at intervals of once every 5 days and separately for each drought stress level. The irrigation treatments were applied at the onset of plants established at the 8–12 leaf stage (on 2–8 February 2019 and 2020 respectively).
2.3 Measurements

2.3.1 Agronomical Traits

At the end of the growing season (on 14–22 June 2019 and 2020), 20 plants from each plot’s inner area \((2 \times 1 \text{ m}^2)\) were selected and air dried at room temperature (away from direct sunlight) for the measurement of grain yield (Gajić et al. 2018).

2.3.2 Root Colonization

The percentage of AMF root colonization was estimated in 5 plants that were randomly selected from each plot after seed maturity (24 May 2019 and 30 May 2020). The roots were washed by distilled water and stored in a 50% ethanol solution. Then root samples were soaked in 100 g/l KOH in a 90 °C water bath for 30 min. After rinsing with distilled water, the samples were soaked in a 2% hydrogen chloride solution for 15 min. The acidified roots were stained in a color solution containing a ration of fuchsine acid and a mixture of lactic acid, glycerol, and distilled water for 24 h. A 1 cm piece of root was separated, and the percentage of AMF colonization was measured using a light microscope (YJ-T101G, China) and using the following Eq. 3 (Kormanik and McGraw 1982):

\[
\text{Root colonization (\%)} = \frac{\text{Total number of infected roots intersecting gridlines}}{\text{Total number of intersecting gridlines}} \times 100
\]

2.3.3 Leaf Chlorophyll Concentration

Leaf chlorophyll (Chl) were measured 30 days after flowering (11 April 2019 and 16 April 2020) on leaves (in 3 plants from each treatment randomly collected) sampled. After cutting, the plant leaves were placed in plastic bags, immediately transported to the laboratory. For measuring chlorophyll concentration, leaf samples were extracted in 80% acetone, and then the extract material was centrifuged at 6000 rpm for 15 min and recorded at 645 and 663 nm (Arnon 1949):

\[
\text{Chl a (mg/g FW) } = 12.7(A_{663.6}) - 2.69(A_{646.6}) \quad (4)
\]

\[
\text{Chl b (mg/g FW) } = 22.9(A_{646}) - 4.68(A_{663.6}) \quad (5)
\]

2.3.4 Oil Extraction

Seed oil was measured using the standard Soxhlet method with hexane solution (ACS grade, Reag. PhEur; obtained from Merck Chemical Co., Germany). The solvent (150 mL) was poured in a Soxhlet apparatus, and then 10 g seeds of each treatment was added. The solvent was boiled and evaporated. This evaporation condensation process continued for 10 h, and after solvent removal, oil was extracted from brown seeds (Visavadiya et al. 2009).

2.3.5 Fatty Acid Composition

Briefly, the composition of the fatty acids in the seed oil of Lallemantia was determined according to the methylation (transformation of fixed oil into fatty acid) and gas chromatography (GC) (Savage et al. 1997). Generally, in a 5-ml screw-top test tube, 0.10 g of the oil sample was weighed. Afterward, 3 ml of heptane and 2 ml of 0.01 M sodium hydroxide solutions were added and shaken at 10,000 rpm for 15 s. Finally, 1 μL of the fatty acid methyl esters (FAME) sample was injected into the gas chromatograph using a microliter syringe. The FAME

Fig. 3 General schema of irrigation system in the research plots with three levels of irrigation regime
were analyzed in an Agilent 7890A GC (Agilent Technologies, Inc. 2010) equipped with a flame ionization detector (FID), using a BPX capillary (part number, 054,980) column (50 m × 0.22 mm internal diameter, 0.2 μm film, nitrogen was the carrier gas with a head pressure at 60 psi, Agilent Technologies, Inc. 2010). The initial column temperature was set at 165 °C and maintained for 10 min and then programmed to increase from 165 to 200 °C at 1.5 °C/min. Injector and detector temperatures were adjusted to 250 °C and 280 °C, respectively.

