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Responses of *Zataria multiflora* Boiss. Ecotypes to Drought Stress and Plant Growth–Promoting Bacteria: Biomass, Antioxidant Capacity, and Photosynthetic Performance

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ABSTRACT

Zataria multiflora Boiss. is an important medicinal plant native to Iran, valued for its bioactive compounds and tolerance to environmental stresses. This study aimed to investigate the interactive effects of drought stress and plant growth–promoting rhizobacteria (PGPR) on growth, non-enzymatic antioxidants, and photosynthetic traits in different ecotypes of *Z. multiflora*. A three-factor factorial experiment was conducted in a completely randomized design with three replications, including ecotype (Isfahan, Kerman, Darab, Jahrom, and Khorramabad), drought stress levels (100, 75, and 50% field capacity), and PGPR treatments (control, *Arthrobacter* sp., and *Curtobacterium* sp.). Drought stress significantly reduced fresh and dry shoot biomass across all ecotypes, while PGPR inoculation alleviated biomass reduction at all stress levels, with *Curtobacterium* sp. showing the strongest growth-promoting effect under non-stress conditions. Total phenolic and flavonoid contents increased with increasing drought intensity in all ecotypes, whereas PGPR enhanced their accumulation under non-stress conditions but generally reduced these compounds under drought stress. Antioxidant activity and chlorophyll fluorescence parameters varied depending on ecotype and PGPR strain. Drought stress decreased chlorophyll a, chlorophyll b, and total chlorophyll contents, while PGPR application increased chlorophyll b and total chlorophyll and mitigated drought-induced damage. Carotenoid content increased under drought stress in most ecotypes. Overall, the results demonstrate that PGPR application, in a genotype- and stress-dependent manner, represents a sustainable biological approach for improving growth, maintaining photosynthetic efficiency, and enhancing drought tolerance in *Z. multiflora*.

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1. Introduction

Zataria multiflora Boiss. (Lamiaceae) is the only recognized species within the genus *Zataria* (Edalat *et al*., 2019). This medicinal plant has long been used in traditional medicine, and its aerial parts exhibit a wide range of biological activities, including antimicrobial, analgesic, antispasmodic, and anti-inflammatory effects, which have led to its incorporation into pharmaceutical formulations such as syrups, oral drops, and topical creams (Aryaeian *et al*., 2025). Owing to its significant medicinal and economic value, increasing attention has been directed toward the cultivation and sustainable utilization of this species. In recent years, climate change and the depletion of water resources have made drought stress one of the most critical constraints limiting the production of agricultural and medicinal plants worldwide (Talbi *et al*., 2020). Drought stress arises from reduced soil moisture availability or increased plant water loss and is often accompanied by salinity and osmotic stresses (Akbarzadeh *et al*., 2023). Water deficit can induce profound morphological, physiological, and biochemical alterations in plants, ultimately leading to reduced growth and productivity (Mumivand *et al*., 2021b). One of the major physiological consequences of drought stress is the degradation of photosynthetic pigments, including chlorophylls and carotenoids. Declines in pigment content reduce photosynthetic

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capacity, impair photosystem efficiency, and consequently decrease biomass accumulation and yield (Shirvani *et al*., 2024). Drought-induced damage to chloroplast ultrastructure and enhanced chlorophyllase activity have been reported as key mechanisms underlying pigment loss (Mumivand *et al*., 2021a; Wang *et al*., 2025). Moreover, drought stress triggers stomatal closure and reduces net photosynthesis, leading to decreased utilization of ATP and NADPH in the Calvin cycle and disruption of the electron transport chain within chloroplasts. This imbalance promotes the accumulation of excess electrons in photosystems and increases their transfer to molecular oxygen, resulting in elevated production of reactive oxygen species (ROS) (Qiao *et al*., 2024). Excessive ROS accumulation causes oxidative damage to photosynthetic pigments, membrane lipid peroxidation, and metabolic dysfunction, ultimately suppressing plant growth and performance (Wang *et al*., 2025; Sood, 2025). To counteract oxidative stress, plants enhance the synthesis of antioxidant compounds such as phenolics and flavonoids, which play a crucial role in ROS scavenging and stress tolerance (Beiranvandi *et al*., 2022). In addition to their protective function, these compounds contribute to pigment stability and the maintenance of photosynthetic efficiency under stress conditions (Mumivand *et al*., 2021a).

The application of plant growth–promoting rhizobacteria (PGPR) has emerged as a sustainable and cost-effective strategy to mitigate drought stress in plants. PGPR enhances nutrient acquisition, improves plant physiological status, and protects photosynthetic pigments, thereby promoting growth and drought tolerance (Karimi Sernawi *et al*., 2024; Mumivand *et al*., 2025). These beneficial microorganisms can also stimulate the biosynthesis of phenolic and flavonoid compounds, increasing the antioxidant capacity of plants and alleviating drought-induced damage (Mumivand *et al*., 2025; Asghari *et al*., 2020). Previous studies have demonstrated that PGPR inoculation improves growth traits, biomass accumulation, chlorophyll content, and antioxidant capacity in medicinal plants under water deficit conditions. For instance, Pagnani et al. (2018) reported that inoculation with *Azospirillum brasilense* and *Gluconacetobacter diazotrophicus* enhanced growth, yield, and secondary metabolite production in *Cannabis sativa*. Similarly, Mirzaei et al. (2020) observed increased dry weight and antioxidant capacity in lemongrass following inoculation with *Pseudomonas* sp. and *Azotobacter* sp. Enhanced chlorophyll content under drought stress has also been reported in *Ocimum basilicum* treated with PGPR (Heidari *et al*., 2012). Comparable results were observed in *Mentha pulegium*, where PGPR inoculation improved nutrient uptake, increased photosynthetic pigments, and promoted secondary metabolite accumulation, thereby mitigating the adverse effects of drought stress (Asghari *et al*., 2020).

Despite its high medicinal and economic importance, *Z. multiflora* populations in Iran are increasingly threatened by overharvesting and declining precipitation in recent years (Shaban *et al*., 2023). Drought stress is considered a major limiting factor for the growth and productivity of this species. Therefore, identifying drought-tolerant ecotypes represents a key strategy for domestication, cultivation expansion, and yield improvement. Recent evidence suggests that inoculation with growth-promoting microorganisms can enhance drought tolerance and improve plant performance through modulation of physiological and biochemical processes (Mumivand *et al*., 2025). Accordingly, the present study aimed to evaluate the responses of five *Z. multiflora* ecotypes to drought stress and PGPR inoculation (*Arthrobacter* sp. and *Curtobacterium* sp.) with respect to growth traits, photosynthetic pigments, non-enzymatic antioxidant indicators, and chlorophyll fluorescence parameters.

2. Materials and methods

2.1. Plant material and experimental treatments

Seeds of five ecotypes of *Zataria multiflora* Boiss. —Isfahan, Kerman, Darab, Jahrom, and Khorramabad ecotypes— were used in this study. The geographical characteristics of seed collection sites are presented in Table 1.

Table 1. Characteristics of the Seed Collection Sites of Different *Z. multiflora* Ecotypes

No	Genotype	Longitude (E)	Laitude (N)	Altitude (m a.s.l.)
1	Esfahan	54° 31' 02"	33° 57' 44"	1235
2	Kerman	57° 07^0 16.3″	30° 01^0 09.4″	2560
3	Darab	51° 230 00.3″	28° 43^0 00.2″	1557
4	Jahrom	28° 30′ 0″	53° 33′ 38″	1045
5	Khoramabad	48° 23^0 17″	33° 27^0 33″	1400

Seeds were sown in September 2022 in seedling trays filled with a cocopeat–perlite substrate and grown

under greenhouse conditions at the research greenhouses of the Faculty of Agriculture, Lorestan University. At the six–true-leaf stage, seedlings were fertilized with a balanced N–P–K fertilizer (20–20–20). In May 2023, uniform seedlings were transplanted into plastic pots (30 cm height × 25 cm diameter) containing a growth medium composed of field soil, well-rotted farmyard manure, and sand in a 1:1:1 (v/v/v) ratio. The physicochemical properties of the potting soil are shown in Table 2.