### 2.4 Statistical Analysis

Data were submitted to statistical analysis using SAS software version 9.3. A combined analysis of variance (ANOVA) was carried out, and mean values were compared using Duncan’s multiple range test at $p < 0.05$.

### 3 Results

The analysis of variance for the 2-year data indicated that the three-way interaction of irrigation, fertilizer, and plant species had a significant on grain yield, root colonization, chlorophyll concentration, and oil content (Table 3) and fatty acid composition (Table 4).

#### 3.1 Grain Yield

By increasing the severity of drought, grain yield reduced in both species, and the most increasing grain yield was observed when both species were grown under 60% irrigation regime conditions. The application of AMF more significantly influenced grain yield of both species under irrigation deficit compared with that of the without fertilizer. With AMF biofertilizer application, the highest grain yield for *L. iberica* was obtained at 60% and 90% irrigation treatments, while for *L. royleana* species, the highest grain yield were obtained from 30 to 90% irrigation regime. The amount of grain yield of *L. iberica* was higher than that of *L. royleana* across all irrigation regimes and fertilizer treatments (Fig. 4).

#### 3.2 Root Colonization

A significant reduction was observed in the root colonization of *Lallemantia* species under water deficiency stress, especially under 90% irrigation regime. On average, both species under the 60% irrigation regime condition had more root colonization than that with 30% and 90% irrigation regime. More differences in root colonization were found in plants inoculated by AMF. Colonization in both species of *Lallemantia* roots improved by AMF inoculation in any irrigation regime treatments; however, *L. royleana* roots had the highest colonization (Fig. 5). Also, we observed a layer

### Table 3 The combined analysis of variance for the effect of year, irrigation regime, fertilizer, and plant species on yield, root colonization, leaf chlorophyll concentration, and oil percentage in the 2-year experiment

| S.V                  | d.f | GY     | C        | Chl a     | Chl b | Oil percentage |
|----------------------|-----|--------|----------|-----------|-------|----------------|
| Year (Y)             | 1   | 1131.31| 4.62n.s  | 0.003n.s  | 0.229n.s | 0.98n.s |
| Block (year)         | 4   | 17,201.58| 0.26   | 1.718     | 0.995  | 0.45           |
| Irrigation regime (I)| 2   | 1,098,031.27** | 897.17** | 150.16** | 47.484** | 24.19** |
| Y×I                  | 2   | 28.95  | 0.04n.s  | 0.027n.s  | 0.028n.s | 1.08*          |
| Block×I (year) (error a) | 8   | 4868.75| 4.05   | 1.949     | 0.374  | 0.53           |
| Fertilizer (F)       | 1   | 482,136.37** | 3676.49** | 203.053** | 93.422** | 3958.46** |
| Plant species (S)    | 2   | 3,660,665.97** | 22,783.31** | 307.016** | 78.345** | 88.99** |
| Y×F                  | 1   | 117.91n.s | 0.01n.s | 0.654n.s  | 0.225n.s | 0.39n.s |
| Y×S                  | 2   | 44.44n.s | 0.14n.s | 0.079n.s  | 0.061n.s | 0.4n.s |
| I×F                  | 2   | 162,190.22** | 12.63*  | 67.674** | 5.196** | 1.32* |
| I×S                  | 4   | 610,270.17** | 373.96** | 76**      | 17.673** | 2.75** |
| F×S                  | 2   | 17,997.91n.s | 527.75** | 146.691** | 13.959** | 35.98** |
| I×F×S                | 4   | 72,240.44** | 30.05** | 75.492** | 13.687** | 2.76** |
| Y×1×F                | 2   | 2.43n.s  | 0.52n.s  | 0.02n.s   | 0.1n.s  | 0.52n.s |
| Y×l×S                | 4   | 62.15n.s | 0.37n.s  | 0.078n.s  | 0.002n.s | 0.3n.s |
| Y×F×S                | 2   | 24.43n.s | 0.01n.s  | 0.097n.s  | 0.049n.s | 0.29n.s |
| Y×1×F×S              | 8   | 74.8n.s  | 0.31n.s  | 0.099n.s  | 0.054n.s | 0.19n.s |
| Error (b)            | 60  | 9556.08 | 3.18   | 0.86      | 0.66     | 0.27     |
| C.V. (%)             | 9.17 | 4.88   | 5.26    | 15.99     | 2.06     |

S.V., source of variation; d.f., degree of freedom; GY, grain yield; C, root colonization; Chl a, chlorophyll a; Chl b, chlorophyll b; C.V., coefficient of variation; ns, *, and ***, not significant and significant at 5 and 1% probability levels, respectively.
of mucilage around roots of inoculated (Fig. 6a) and non-
inoculated (Fig. 6b) L. royleana, which is not reported so far.

### 3.3 Leaf Chlorophyll Concentration

Increasing available soil water depletion caused a reduction in leaf Chl a in both species of Lallemantia. Nano-iron chelate application was effective in improving Chl a concentration of both species across all irrigation treatments. Compared with L. royleana, the Chl a concentration in L. iberica species was higher across all irrigation regimes and fertilizer treatments (Fig. 7). In Lallemantia species, Chl b concentration was reduced in irrigation regimes from 30 to 90% irrigation regime. Across all irrigation treatments, the highest Chl b

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**Table 4** The combined analysis of variance for the effect of year, irrigation regime, fertilizer, and plant species on fatty acid compositions in the 2-year experiment

| S.V.          | df | EA | AA | LNA | LA | OA | SA | POA | PA |
|---------------|----|----|----|-----|----|----|----|-----|----|
| Year (Y)      | 1  | 0.004n.s | 0.0000002n.s | 0.0000002n.s | 0.0005n.s | 0.000926n.s | 0.0000002n.s | 0.0003n.s |
| Block (year)  | 4  | 0.024 | 0.000165 | 0.18 | 0.326 | 0.511 | 0.002545 | 0.0000088 | 0.673 |
| Irrigation regime (I) | 2  | 0.191** | 0.017612** | 160.82** | 16.142** | 40.136** | 0.857121** | 0.0187628** | 28.013** |
| Y×I           | 2  | 0.0001n.s | 0.000001n.s | 0.04n.s | 0.007n.s | 0.003n.s | 0.000713n.s | 0.0000057n.s | 0.005n.s |
| Block×I (year) error a | 8  | 0.008 | 0.000042 | 0.52 | 0.25 | 0.025 | 0.00031 | 0.0000189 | 0.104 |
| Fertilizer (F) | 1  | 0.811** | 0.058899** | 663.77** | 130.727** | 40.136** | 0.877339** | 0.02241362** | 56.385** |
| Plant species (S) | 2  | 3.45** | 0.046265** | 206.43** | 39.361** | 68.25** | 0.877339** | 0.02241362** | 56.385** |

Fig. 4 The effect of AMF and nano-iron chelate application on grain yield of L. iberica and L. royleana species under different water treatments. Means followed by the same letter are not significantly different (p<0.05) by Duncan’s multiple range test. The bars indicate the standard error of the means (±SE)
in Lallemantia species was obtained in plants inoculated by AMF. Simultaneously, the lowest Chl b was observed in L. iberica and L. royleana at control treatment (neither biofertilizer nor nano-iron chelate fertilizer). Higher Chl a and Chl b were observed in L. iberica leaves, compared with L. royleana under all irrigation regimes and fertilizer treatments (Fig. 8).

### 3.4 Oil Percentage

As the availability of irrigation water reduced, the oil percentage of Lallemantia species followed a decreasing trend. Fertilizer application (especially AMF) significantly increased oil percentage. In all irrigation regimes (30% and 90% levels of irrigation regime) in
both Lallemantia species, the highest and lowest oil percentage of seeds was obtained in plants inoculated by AMF fertilizer and control (without fertilizer), respectively. Across all irrigation regimes and fertilizer treatments, L. iberica performed significantly higher seed oil percentage compared with L. royleana (Fig. 9).