Table 2. Physicochemical properties of the potting soils used

No.	Soil properties	Unit
1	Total nitrogen (%)	0.23
2	Available potassium (mg.kg^{-1})	277
3	Available phosphorus (mg.kg^{-1})	6.6
4	Iron (mg.kg^{-1})	1.71
5	Magnesium (mg.kg^{-1})	99.4
6	Zinc (mg.kg^{-1})	0.83
7	Copper (mg.kg^{-1})	0.41
8	Boron (mg.kg^{-1})	0.41
9	Organic carbon (%)	1.17
10	pH	7.7
11	EC (ds/m)	2.03
12	Sand (%)	55.6
13	Clay (%)	19.2
14	Silt (%)	25.2
15	Calcium carbonate (%)	7.8

The experiment was conducted as a three-factor factorial arranged in a completely randomized design with three replications, each replication consisting of five pots. The experimental factors included: (i) five *Z. multiflora* ecotypes (Isfahan, Kerman, Darab, Jahrom, and Khorramabad), (ii) plant growth–promoting rhizobacteria (PGPR) at three levels (non-inoculated control, *Arthrobacter* sp., and *Curtobacterium* sp.) (Table 3), and (iii) drought stress at three levels (100, 75, and 50% of field capacity). PGPR inoculation was applied twice: first at transplanting and again 20 days later. Drought stress levels were imposed based on percentage reductions in soil moisture relative to field capacity (FC) and maintained using a gravimetric method. FC was determined for each pot, and daily water loss was compensated for by weighing pots and adding the required amount of water to reach the target moisture level. Throughout the experimental period, greenhouse conditions were carefully monitored, and weeds, pests, and diseases were controlled as required. The greenhouse was oriented north–south, with average day/night temperatures of approximately 30/20°C, relative humidity ranging from 55 to 85%, and a mean photosynthetic photon flux density (PPFD) of 700 ± 100 µmol m^{-2}s^{-1}.

Table 3. Characteristics of plant growth-promoting bacteria used

Characteristics		*Curtobacterium*	*Arthrobacter*
Gram stain		+	+
Type of metabolism		O	O
Oxidase		-	+
Catalase		+	+
Starch hydrolysis		-	-
Growth in NaCl (%)	5	+	+
	7	+	+
	10	+	-
	15	+	-
Gelatin hydrolysis		+	+
ACC-deaminase activity		+	+
Siderophore production		+	+
Growth at temperature (°C)		10–37°C (optimum 28–30°C)	4–37°C (weak growth at 45°C)
Indole-3-acetic acid (IAA)		+	+

2.2. Sampling and growth measurements

At the end of the experiment (October 2023), during the full flowering stage, the young fully expanded leaves were sampled for biochemical analyses, including chlorophyll a, chlorophyll b, total chlorophyll, carotenoids, total phenolics, total flavonoids, and antioxidant activity (Aghamirzaei *et al*., 2024). Leaf samples were immediately frozen in liquid nitrogen and stored at −80°C until analysis. Four plants per treatment were randomly harvested to determine shoot fresh weight. Samples were then air-dried under shade at room temperature until constant weight was achieved, and shoot dry weight was recorded.

2.3. Total phenolic content

Leaf extracts were prepared by homogenizing 100 mg of dried leaf tissue with 2 mL of 80% methanol and incubating the mixture for 16 h in darkness. After centrifugation at 14,000 rpm for 20 min, the supernatant was collected for analysis of total phenolics, flavonoids, and antioxidant activity (Babaei-Rad *et al*., 2025). Total phenolic content was determined using the Folin–Ciocalteu reagent following McDonald et al. (2001). Briefly, 0.4 mL of diluted extract was mixed with 1.6 mL sodium carbonate solution and 2 mL Folin–Ciocalteu reagent. After incubation for 30 min at room temperature, absorbance was measured at 760 nm. Results were expressed as milligrams of gallic acid equivalents per gram of dry weight (mg GAE g^{-1} DW).

2.4. Total flavonoid content

Total flavonoid content was determined using the aluminum chloride colorimetric method according to Chang et al. (2002). Briefly, 200 µL of plant extract was mixed with 100 µL aluminum chloride solution and 100 µL potassium acetate. The mixture was vortexed and incubated for 30 min in darkness at room temperature, and absorbance was recorded at 415 nm. A rutin standard curve (0, 2.5, 5, 10, 20, and 320 mg L^{-1}) was used for quantification. Results were expressed as milligrams of rutin equivalents per gram of dry weight (mg RE g^{-1} DW).

2.5. Total antioxidant activity

Antioxidant activity was assessed using the ferric reducing antioxidant power (FRAP) assay following Benzie and Strain (1996). A 300 mM acetate buffer (pH 3.6), 10 mM TPTZ solution (in 40 mM HCl), and 20 mM $FeCl_3 \cdot 6H_2O$ were mixed at a ratio of 10:1:1 to prepare the FRAP working solution. For the assay, 180 µL of freshly prepared FRAP reagent was mixed with 20 µL of methanolic extract and incubated at 37°C for 8 min. Absorbance was measured at 593 nm. $FeSO_4 \cdot 7H_2O$ was used as the standard, and results were expressed as mmol Fe g^{-1} DW.

2.6. Photosynthetic pigments

Chlorophyll a, chlorophyll b, total chlorophyll, and carotenoid contents were determined according to Lichtenthaler (1987). Leaf tissue was extracted with 80% acetone and centrifuged at 3,000 rpm for 10 min. Absorbance of the supernatant was measured at 663, 646, and 470 nm using a spectrophotometer. Pigment concentrations were calculated using Equations 1-4.

(1) $$\text{Chl a} = [12.21 \times A_{663} - 2.81 \times A_{646}] \times \frac{V}{W}$$

(2) $$\text{Chl b} = [20.13 \times A_{646} - 5.03 \times A_{663}] \times \frac{V}{W}$$

(3) $$\text{Total Chlorophyll} = \text{Chl a} + \text{Chl b}$$

(4) $$\text{Carotenoids} = \frac{100 \times A_{470} - 1.8 \times \text{Chl a} - 85.02 \times \text{Chl b}}{198} \times \frac{V}{W}$$

Where A663, A646, and A470 are absorbance values at the respective wavelengths, V is the final volume of extract (mL), and W is fresh leaf weight (mg).

2.7. Chlorophyll fluorescence

Chlorophyll fluorescence parameters were measured using a Pocket PEA fluorimeter (Hansatech Instruments Ltd., UK). Fully expanded leaves were dark-adapted for 20 min using leaf clips prior to measurement. Minimum fluorescence (F_0), maximum fluorescence (F_m), variable fluorescence (Fv), and maximum quantum efficiency of PSII (Fv/F_m) were recorded. Measurements were conducted between 10:00 and 13:00 h (Hajipour *et al*., 2025).

2.8. Statistical analysis

Data were subjected to analysis of variance (ANOVA) using SAS software (version 9.1) according to the experimental design. Mean comparisons were performed using Duncan's multiple range test at a significance level of $p \leq 0.05$.

3. Results and discussion

3.1. Shoot fresh and dry weight

Analysis of variance (ANOVA) revealed that the main effects of drought stress and bacterial inoculation were significant for both shoot fresh and dry weights, whereas genotype had no significant effect on either trait. The interaction of drought stress × genotype significantly affected shoot dry weight but had no significant effect on shoot fresh weight. Shoot fresh and dry weights were significantly influenced by the interaction of drought stress × bacterial inoculation. In contrast, the genotype × bacterial inoculation interaction was not significant for either trait. Moreover, the three-way interaction of drought stress × genotype × bacterial inoculation significantly affected both shoot fresh and dry weights (Table 4). Shoot fresh and dry weights significantly decreased in all genotypes with increasing drought stress. However, PGPR inoculation significantly increased both traits across all genotypes and at all drought levels. The positive effect of *Curtobacterium* was particularly pronounced under non-stress conditions. Overall, the highest shoot fresh and dry weights were observed under non-stress conditions in the Isfahan, Jahrom, and Kerman genotypes inoculated with *Curtobacterium* (Table 5).

Table 4. Analysis of variance of the effects of drought stress, bacterial inoculation, and genotype on yield, total phenolics, flavonoids, and antioxidant activity in *Z. multiflora*.

Source	DF	Shoot fresh weight	Shoot dry weight	Total Phenol	Total flavonoid	Antioxidant activity
Drought	2	37598.71**	7205.01**	10422.16**	80305.58**	0.34**
Genotype	4	10.45^{ns}	10.44^{ns}	42.81*	209.08^{ns}	0.20**
Inoculation	2	1815.58**	433.31**	945.35**	3219.88**	0.16905^{ns}
Drought × Genotype	8	57.97^{ns}	19.31**	170.41**	1510.65**	0.16728**
Drought × Inoculation	4	304.09**	205.88**	829.29**	1735.04**	0.14575**
Genotype × Inoculation	8	20.60^{ns}	9.10^{ns}	106.64**	502.27**	0.09095*
Drought × Genotype × Inoculation	16	66.58**	12.26*	44.05**	608.94**	0.08052**
Error	90	29.78	6.64	12.20	160.91	0.03336
CV (%)	-	8.12	8.65	8.42	8.62	10.5

*, **, and ns: significant at the 1% level, significant at the 5% level, and not significant, respectively.

Table 5. Mean comparison of the interaction effects of drought stress, bacterial inoculation, and genotype on yield, total phenolics, flavonoids, antioxidant activity, and carotenoids in *Z. multiflora*

Genotype	Drought (FC %)	Inoculation	Shoot fresh weight (g)	Shoot dry weight (g)	Total Phenol (mg GAE g^{-1} DW)	Total flavonoid (mg RE g^{-1} DW)	Antioxidant activity (µmol Fe^{+2} g^{-1} DW)	Carotenoid (mg g^{-1} FW)
Darab	100%	No Inoculation	83.07±5.13^{h}	38.13±2.66^{gh}	25.53±2.05^{tuv}	12.75±1.02^{mno}	1.758±0.26^{e-m}	75.56±5.36^{f-l}
		Curtobacterium	106.47±7.5^{bcd}	47.87±2.27^{de}	34.56±0.91^{qr}	8.7.57±0.77^{stu}	1.780±0.16^{d-m}	67.32±2.23^{k-o}
		Arthrobacter	107.6±3.46^{bcd}	44.13±2.73^{de}	28.76±3.06^{stu}	10.06±1.21^{q-t}	1.655±0.4^{h-n}	61.87±4.89^{nop}
	75%	No Inoculation	56.27±2.1^{k-n}	24.13±2.1^{j-n}	55.71±2.96^{efg}	18.18±0.37^{b-g}	1.696±0.16^{f-n}	86.89±4.10^{cde}
		Curtobacterium	60.2±1.70^{i-m}	26.13±2.13^{i-l}	47.72±3^{i-m}	16.49±0.32^{g-j}	1.492±0.15^{lmn}	80.66±1.02^{e-h}
		Arthrobacter	57.87±1.6^{j-n}	21.67±3.07^{m-p}	40.76±1.93^{nop}	12.94±0.28^{mno}	1.672±0.15^{g-n}	79.20±11.12^{e-i}
	50%	No Inoculation	43±3^{rst}	18.4±2.62^{p}	51.67±4.38^{g-k}	19.74±0.98^{abc}	1.638±0.14^{h-n}	97.43±12.82^{ab}
		Curtobacterium	49.67±2.34^{n-r}	20.43±1.27^{nop}	54.51±4.27^{efg}	18.70±1.56^{a-f}	1.537±0.11^{lmn}	80.64±8.76^{e-h}
		Arthrobacter	44.13±5.47^{p-t}	19.26±1.26^{p}	43.77± 3.72^{l-o}	16.55±0.52^{g-j}	1.614±0.08^{j-n}	76.23±7.52^{f-k}
Esfahan	100%	No Inoculation	86±3.81^{h}	36.67±2.30^{h}	20.31±3.79^{vwx}	8.01±3.37^{tu}	1.894±0.43^{b-j}	72.08±2.16^{h-m}
		Curtobacterium	112.4±9.27^{abc}	52.74±4.16^{ab}	20.43±3.45^{vwx}	12.30±1.78^{mno}	1.750±0.19^{f-m}	60.78±1.91^{nop}
		Arthrobacter	91.73±10.02^{fgh}	41.13±1.33^{fg}	24.93±3.26^{tuvw}	9.67±2.52^{q-u}	1.966±0.26^{b-g}	63.96±3.12^{m-p}
	75%	No Inoculation	56.47±8.46^{j-n}	24.87±3.18^{i-m}	59.25±4.11^{cde}	15.94±0.46^{h-k}	1.617±017^{j-n}	80.59±2.3^{e-h}
		Curtobacterium	65.13±3.71^{ij}	26.87±0.46^{i-l}	35.49±4.6^{pq}	12.76±0.45^{mno}	1.536±0.1^{lmn}	63.67±2.25^{m-p}
		Arthrobacter	62±3.60^{i-l}	28.13±0.50^{ij}	38.77±2.78^{opq}	13.98±1.03^{klm}	1.558±0.12^{lmn}	77.17±4.08^{f-j}
	50%	No Inoculation	37.67±2.08^{tu}	17.67±2.13^{pq}	69.36±3.99^{a}	20.36±0.46^{a}	1.496±0.16^{mn}	95.30±5.01^{abc}
		Curtobacterium	43.17±1.88^{rst}	18.531.66^{p}	46.34±3.82^{j-n}	19.88±1.21^{ab}	1.605±0.15^{j-n}	75.33±6.76^{f-l}
		Arthrobacter	42.73±6.37^{rst}	19.26±1.84^{op}	54.97±6.46^{efg}	19.85±0.69^{ab}	1.786±0.2^{d-l}	80.53±6.37^{e-h}
Khoramabad	100%	No Inoculation	89.33±8.78^{gh}	37.53±2.50^{gh}	18.95±2.096^{x}	7.99±0.94^{u}	1.784±0.18^{d-l}	79.36±5.01^{e-h}
		Curtobacterium	104.33±5.6^{cde}	49.87±3.72^{bcd}	26.32±2.15^{tu}	10.31±1.26^{p-s}	1.784±0.05^{d-l}	68.59±3.89^{j-o}
		Arthrobacter	99.06±7.1^{def}	42.73±2.60^{f}	27.26±2.95^{tu}	11.16±1.15^{n-q}	2.115±0.06^{abc}	59.59±5.92^{op}
	75%	No Inoculation	55.2±4.71^{k-o}	23.60±2.88^{k-n}	61.38±5.08^{cd}	19.60±1.23^{a-d}	1.979±0.12^{b-f}	74.97±3.32^{g-l}
		Curtobacterium	61.93±5.70^{i-l}	23.13±1.72^{l-o}	40.71±6^{nop}	15.56±0.18^{ijk}	1.634±0.06^{i-n}	80.50±5.23^{e-h}
		Arthrobacter	57.2±3.30^{j-n}	27.13±1.52^{i-l}	28.94±1.3^{rst}	13.22±0.63^{lmn}	2.358±0.17^{a}	79.99±6.43^{e-h}
	50%	No Inoculation	39.33±5.77^{stu}	18.73±1.81^{p}	67.88±3.73^{ab}	19.60±0.81^{a-d}	2.049±0.1^{b-e}	92.43±4.66^{bcd}
		Curtobacterium	52.07±2.65^{m-q}	23.4±1.9^{k-o}	51.1±3.26^{g-j}	17.78±0.39^{c-h}	1.560±0.13^{lmn}	69.51±7.21^{i-n}
		Arthrobacter	43.60±7.07^{q-t}	21.66±3.07^{m-p}	63.16±5.32^{cd}	16.59±0.44^{g-j}	1.630±0.12^{i-n}	80.49±3.80^{e-h}
Jahrom	100%	No Inoculation	89.8±8.43^{gh}	35.33±2.99^{h}	19.75±1.05^{wx}	8.56±1.86^{stu}	1.868±0.16^{c-k}	67.20±4.14^{k-p}
		Curtobacterium	113.6±8^{ab}	54.27±2.38^{a}	23.22±1.89^{u-x}	10.92±1.95^{o-r}	1.915±0.09^{b-i}	75.27±5.61^{f-l}
		Arthrobacter	102±6.12^{de}	48.86±3.85^{cd}	25.20±4.16^{tuvw}	9.76±1.50^{q-u}	2.183±0.25^{ab}	57.53±12.72^{p}
	75%	No Inoculation	56.27±2.13^{k-n}	26.8±2.07^{i-l}	56.81±1.47^{d-g}	17.19±0.62^{e-i}	1.579±0.1^{k-n}	77.69±2.27^{e-j}
		Curtobacterium	67.93±2.08^{i}	27.27±0.8^{ijk}	46.18±2.93^{k-n}	15.96±0.33^{h-k}	1.448±0.07^{n}	62.81±4.95^{m-p}
		Arthrobacter	58.54±6.4^{j-m}	27.53±3.3^{ijk}	43.45±1.75^{mno}	14.22±0.5.0^{klm}	1.703±0.13^{f-n}	66.43±3.11^{l-p}
	50%	No Inoculation	32±2^{u}	14.13±0.41^{q}	53.22±1.43^{f-i}	17.72±1.07^{c-h}	2.057±0.13^{bcd}	102.87±9.73^{a}
		Curtobacterium	44.46±5.49^{p-t}	19.33±2.30^{op}	49.28±3.46^{h-k}	16.76±1.59^{f-j}	1.633±0.1^{i-n}	83.49±5.64^{d-g}
		Arthrobacter	47.06±6.92^{o-s}	20.67±3.05^{nop}	46.92±3.09^{j-m}	17.37±1.03^{e-i}	1.506±0.17^{lmn}	84.94±9.01^{def}
Kerman	100%	No Inoculation	90.66±2.71^{fgh}	36.47±0.23^{h}	19.17±2.03^{x}	10.55±1.43^{p-s}	1.509±0.15^{lmn}	74.66±7.65^{g-l}
		Curtobacterium	116.8±8.51^{a}	52.47±4.8^{abc}	23.45±2.54^{t-x}	9.85±1.09^{q-u}	1.867±0.18^{c-k}	87.28±4.56^{cde}
		Arthrobacter	96.8±6.48^{efg}	41.47±5.52^{fg}	26.83±3.2^{tu}	9.09±1.43^{r-u}	1.648±0.46^{h-n}	75.514±2.52^{f-l}
	75%	No Inoculation	53.4±3.07^{l-o}	24.13±2.0^{j-n}	63.29±4.28^{bc}	18.95±0.36^{a-d}	1.932±0.08^{b-h}	78.28±4.7^{e-j}
		Curtobacterium	53.4±3.07^{l-o}	26.33±2.13^{i-l}	46.32±4.27^{k-n}	18.01 ±1.29^{b-g}	1.975±0.11^{b-f}	63.05±4.32^{m-p}
		Arthrobacter	62.26±5^{ijk}	28.33±2.27^{i}	34.05±1.34^{qrs}	17.61±1.59^{d-i}	1.757±0.06^{e-m}	66.04±5.65^{l-p}
	50%	No Inoculation	41±1^{rst}	20.67±2.30^{nop}	58.04±4.75^{c-f}	18.88±0.99^{a-e}	1.759±0.15^{e-m}	100.02±5.58^{ab}
		Curtobacterium	47.2±3.53^{o-s}	21.33±3.05^{m-p}	44.26±3.72^{l-o}	15.09±0.26^{jkl}	1.517±0.09^{lmn}	72.04±6.5^{h-m}
		Arthrobacter	42.6±2.22^{rst}	21.6±0.7^{m-p}	45.81±3.53^{lmn}	16.76±1.77^{f-j}	1.486±0.16^{lmn}	78.011±4.27^{e-j}