3.5 Fatty Acid Composition

In both Lallemantia species by increasing water deficit, the relative percentage of eicosenoic acid (EA), arachidic acid (AA), linolenic acid (LNA), linoleic acid (LA), oleic acid (OA), and stearic acid (SA) fatty acid significantly reduced, while palmitic acid (PA) and arachidic acid (AA) increased. Using AMF and nano-iron chelate leads to a significant enhancement in the fatty acid relative percentage compared with that of control plants. The amount of palmitoleic acid (POA) and LA by using nano-iron chelate and fatty acids of EA, AA, LNA, OA, SA, and PA with inoculation AMF significantly increased during drought stress. The highest value of AA, LNA, and POA was observed in L. royleana species. Additionally, the EA, LA, OA, and SA relative percentage in L. iberica species was significantly higher than L. royleana (Table 5).

4 Discussion

Drought stress is one of the environmental stresses that influences growth and crop production; however, plants can create beneficial associations that reduce drought stress.
effects (Zhang et al. 2020). Increasing rates in grain yield for both species of *Lallemantia* under the 60% irrigation regime and, in contrast, increasing severity of water deficit (90% irrigation regime) caused a considerable reduction in grain yield. This may be due to the reduction of water and nutrient absorption (Ghanbarzadeh et al. 2020). In addition, it has been reported that reduction of yield is probably related to reduction in photosynthesis rate due to stomata closure and carbon dioxide (CO₂) uptake reduction (Kademian et al. 2019). However, AMF inoculation noticeably enhanced grain yield in both species. Improvement of yield in plant inoculated under drought stress may be due to uptake of microelements from the soil and, subsequently, metabolite production and enzyme activity could change positively (Symanczik et al. 2018; Xie et al. 2018) and facilitated assimilate transition to grain (Taghizadeh et al. 2019). Compared with *L. royleana*, a higher grain yield in *L. iberica* across all irrigation regimes and fertilizer treatments is probably due to increase uptake more water from the soil and provides energy needed for growth (Paravar et al. 2021).