Means in each column followed by the same letter are not significantly different at the 1% probability level according to Duncan's multiple range test.

3.2. Total phenolic content

ANOVA showed that the main effects as well as all two-way and three-way interactions among drought stress, bacterial inoculation, and genotype had significant effects on total phenolic content (Table 4). Mean comparisons indicated that total phenolic content significantly increased with increasing drought intensity in all genotypes. PGPR inoculation exerted contrasting effects on total phenolic content depending on water availability. Under non-stress conditions, PGPR generally increased total phenolic content in most genotypes, whereas under drought stress, PGPR application resulted in a reduction of total phenolics in the majority of genotypes. The highest total phenolic content was recorded in the Isfahan genotype under 50% FC without bacterial inoculation (36.69 mg GAE g^{-1} DW); however, this value was not statistically different from that of the Khorramabad genotype under the same drought level and without bacterial inoculation (Table 5).

3.3. Total flavonoids

ANOVA indicated that the main effects of drought stress and inoculation with PGPR, as well as the two-way and three-way interactions among drought stress, PGPR inoculation, and genotype, were significant for total flavonoid content (Table 4). Mean comparisons revealed that drought stress increased total flavonoid content across all *Z. multiflora* genotypes. PGPR inoculation, however, did not have a consistent effect on flavonoid content. Under non-stress conditions, PGPR inoculation enhanced total flavonoid content in the Khorram, Jahrom, and Isfahan genotypes. In contrast, under drought stress, the effect of PGPR on total flavonoid content was generally negative or non-significant in most genotypes. Overall, the Isfahan genotype exhibited the highest total flavonoid content under 50% FC, regardless of the PGPR treatment (Table 5).

3.4. Antioxidant activity

ANOVA revealed that both drought stress and genotype had significant effects on antioxidant activity. Moreover, the two-way and three-way interactions among drought stress, genotype, and inoculation with PGPR were also statistically significant (Table 4). Mean comparisons indicated that the response of antioxidant activity to drought stress varied depending on the genotype and PGPR treatment. Specifically, in the Darab and Khorramabad genotypes under non-inoculated conditions, drought stress at 50% and 75% FC did not induce significant changes in antioxidant activity. In contrast, severe drought stress (50% FC) reduced antioxidant activity in the Isfahan genotype, while in the Kerman genotype, drought stress at 75% FC led to an increase in antioxidant activity. The effect of PGPR inoculation also differed among genotypes and drought levels, highlighting the genotype-dependent nature of the response. Overall, the highest antioxidant activity was observed in the Khorramabad genotype under 75% FC when inoculated with *Arthrobacter* (35.2 µmol Fe^{2+} g^{-1} DW), which was not significantly different from that of the Jahrom genotype inoculated with *Arthrobacter* under non-stress conditions (Table 5). These results suggest that PGPR inoculation can modulate antioxidant responses in a genotype- and stress-dependent manner.

3.5. Photosynthetic pigments

ANOVA revealed that the main effect of drought stress was significant for chlorophyll a, total chlorophyll, and carotenoid content. Chlorophyll a, chlorophyll b, total chlorophyll, and carotenoid content were significantly influenced by the main effect of bacterial inoculation and the interaction of drought stress × genotype. The interaction of drought stress × bacterial inoculation was also significant for chlorophyll b, total chlorophyll, and carotenoids. Furthermore, the three-way interaction of drought stress × genotype × bacterial inoculation significantly affected carotenoid content (Table 6). Mean comparisons indicated that inoculation with PGPR, regardless of bacterial type, increased chlorophyll a content. Specifically, inoculation with *Curtobacterium* increased chlorophyll a by 32.61%, while *Arthrobacter* inoculation led to a 37.60% increase compared to non-inoculated plants (Fig. 1).

The effect of drought stress on chlorophyll content varied among genotypes. For instance, in the Khorramabad genotype, severe drought stress (50% FC) led to reductions in chlorophyll a, chlorophyll b, and total chlorophyll. In the Kerman genotype, decreases in chlorophyll a and total chlorophyll were observed at both levels of drought stress. Similarly, severe drought stress reduced chlorophyll a content in the Jahrom genotype. However, in the remaining

genotypes, drought stress did not result in significant changes in the measured pigments (Fig. 2A-C). Mean comparisons indicated that drought stress generally decreased chlorophyll b and total chlorophyll content. Nevertheless, inoculation with PGPR largely mitigated the negative effects of drought stress, leading to increases in chlorophyll b and total chlorophyll. Overall, PGPR inoculation enhanced chlorophyll b and total chlorophyll content across all levels of drought stress (Fig. 3A, B). Mean comparisons indicated that drought stress had a variable effect on carotenoid content. In most genotypes and across many PGPR treatments, drought stress tended to increase carotenoid levels, although in some cases, changes were not statistically significant. The effect of PGPR inoculation on carotenoid content was also genotype- and bacteria-dependent. For example, *Arthrobacter* inoculation under non-stress conditions significantly decreased carotenoid content in the Darab and Jahrom genotypes, whereas *Curtobacterium* inoculation in these genotypes did not result in significant differences compared to non-inoculated plants. In contrast, in the Isfahan genotype, *Curtobacterium* inoculation reduced carotenoid content, while *Arthrobacter* had no significant effect. In the Khorramabad genotype, both bacterial inoculations separately led to significant reductions in carotenoid content, whereas in the Kerman genotype, *Curtobacterium* inoculation increased carotenoid levels. Overall, the highest carotenoid content was observed in the Jahrom, Kerman, and Isfahan genotypes under severe drought stress (50% FC) without PGPR inoculation (Table 5).