This study showed that the percentage of root colonization of AMF inoculation in both species of *Lallemantia* significantly decreased from 30 to 90% level of irrigation regime which in agreement with previous reports in *Camelina sativa* L. (Borzoo et al. 2021), *Dracocephalum moldavica* L. (Ghanbarzadeh et al. 2020), *Lavandula officinalis* L. and *Rosmarinus officinalis* L. (Pirzad and Mohammadzadeh 2018), and *Lallemantia iberica* L. (Heydari and Pirzad 2021). The decrease in root colonization of both *Lallemantia* species under severe water deficit could be attributed to fewer carbohydrates produced by photosynthesis (Sheteiwy et al. 2021; Symanczik et al. 2018). Accordingly, it has been reported that one of the main reasons for the reduction of root colonization in *Trifolium subterraneum* L., *Trifolium incarnatum* L. (Jongen et al. 2022), and *Glycine max* L. (Amani Machiani et al. 2021) under drought stress was the provision of lower carbon by the host plant for mycorrhizal. It has been proved that increase in the functional of root mycorrhizal depends on more colonized of roots by extraradical mycelium (Vallejos-Torres et al. 2021). In fact, after AMF forms a symbiotic structure with the roots of the host plant, spores germinate, and extraradical mycelium is produced and spread by the host plant’s roots throughout the surrounding soil (Bhantana et al. 2021). Expanding of extraradical mycelium from colonized roots into the soil induces the exploring and uptaking of soil nutrient as well as their translocating to the host plant (Floc’h et al. 2022; Ujvári et al. 2021). In light of this, the colonized roots of host plant provide 4% and up to 25% of produced photosynthates by leaves as a reward for the completion of AMF’s life cycles and the greater growth of extraradical mycelium (Wipf et al. 2019). In addition, higher root colonization in plants inoculated of *Lallemantia* may due to release mucilaginous polymers into the soil via living roots of host plants which provide a suitable habitats for microbes (Guhra et al. 2022). Moreover, the presence of mucilage chemical compositions in soil causes hyphae adhesion of AMF to root surface of host plant and increases root colonization (Paravar et al. 2021). It has been reported that mucilage around roots of host plant consists source of carbon which is utilized by soil microbes and effectively causes the increase in root colonization (Vora et al. 2021). Compared with *L. iberica*, higher root colonization in *L. royleana* can be due to the existence of mucilage layer around theirs roots which provide a carbon source for soil microbial community (Paravar et al. 2021). It has been reported that higher root colonization in *L. royleana* was probably related to the much more mucilage in their seeds (Paravar et al. 2022). Mucilage is a polysaccharide-rich substance which is able to stick to solid surfaces and soil particles after release to the rhizosphere, leads to the attracted of beneficial microorganisms in rhizosphere (Landl et al. 2021).
| Irrigation regime | Species      | Fertilizer          | EA     | AA       | LNA     | Fatty acid composition (%) |
|------------------|--------------|---------------------|--------|----------|---------|---------------------------|
|                  |              |                     | LA     | OA       | SA      | POA          | PA       |
| 30%              | *L. iberica* | Without fertilizer  | 0.68 ± 0.02 fg | 0.03 ± 0.002i | 54.08 ± 0.4 h | 13.11 ± 0.09ef | 11.74 ± 0.07 g | 1.55 ± 0.01n | 0.02 ± 0.004 m | 5.45 ± 0.11j |
|                  |              | AMF                 | 1.51 ± 0.03b  | 0.06 ± 0.003 g | 56.92 ± 0.33 fg | 14.18 ± 0.23c | 14.39 ± 0.14d | 1.84 ± 0.02jk | 0.03 ± 0.005 k | 8.48 ± 0.09df |
|                  |              | Nano-iron chelate   | 0.7 ± 0.02 fg | 0.04 ± 0.001 h | 54.77 ± 0.22 h | 14.92 ± 0.05b | 13.3 ± 0.08e | 1.57 ± 0.01n | 0.07 ± 0.002i | 8.36 ± 0.38ef |
|                  | *L. royleana*| Without fertilizer  | 0.72 ± 0.02 fg | 0.04 ± 0.001 h | 61.74 ± 0.23c | 11.48 ± 0.06hi | 9.81 ± 0.12 h | 2.12 ± 0.01 fg | 0.07 ± 0.003i | 4.98 ± 0.11j |
|                  |              | AMF                 | 0.96 ± 0.04de | 0.11 ± 0.004 cd | 62.87 ± 0.06b | 10.53 ± 0.05 k | 13.4 ± 0.04e | 2.3 ± 0.01 bd | 0.08 ± 0.002 g | 7.8 ± 0.06gh |
|                  |              | Nano-iron chelate   | 0.62 ± 0.01 g | 0.11 ± 0.004 cd | 58.11 ± 0.01e | 11.74 ± 0.08 h | 12.52 ± 0.03f | 2.19 ± 0.01 ef | 0.11 ± 0.007e | 7.51 ± 0.02 h |
| 60%              | *L. iberica* | Without fertilizer  | 0.88 ± 0.01e  | 0.04 ± 0.001hi | 54.21 ± 0.28 h | 12.61 ± 0.07 g | 14.52 ± 0.04d | 1.63 ± 0.01 nm | 0.05 ± 0.009j | 6.68 ± 0.14i |
|                  |              | AMF                 | 1.68 ± 0.03a  | 0.1 ± 0.001e  | 59.26 ± 0.25d | 14.96 ± 0.05ab | 16.56 ± 0.19a | 1.93 ± 0.01ij | 0.08 ± 0.001 h | 8.92 ± 0.14ce |
|                  |              | Nano-iron chelate   | 0.68 ± 0.02 fg | 0.06 ± 0.004 g | 56.58 ± 0.36 g | 15.37 ± 0.03a | 15.61 ± 0.21b | 1.69 ± 0.02 lm | 0.11 ± 0.0001f | 6.71 ± 0.06i |
|                  | *L. royleana*| Without fertilizer  | 0.77 ± 0.02f  | 0.07 ± 0.002 g | 59.58 ± 0.04d | 10.57 ± 0.08 k | 11.33 ± 0.06 g | 2.21 ± 0.01 df | 0.12 ± 0.0007d | 6.56 ± 0.07i |
|                  |              | AMF                 | 1.04 ± 0.03d  | 0.14 ± 0.002b | 68.16 ± 0.26a | 12.94 ± 0.09 fg | 14.56 ± 0.08d | 2.39 ± 0.02 b | 0.14 ± 0.0046b | 9.17 ± 0.04bc |
|                  |              | Nano-iron chelate   | 0.74 ± 0.01 fg | 0.1 ± 0.004de | 62.79 ± 0.14b | 13.47 ± 0.03de | 13.39 ± 0.04 e | 2.27 ± 0.01 c e | 0.16 ± 0.002a | 8.83 ± 0.02 e |
| 90%              | *L. iberica* | Without fertilizer  | 0.71 ± 0.04 fg | 0.04 ± 0.002 h | 50.95 ± 0.14i | 10.83 ± 0.02j | 14.56 ± 0.11 d | 1.75 ± 0.01 kl | 0.03 ± 0.001 l | 8.54 ± 0.22 df |
|                  |              | AMF                 | 1.24 ± 0.05c  | 0.12 ± 0.003c | 56.48 ± 0.33 g | 13.78 ± 0.25 cd | 15.79 ± 0.27 b | 2.07 ± 0.04 gh | 0.05 ± 0.005 j | 9.67 ± 0.14b |
|                  |              | Nano-iron chelate   | 0.68 ± 0.03 fg | 0.08 ± 0.001f | 56.58 ± 0.32 g | 14.03 ± 0.04 c | 15.66 ± 0.08 b | 1.98 ± 0.05 hi | 0.08 ± 0.0003 h | 9.05 ± 0.06 cd |
|                  | *L. royleana*| Without fertilizer  | 0.64 ± 0.02 g  | 0.08 ± 0.004f | 53.97 ± 0.16 h | 10.41 ± 0.05 k | 11.58 ± 0.1 g | 2.33 ± 0.02 bc | 0.07 ± 0.0007i | 7.33 ± 0.04 h |
|                  |              | AMF                 | 1.01 ± 0.05d  | 0.2 ± 0.005a  | 59.47 ± 0.04d | 11.13 ± 0.05j | 15.14 ± 0.05 c | 2.86 ± 0.02 a | 0.13 ± 0.004 c | 10.38 ± 0.05 a |
|                  |              | Nano-iron chelate   | 0.68 ± 0.02 fg | 0.13 ± 0.005 c | 57.79 ± 0.07 ef | 11.72 ± 0.08 h | 13.58 ± 0.03 e | 2.39 ± 0.01 b | 0.14 ± 0.004 b | 8.15 ± 0.18 fg |