Table 6. Analysis of variance of the effects of drought stress, bacterial inoculation, and genotype on photosynthetic pigments in *Z. multiflora*.

Source	DF	Chlorophyll a	Chlorophyll b	Total Chlorophyll	Carotenoid
Drought	2	8.2262**	1.6545^{ns}	17.258**	2585.39**
Genotype	4	0.5358^{ns}	0.4448^{ns}	0.211^{ns}	66.94^{ns}
Inoculation	2	99.6429**	48.5752**	287.356**	1840.26**
Drought × Genotype	8	1.9799*	1.5924*	5.093*	308.73**
Drought × Inoculation	4	0.9880^{ns}	2.4278**	5.726*	445.90**
Genotype × Inoculation	8	0.7135^{ns}	0.5609^{ns}	1.066^{ns}	53.94^{ns}
Drought × Genotype × Inoculation	16	1.1356^{ns}	0.7573^{ns}	2.758^{ns}	95.43**
Error	90	0.7276	0.6498	1.696	35.83
CV (%)	-	14.31	18.70	12.68	7.84

*, **, and ns: significant at the 1% level, significant at the 5% level, and not significant, respectively.

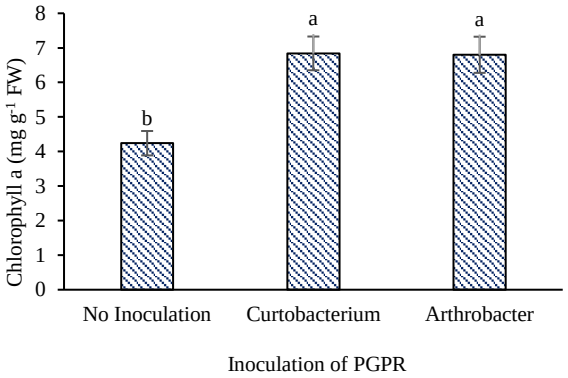


Figure 1. Effect of plant growth-promoting bacteria on chlorophyll a content in *Z. multiflora*

3.6. Chlorophyll fluorescence

ANOVA revealed that drought stress significantly affected minimum fluorescence (F_0), maximum fluorescence (F_m), and variable fluorescence (Fv). The main effect of genotype, as well as the interactions genotype × drought stress and genotype × bacterial inoculation, were significant for Fv/F_m. Additionally, the three-way interaction among drought stress, genotype, and PGPR inoculation significantly influenced all chlorophyll fluorescence parameters (Table 7). Mean comparisons showed that although drought stress and bacterial inoculation altered F_0 and F_m in several cases, these changes were generally inconsistent and mostly non-significant. Fv also showed no consistent trend under drought stress. For example, in most genotypes, drought stress did not significantly affect Fv; however, in the Isfahan and Kerman genotypes under severe stress (50% FC) without PGPR inoculation, Fv increased. Conversely, in the Jahrom genotype, mild drought stress (75% FC) decreased Fv under non-inoculated conditions. Drought stress and bacterial inoculation influenced the Fv/F_m ratio in several cases, but changes were irregular and mostly non-significant. Nevertheless, in the Isfahan genotype under non-stress conditions, inoculation with *Arthrobacter* increased the Fv/F_m ratio, whereas the opposite trend was observed in the Darab genotype under the same conditions (Table 8).

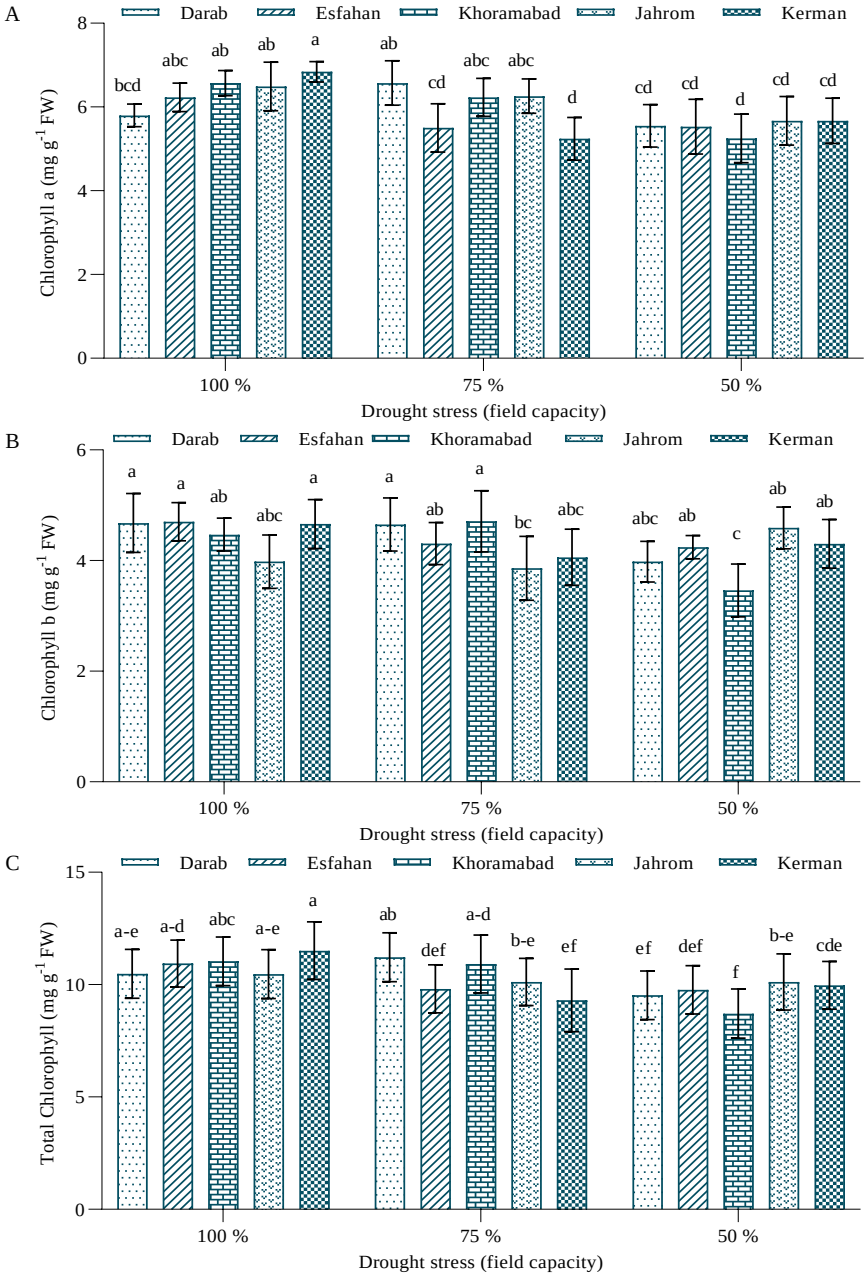


Figure 2. Comparison of the mean effects of the interaction between drought stress and genotype on (A) chlorophyll a, (B) chlorophyll b, and (C) total chlorophyll in *Z. multiflora*