The same letters in each column show non-significant differences at $P<0.05$, analyzed by Tukey's honest test. EA, eicosenoic acid; AA, arachidic acid; LNA, linolenic acid; LA, linoleic acid; OA, oleic acid; SA, stearic acid; POA, palmitoleic acid; PA, palmitic acid.
Decline in Chl a and Chl b concentration by increasing water deficit in both species of *Lallemantia* was due to water shortage which leads to stomata closure and decreasing CO₂ diffusion into leaves, resulting in a reduction of Chl levels and photosynthesis (Zhang et al. 2020). In addition, it has been reported that reduction of Chl a and Chl b concentration is probably due to the destruction of chloroplast and the instability of the chlorophyll protein complex (Ghanbarzadeh et al. 2019). However, Chl a and Chl b concentration increased in response to AMF and nano-iron chelate fertilizer. Increasing Chl a concentration in both species of *Lallemantia* in any irrigation regime by application of nano-iron chelate fertilizer is probably due to improving carbonic anhydrase activity and synthesis of photosynthetic pigments (El-Desouky et al. 2021). Indeed, nano-iron chelate by increasing photosynthesis rates and stomatal conductivity causes that transpiration rates decrease under water efficiency stress (Xie et al. 2018). According to the results, Chl b concentration in both species of *Lallemantia* inoculated significantly increased in any irrigation regime similar to the results of Paravar et al. (2021). It has been reported that AMF by developing the host plants’ root system could keep the stomata open to facilitate the exchange of gases for photosynthesis (Wu et al. 2013). Higher Chl a and Chl b in *L. iberica* leaves are probably due to the reduction in percentage of closed stomata which can provide CO₂ gas for photosynthesis (Paravar et al. 2021).

Based on the results, the highest oil percentage was observed in the 60% irrigation regime. Researchers considered that the enhancement of oil content under mild stress may be due to the increasing of osmotic adjustment in plants (Abdollahi and Maleki Farahani 2019; Tiwari et al. 2021). Osmotic adjustment is an important physiological adaptation to drought stress, resulting in improved extraction from dry soil as well as the maintenance of cell turgor, growth, and leaf exchange under water stress (Bai et al. 2019). Indeed, osmotic adjustments cause root extension into deeper soil and soil water extraction from low soil water potential (Farouk and Al-Amri 2019). Besides, it has been demonstrated *Lallemantia* plants are grown in dry regions, and water deficits are one of the main problems for the growth of plants in these regions (Abdollahi and Maleki Farahani 2019; Naservafaei et al. 2021). However, it has been proven that *Lallemantia* plants are able to cope with water shortages through changes in cell wall properties, closure stomata, osmotic adjustment, production of antioxidants, and secondary metabolites (Fazli et al. 2021; Omidi et al. 2018). A reduction in soil water (i.e., 90% irrigation regime) declined oil percentage which is consistent with reports by other (Bor zoo et al. 2021; Paravar et al. 2021). These reports showed that reduction in oil percentage was probably due to the decreasing in photosynthesis under irrigation deficit (Farouk and Al-Amri 2019). Indeed, plant availability to water and CO₂ limits under severe water deficit and fewer photosynthates dedicate to the parts of growing plant (Paravar et al. 2021). It is proved that enhanced photosynthesis can provide more carbon for oil synthesis (Rahimzadeh and Pirzad 2019). It seems water deficit could induce a specific defense mechanism in seeds of groundnuts through fatty acid synthesis as osmotic regulator metabolites (Pawar et al. 2018). Compared with *L. iberica*, the oil percentage of *L. royleana*, which is treated by nano-iron chelate, was higher across all irrigation regimes. The results obtained by other researchers showed that increasing in oil percentage in *Arachis hypogaea* L. (Nobahar et al. 2019) was due to the application of nano-iron chelate which caused the improvement of photosynthetic products under drought stress. It has been showed that increasing of Chl content caused the providing more carbohydrates (Keymer et al. 2017). Export of carbohydrates from photosynthesizing leaves to seeds of *L. royleana* may be caused by the increasing oil percentage because carbohydrates are precursors of fatty acid biosynthesis pathways (Mahmoud and Taha 2018). The AMF significantly enhanced the oil percentage in *L. iberica* species across all irrigation regimes. The present research findings are consistent with results, which found drought stress-induced reduction of fatty acid component, whereas mycorrhizal treatment increased the unsaturated fatty acid relative percentage in drought-stressed *Lavandula officinalis* L. and *Rosmarinus officinalis* L. seeds (Pirzad and Mohammadzadeh 2018). The extension of mycorrhizal hyphae may cause this ability, thereby increasing water and microelements (e.g., phosphorus) absorption from soil (Rahimzadeh and Pirzad 2019). Generally, higher oil percentage in *L. iberica* seeds than *L. royleana* is probably due to the higher chlorophyll concentration in leaves of *L. iberica* (Paravar et al. 2021). Chlorophyll is magnesium–tetrapyrrole molecules which plays fundamental roles during photosynthesis by absorption light and assembly with photosynthetic protein complexes (Liu et al. 2020). It has been demonstrated that enhancement of chlorophyll concentration could lead to the increasing photosynthesis activities and carbohydrate availability to developing seeds (Paravar et al. 2021).