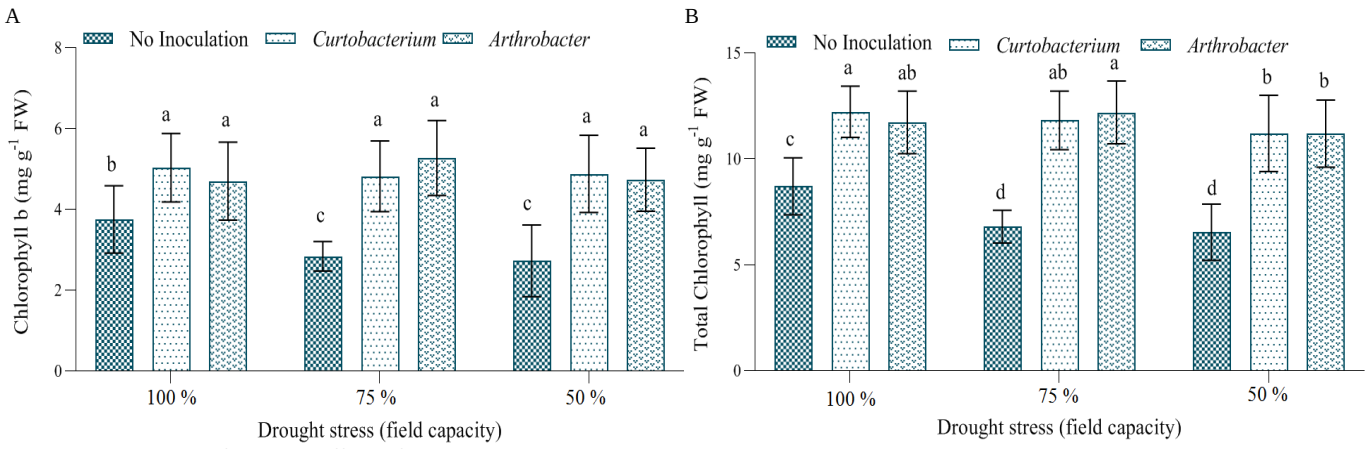


Figure 3. Comparison of the mean effects of the interaction between drought stress and plant growth-promoting bacteria on (A) chlorophyll b and (B) total chlorophyll in *Z. multiflora*

Table 7. Analysis of variance of the effects of drought stress, bacterial inoculation, and genotype on chlorophyll fluorescence parameters in *Z. multiflora*

Source	DF	F_0	Fm	Fv	Fv/Fm
Drought	2	564509.18*	28250469.1**	20862196.44**	0.00005^{ns}
Genotype	4	30792.21^{ns}	4276815.5^{ns}	4025409.27^{ns}	0.0002**
Inoculation	2	239962.10^{ns}	2391633.1^{ns}	1119880.37^{ns}	0.0001^{ns}
Drought × Genotype	8	220285.19^{ns}	7181740.6^{ns}	5386280.56^{ns}	0.0001**
Drought × Inoculation	4	139887.75^{ns}	4326311.8^{ns}	2978064.24^{ns}	0.00003^{ns}
Genotype × Inoculation	8	72027.28^{ns}	3970489^{ns}	3251203.50^{ns}	0.0001*
Drought × Genotype × Inoculation	16	149450.22*	7530736.1*	5896709.58*	0.0001**
Error	90	131930.13	4121693.9	2926105.9	0.00005
CV (%)	-	9.62	8.94	9.03	0.90

*, **, and ns: significant at the 1% level, significant at the 5% level, and not significant, respectively.

Table 8. Mean comparison of the interaction effects of drought stress, bacterial inoculation, and genotype on chlorophyll fluorescence parameters

Genotype	Drought (FC %)	Inoculation	F_0	Fm	Fv	Fv/Fm
Darab	100%	No Inoculation	3630.6±316.56^{a-d}	21537.3±750.46^{b-f}	17906.6±554.86^{b-f}	0.8313±0.01^{a-g}
		Curtobacterium	3673.1±8.14^{a-d}	22099.1±344.35^{a-f}	18426±336.2^{b-f}	0.8338±0.002^{a-g}
		Arthrobacter	3588.3±653.68^{bcd}	19826.8±2639.15^{ef}	16238.5±2037.6^{ef}	0.8198±0.01^{hi}
	75%	No Inoculation	3680.5±161.42^{a-d}	22810.3±544.14^{a-f}	19129.8±400.07^{a-f}	0.8385±0.004^{a-e}
		Curtobacterium	3089.1±766.45^{d}	19629.8±4701.63^{f}	16540.6±3941.48^{def}	0.8440±0.005^{ab}
		Arthrobacter	3911.8±392.77^{abc}	23559.3±1345.10^{a-f}	19647.5±969.52^{a-e}	0.8341±0.007^{a-g}
	50%	No Inoculation	3928.8±132.31^{abc}	23754±1587.92^{a-f}	19825.1±1503.09^{a-d}	0.8348±0.008^{a-g}
		Curtobacterium	4191.5±539.5^{ab}	25327.8±2976.66^{ab}	21136.3±2438.25^{ab}	0.8288±0.002^{b-g}
		Arthrobacter	4087.1±321.95^{abc}	23863.1±1382.68^{a-e}	19776±1094.79^{a-d}	0.842±0.005^{abc}
Esfahan	100%	No Inoculation	3654.8±394.26^{a-d}	20893.8±1760.78^{a-f}	17239±1395.59^{c-f}	0.8253±0.007^{d-g}
		Curtobacterium	3764.6±232.19^{a-d}	23630.1±1795.33^{a-f}	19865.5±1564.83^{a-d}	0.8403±0.002^{a-d}
		Arthrobacter	4036.6±264.1^{abc}	26055.1±1061.03^{a}	22018.5±800.32^{a}	0.8451±0.004^{a}
	75%	No Inoculation	3623.1±68.84^{a-d}	22473.6±906.43^{a-f}	18850.5±839.13^{a-f}	0.8385±0.003^{a-e}
		Curtobacterium	3464.6±123.98^{bcd}	21611.6±393.6^{b-f}	18147±314.31^{b-f}	0.84±0.004^{a-d}
		Arthrobacter	4332.5±711.38^{a}	25401.5±1788.92^{ab}	21069±1078.26^{ab}	0.8303±0.01^{a-g}
	50%	No Inoculation	3942.6±150.77^{abc}	24982.5±1650.24^{abc}	21039.8±1503.64^{ab}	0.842±0.004^{abc}
		Curtobacterium	3622±163.38^{a-d}	21974±1078.9^{a-f}	18352±931.69^{b-f}	0.8346±0.003^{a-f}
		Arthrobacter	3485±404.93^{bcd}	21829.8±2252.4^{b-f}	18344.8±1863.66^{b-f}	0.8405±0.005^{a-d}
Khoramabad	100%	No Inoculation	3742.8±373.77^{a-d}	23132.6±2314.2^{a-f}	19389.8±1956.45^{a-f}	0.8380±0.004^{a-f}
		Curtobacterium	3791±319.71^{a-d}	23115.6±1122.41^{a-f}	19324.6±804.67^{a-f}	0.8358±0.006^{a-f}
		Arthrobacter	3779.1±202.49^{a-d}	22857.8±1168.87^{a-f}	19078.6±966.52^{a-f}	0.8340±0.0005^{a-g}
	75%	No Inoculation	3515±200.56^{bcd}	22274±1778.78^{a-f}	18759±1589.28^{a-f}	0.8421±0.005^{abc}
		Curtobacterium	3637.6±361.58^{a-d}	22864.1±2080.73^{a-f}	19226.5±1720.94^{a-f}	0.8408±0.002^{abc}
		Arthrobacter	3600.6±181.59^{a-d}	20969±2781.14^{c-f}	17368.3±2627.25^{c-f}	0.8235±0.02^{efg}
	50%	No Inoculation	3869±471.79^{abc}	23460.1±2601.84^{a-f}	19591.1±2134.30^{a-e}	0.8356±0.003^{a-f}
		Curtobacterium	3979.3±435.56^{abc}	23901.3±2737.94^{a-e}	19922±2316^{a-d}	0.8338±0.004^{a-g}
		Arthrobacter	4016.8±362.19^{abc}	23691.1±2580.83^{a-f}	19674.3±2229.2^{a-e}	0.8330±0.005^{a-g}
Jahrom	100%	No Inoculation	3985.6±85.99^{abc}	24720.1±573.85^{abc}	20734.5±487.92^{abc}	0.8386±0.0002^{a-e}
		Curtobacterium	3548.5±641.40^{bc}	21588±3589.22^{b-f}	18039.5±2951.75^{b-f}	0.8358±0.003^{a-f}
		Arthrobacter	3936.2±343.25^{abc}	22630.2±379.25^{a-f}	18694±36^{a-f}	0.8267±0.01^{c-g}
	75%	No Inoculation	3421.8±779.61^{cd}	19994.3±3851.72^{def}	16572.5±3072.11^{def}	0.8291±0.006^{b-g}
		Curtobacterium	3687.5±509.30^{a-d}	20928±3344.97^{c-f}	17240.5±2838.35^{c-f}	0.8230±0.005^{fg}
		Arthrobacter	3579.3±416.78^{bc}	21054.6±1984.45^{b-f}	17475.3±1578.30^{c-f}	0.8301±0.006^{a-g}
	50%	No Inoculation	3917.3±453.24^{abc}	23122.1±3125.47^{a-f}	19204.8±2690.2^{a-f}	0.8303±0.007^{a-g}
		Curtobacterium	3585±335.84^{bcd}	21896±2847.89^{b-f}	18311±2524.22^{b-f}	0.8360±0.007^{a-f}
		Arthrobacter	4008.3±78.54^{abc}	23566.1±551.99^{a-f}	19557.8±486.81^{a-e}	0.830±0.001^{a-g}
Kerman	100%	No Inoculation	3631.1±103.21^{a-d}	22172±1314.92^{a-f}	18540.8±1230.7^{b-f}	0.836±0.006^{a-f}
		Curtobacterium	3738.3±81.12^{a-d}	22246.1±422.75^{a-f}	18507.8±454.73^{b-f}	0.832±0.005^{a-g}
		Arthrobacter	3628.1±80.30^{a-d}	22036.50±1^{a-f}	18408.3±1079.14^{b-f}	0.8351±0.01^{a-f}
	75%	No Inoculation	3778.6±259.45^{a-d}	19796.8±660.47^{ef}	16018.1±901.9^{f}	0.8088±0.01^{i}
		Curtobacterium	3879.1±166.87^{abc}	22960.3±1278.23^{a-f}	19081.1±1112.36^{a-f}	0.8308±0.002^{a-g}
		Arthrobacter	3986.6±171.19^{abc}	23478.1±819.85^{a-f}	19491.5±651.54^{a-f}	0.83±0.002^{a-g}
	50%	No Inoculation	3997.5±274.67^{abc}	24318.1±2147.33^{abc}	20320.6±1873.55^{abc}	0.8353±0.003^{a-f}
		Curtobacterium	4003.5±211.48^{abc}	24018.6±1254.79^{a-d}	20015.1±1043.31^{a-d}	0.8331±0.0002^{a-g}
		Arthrobacter	3818.3±99.81^{a-d}	23613.3±1504.45^{a-f}	19795±1423.88^{a-d}	0.8381±0.007^{a-f}