Alterations in fatty acid compositions of both *Lallemantia* species under irrigation deficit are probably due to the decline in the activity of oleate desaturase enzyme, lipid metabolism, and transportation of lipids (Khademian et al. 2019). The present research findings are consistent with results reported that severe water deficits caused an enhancement in saturated fatty acids (PA, SA, and AA) and decreased unsaturated fatty acids, including POA, OA, LA, LNA, and EA (Wu et al. 2019). In addition, it has been reported that changes of fatty acid components under drought stress may be due to the inhibition of fatty acid and denaturizing activities that can lead to the alternated in oil concentration (Paravar et al. 2021). Many studies showed drought stress changed fatty acid components on *Silybum marianum* L. (Wu et al. 2019) and *Nigella sativa* L. (Bayati et al. 2020). In this present study, mycorrhizal inoculation enhanced the relative percentages of PA, SA, OA, LNA, AA, and EA under drought stress. According to our findings,
one major reason for the increasing relative percentages of PA, SA, OA, LNA, AA, and EA by AMF can be attributed to increased colonization (Jerbi et al. 2022). In light of this, it has been demonstrated that the diffusion of mycorrhizal mycelium into the roots’ inner tissues not only induces the reinforcing and expanding of root system in deeper soil layers but also facilitates the absorption of water and nutrients from large soil surface area through developed roots (Kheyri et al. 2022; Paravar et al. 2021). Thus, water and nutrient uptake can contribute to the boosted time to produce fatty acids in oil seeds via enhanced photosynthesis content, growth period, and sink capacity (Farouk and Al-Huqail 2022; Gholinezhad et al. 2020). Furthermore, previous research reported that fatty acid enhancement in plants treated with mycorrhizae may be related to the increased solubility and availability to phosphorus (Jones and French 2021), because phosphorus absorption from the deeper soil layer supplies the ATP and NADPH required for the fatty acid synthesis pathway (Carvalho et al. 2022). Our findings are in line with studies that reported the application of nano-iron chelate could change the relative percentage of POA and LA under irrigation deficit (Nobahar et al. 2019). Iron is a micronutrient that can lead to the protection of treated plants across irrigation deficit. It is reported that nano-iron by improving photosynthesis and stomatal conductance under deficit irrigation causes the provision of more carbohydrates for fatty acid biosynthesis (Khan et al. 2017; Ma et al. 2019). Across all irrigation regimes, the POA, PA, SA, LA, and AA relative percentage was higher in L. royleana than that of in L. iberica. However, the higher OA, LNA, and EA relative percentage in L. iberica than that of L. royleana may be because of different genetic backgrounds (Thokchom et al. 2020).

5 Conclusion

Results of this study demonstrated that increasing irrigation regime significantly reduced grain yield, chlorophyll concentration oil content, and fatty acid components of both Lallemantia species. However, compared with nano-iron fertilizer, AMF inoculation was an effective way in reducing the negative effects of drought stress on both Lallemantia species. Indeed, AMF inoculation caused the increasing grain yield and chlorophyll b concentration, as well as oil content and fatty acid components by improving soil condition and increasing root colonization under deficit irrigation. In addition, it showed that L. royleana plants due to the better response to AMF inoculation were higher tolerant against deficit irrigation compared with L. iberica. All in all, 60% irrigation regime was the optimal irrigation for producing both Lallemantia species, and AMF inoculation had the most effectiveness on improvement of the production of both Lallemantia species especially when these plants were exposed to 90% irrigation regime.

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Author Contribution AP, SMF, and ARR designed the concept of the study. AP carried and executed the experimental work. AP, SMF, and ARR jointly wrote the manuscript. All the authors have approved the manuscript and agree with the submission.

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Declarations

Conflict of Interest The authors declare no competing interests.

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