Means in each column followed by the same letter are not significantly different at the 1% probability level according to Duncan's multiple range test.

The results of the present study demonstrated that drought stress significantly reduced shoot fresh and dry biomass across all *Z. multiflora* genotypes, a response that can be attributed to well-established physiological mechanisms associated with water deficit (Soufan *et al*., 2023). These mechanisms include impaired cellular turgor, stomatal closure to limit transpiration, restricted CO_2 uptake, and reduced photosynthetic efficiency (Shil and Dewanjee, 2022), ultimately constraining vegetative growth and biomass accumulation (Elsherif *et al*., 2025). However, the magnitude of biomass reduction was not uniform among different *Z. multiflora* genotypes. This intraspecific variation indicates the presence of considerable genetic potential for drought tolerance in this species native to arid regions, which could serve as a basis for targeted breeding programs (Mumivand *et al*., 2026). This pattern has been widely reported in medicinal plants of the Lamiaceae family, including thyme, where drought stress disrupts mineral uptake and enhances ROS production, leading to oxidative damage and yield loss (Bistgani *et al*., 2024). For instance, in *Mentha piperita*, drought stress reduced glandular trichome density and volatile compound production, changes that were accompanied by a general decline in biomass (Chiappero *et al*., 2022). Despite familial similarities, *Z. multiflora* may exhibit a different trade-off between carbon allocation to defensive secondary metabolites and vegetative growth due to its richer phenolic and essential oil profile—a concurrent investigation of which in the present study could have provided considerable added value (Alipour *et al*., 2026).

In contrast, inoculation with plant PGPR, particularly *Curtobacterium* spp., significantly increased shoot fresh and dry weights across all genotypes and drought levels, effectively mitigating drought-induced growth inhibition. This improvement likely results from multiple synergistic mechanisms, including the production of phytohormones such as indole-3-acetic acid (IAA) and cytokinins that enhance root growth and water uptake, osmotic adjustment through the accumulation of compatible solutes (e.g., proline and soluble sugars), and reduced oxidative damage via stimulation of antioxidant enzymes (Verma *et al*., 2024). Collectively, these processes contribute to maintaining cellular hydration and metabolic stability under water-limited conditions (Notununu *et al*., 2024). Additionally, PGPR are known to produce extracellular polymeric substances, which improve soil structure and enhance water-holding capacity, thereby supporting greater shoot and root biomass in inoculated plants compared with non-inoculated controls under drought stress (Vaghela *et al*., 2026). *Curtobacterium* strains, in particular, have been shown to reduce lipid peroxidation (lower malondialdehyde content) and regulate osmolyte accumulation (Chen *et al*., 2025). For example, *C. albidum* SRV4 increased biomass by 15–30% and improved photosynthetic performance in *Oryza sativa* under salinity stress—an osmotic stress comparable to drought (Vimal *et al*., 2019). Similarly, *C. herbarum* CAH5 reduced malondialdehyde levels and enhanced antioxidant enzyme activities in *Lactuca sativa*, leading to improved biomass under stress conditions (Silambarasan *et al*., 2019). The more pronounced positive effects of *Curtobacterium* under non-stress conditions may reflect its optimal functioning in resource-rich environments, where bacterial growth-promoting activities—particularly hormonal stimulation—can operate without competition from plant stress responses (Chen *et al*., 2025). Under severe drought, elevated ethylene levels may limit plant growth; although PGPR can reduce ethylene via ACC deaminase activity, the effectiveness of this mechanism may decline under intense stress, resulting in relatively smaller growth benefits compared with non-stressed conditions (Verma *et al*., 2024). A similar pattern has been reported in *M. piperita*, where PGPR maintained biomass under drought stress but induced greater growth stimulation under optimal conditions (Santoro *et al*., 2015). Overall, these complex genotype–microbe–stress interactions highlight the potential of *Curtobacterium* as an effective and sustainable biofertilizer for arid and semi-arid environments. Future omics-based studies could further elucidate the molecular mechanisms underlying this symbiosis and support the selection and breeding of more drought-tolerant ecotypes.

Across all *Z. multiflora* genotypes, increasing drought intensity resulted in a significant increase in total phenolic content, reflecting a key defensive strategy against drought-induced oxidative stress (Mansinhos *et al*., 2024). Water deficit is associated with excessive ROS generation, which can damage cellular membranes, proteins, and DNA (Ahmadi *et al*., 2024). Consequently, plants enhance the synthesis of

phenolic compounds—non-enzymatic antioxidants that scavenge ROS and help maintain redox homeostasis (Hosseini and Heidari, 2025). This increase, observed in many genotypes, indicates the activation of the phenylpropanoid pathway as an important adaptive mechanism; however, the intensity of this response varied among genotypes and suggests the existence of genetic diversity in the capacity for defensive secondary metabolite synthesis (Dalvand *et al*., 2026; Alipour *et al*., 2026). This response is well documented in Lamiaceae medicinal plants, where phenolics not only confer stress tolerance but also enhance medicinal quality. In *Artemisia dracunculus*, total phenolics increased proportionally with drought severity due to activation of the phenylpropanoid pathway (Mumivand *et al*., 2021b; Khanizadeh *et al*., 2026), while in *Thymus daenensis*, drought-induced phenolic accumulation was associated with reduced oxidative enzyme activity and improved cellular integrity (Bistgani *et al*., 2023). PGPR inoculation exerted contrasting effects on total phenols and flavonoids depending on water availability. Under non-stress conditions, PGPR generally enhanced the accumulation of these compounds, whereas under drought stress, a relative reduction was observed in many genotypes. In non-stress conditions, PGPR promote nutrient uptake, phytohormone production (e.g., IAA and cytokinins), and metabolic activation, thereby stimulating secondary metabolite biosynthesis and improving plant quality (Verma *et al*., 2024). Under drought stress, however, PGPR may redirect plant energy toward fundamental survival mechanisms—such as osmotic adjustment and root system development—leading to reduced investment in secondary metabolite production, as survival becomes the primary priority (Vaghela *et al*., 2026). This dual response has been reported in other Lamiaceae species, including M. piperita, where PGPR preserved essential oil yield under drought while reducing phenolic content, likely due to altered carbon allocation (Ozhuner, 2025). The response of antioxidant activity to drought stress and PGPR inoculation was strongly genotype-dependent. Genetic variation in the expression of antioxidant defense–related genes resulted in increased antioxidant activity in some genotypes and decreases in others. Similar genotype-specific responses to PGPR under osmotic stress have been reported in *Cicer arietinum* (Naseri *et al*., 2020) and Lavandula angustifolia, where drought-induced changes in antioxidant activity varied among genotypes and aligned with differential PGPR effects (Hosseini and Heidari, 2025). These findings underscore the complexity of interactions among drought stress, PGPR, and genotype in regulating antioxidant metabolism.

PGPR inoculation, regardless of bacterial strain, increased chlorophyll a content, likely through multiple physiological mechanisms, including enhanced uptake of magnesium (a core component of chlorophyll), phytohormone-mediated stimulation of chlorophyll biosynthesis, and reduced oxidative damage to chloroplasts via ROS regulation (Verma *et al*., 2024; Khanizadeh *et al*., 2024). These processes collectively support photosynthetic efficiency and chlorophyll stability (Notununu *et al*., 2024). In medicinal plants such as M. piperita, inoculation with Bacillus and Pseudomonas strains increased chlorophyll a content by 30–40%, consistent with enhanced expression of chlorophyll biosynthesis genes (Ozhuner, 2025). In contrast, drought stress generally reduced chlorophyll a, chlorophyll b, and total chlorophyll contents across most genotypes, reflecting chloroplast structural damage, inhibited porphyrin synthesis, and accelerated chlorophyll degradation driven by drought-induced ROS (Bistgani *et al*., 2024). Stomatal closure and reduced CO_2 assimilation further impair photosynthesis and promote chlorophyll breakdown, a common response in drought-sensitive plants (El-Saadony *et al*., 2024). Similar reductions in chlorophyll content have been reported in T. vulgaris under drought stress and were associated with decreased growth and productivity (Kamyab and Samsampour, 2025). Genotypic differences in chlorophyll stability are likely linked to variation in stress-responsive gene expression, with more tolerant genotypes exhibiting smaller declines (Han *et al*., 2025). Notably, PGPR application increased chlorophyll b and total chlorophyll contents across all drought levels, substantially alleviating drought-induced damage to the photosynthetic apparatus. This protective effect can be attributed to improved water and nutrient uptake, osmolyte production that maintains cellular turgor, and ethylene reduction via ACC deaminase activity, all of which support chlorophyll synthesis and stability (Kesavardhini *et al*., 2026). Similar results were reported in Allium ascalonicum, where PGPR

increased chlorophyll content by up to 67% under drought stress, coinciding with reduced malondialdehyde levels (Pratiwi *et al*., 2024). Drought stress exerted variable effects on carotenoid content; however, increases were observed in most genotypes and PGPR treatments. This response reflects the role of carotenoids as non-enzymatic antioxidants that protect chlorophyll from photooxidative damage and stabilize chloroplast membranes under stress (Gowtham *et al*., 2022). Carotenoids are generally less sensitive to drought than chlorophylls and often accumulate to strengthen plant defense systems (Hosseini and Heidari, 2025; Khanizadeh *et al*., 2025). The interaction between PGPR and carotenoid metabolism appeared genotype-dependent, likely reflecting differences in carbon allocation to protective pathways (Kesavardhini *et al*., 2026).

Although drought stress and PGPR inoculation influenced chlorophyll fluorescence parameters (F_0, Fm, Fv, and Fv/Fm), these changes were often inconsistent and not statistically significant. This variability may result from complex interactions among ecotype genetics, stress intensity, and PGPR-mediated mechanisms (Hajipour *et al*., 2025). However, the lack of a uniform chlorophyll fluorescence response despite the observed changes in chlorophyll a and b contents (previous sections) suggests that the protective mechanisms of this species are primarily based on non-enzymatic antioxidants (phenolics and carotenoids) and osmotic adjustment rather than the direct maintenance of PSII efficiency (Dalvand *et al*., 2026). Chlorophyll fluorescence, as an indicator of PSII efficiency, is closely linked to pigment content and chloroplast integrity, both of which are affected by ROS accumulation under drought stress (Rasouli *et al*., 2023). While drought typically increases F_0 and decreases Fv/Fm, these responses are highly genotype- and stress-level dependent (Lotfi *et al*., 2024). Similar irregular patterns have been reported in T. vulgaris and Satureja hortensis under moderate drought stress (Rasouli *et al*., 2023; Kamyab *et al*., 2025). PGPR inoculation may moderate these changes, although its primary effects appear to operate through improvements in nutrient uptake and osmotic regulation rather than direct modulation of fluorescence parameters, particularly under mild stress where PSII damage is limited (Jofré *et al*., 2024). Overall, the lack of a consistent fluorescence pattern suggests a relatively high tolerance of *Z. multiflora* to moderate drought stress, warranting further investigation using molecular and transcriptomic approaches.

4. Conclusion

This study demonstrated that drought stress, as a major abiotic constraint, significantly reduced vegetative growth and biomass accumulation in different *Z. multiflora* genotypes. In contrast, PGPR inoculation markedly improved these traits across all genotypes and drought levels, with *Curtobacterium* showing the strongest positive effect on biomass, particularly under non-stress conditions. Increasing drought severity significantly enhanced total phenolic content in all genotypes, whereas the effects of PGPR on phenols and flavonoids were stress-dependent, promoting their accumulation under non-stress conditions but generally reducing them under drought stress. Antioxidant activity responses were strongly genotype-specific, reflecting genetic variation in antioxidant regulation capacity.

Drought stress reduced chlorophyll content in most genotypes, while PGPR inoculation increased chlorophyll a and consistently enhanced chlorophyll b and total chlorophyll across all drought levels, effectively mitigating drought-induced damage to the photosynthetic system. In contrast, carotenoid content generally increased under drought stress, supporting their protective role against oxidative damage. Changes in chlorophyll fluorescence parameters were observed, but did not follow a uniform pattern. Overall, the findings highlight the effectiveness of PGPR as a sustainable biological strategy for improving growth, modulating physiological responses, and enhancing drought tolerance in *Z. multiflora*, with strong dependence on genotype and stress intensity. The application of PGPR therefore represents a promising approach for maintaining productivity and photosynthetic efficiency of *Z. multiflora* under water-limited conditions.

Abbreviation

PGPR: Plant Growth-Promoting Rhizobacteria; F_0: Minimum Fluorescence in Dark-Adapted State; Fm: Maximum Fluorescence in Dark-Adapted State; Fv: Variable Fluorescence; Fv/Fm: Maximum Quantum Efficiency of PSII; ROS: Reactive Oxygen Species;

IAA: Indole-3-Acetic Acid; FC: Field Capacity; ACC deaminase: Aminocyclopropane-1-Carboxylate Deaminase.

Conflict of interests

The authors declare no conflict of interest.

Ethics approval and consent to participate

No humans or animals were used in the present research. The authors have adhered to ethical standards, including avoiding plagiarism, data fabrication, and double publication.

Consent for publications

All authors read and approved the final manuscript for publication.

Availability of data and material

The data presented in this study are available on request from the corresponding author.

Authors' contributions

Abuzar Alizadeh: Investigation, Visualization and Writing original draft; Hasan Mumivand: Project administration, Methodology, Conceptualization, Planned the experiments, Validation, and Writing–review & editing; Sadegh Mousavi-Fard: Writing - Review & Editing, Software, and Formal analysis; Abdolhossein Rezaei Nejad: Writing -Review & Editing, and Validation.

Informed consent

The authors declare not to use any patients in this research.

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