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Bacterial siderophore improves nutrient uptake, leaf physiochemical characteristics, and grain yield of cumin (*Cuminum cyminum* L.) ecotypes

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ABSTRACT

Cumin is one of the most popular herbs that is used widely as a spice and medicinal purposes. In Iran, cumin is mainly cultivated in high pH soils in arid regions where some elements such as iron (Fe) and zinc (Zn) cannot be adequately absorbed. Accordingly, we hypothesized that using chelating agents like bacterial siderophore could alleviate nutrient deficiency under such conditions. Cumin ecotypes (Sabzevar, Torbat-e-Jam, Taibad, and Shiraz) and bacterial siderophore treatments (control, seed priming, foliar spray, and seed priming + foliar spray (combined); 0.2%) were considered as the experimental factors. The application of siderophore increased the concentration of Fe, Zn, and nitrogen (N) in leaves and grains compared with the control. The highest leaf Fe concentration was observed when the combined treatment was applied. Sabzevar showed the highest grain Fe and Zn concentrations by 110 and 50%, respectively, over the control in the combined treatment. The highest grain yield was obtained from the combined-treated Taibad plants by a 28% increase over the control. Compared with the control, essential oil yield was increased by 22% in the combined-treated plants. The results showed that the combined application of siderophore had a higher efficiency among the other treatments. Furthermore, bacterial siderophore could be usefully applied to improve physiological traits, nutrient absorption, and grain yield in cumin under an arid region.

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Chelating agents; fortification; iron; nitrogen; zinc

Introduction

Cumin (*Cuminum cyminum* L.), belonging to the *Apiaceae* family and well known as the king of grain spice, is among the most critical and economic medicinal herbs worldwide (Lal et al. 2014). After black pepper, it ranks as the second most popular spice and widely used as an ingredient in many foods, mainly for its aroma and medicinal purposes (Lodha and Mawar 2014; Sowbhagya 2013). Due to the presence of various varieties of medicinal plants, greater attention has recently been paid to these plants. Iran is one of the leading producers of cumin in the world (Sowbhagya 2013). Grains are an essential part of the plant and a good source of Fe and manganese (Mn) (Parthasarathy, Chempakam, and Zachariah 2008). Cumin grains also contain oil (7%), resin (13%), essential oil (2–4%), and aleurone (24%) (Dhaliwal et al. 2016). The antibacterial and

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antioxidant activity of cumin has also previously been reported (Akrami et al. 2015; Ravi, Prakash, and, Bhat 2013). Cumin seeds contain a volatile oil that is the source of flavor, varying among ecotypes, depending on origin and the genotype (Sowbhagya 2013).

The quality and yield of medicinal plants are affected by many factors. Nutrients can significantly affect the quality and quantity of the cumin yield. Fe, Zn, and N are essential elements for the plant growth, with their effect being reported on chlorophyll synthesis and the rate of photosynthesis (Fathi-Amirkhiz, Amini Dehaghi, and Heshmati 2015). Although Fe is the most abundant microelement in the soil, plants often suffer from Fe deficiency. Fe has a positive effect on dry matter production and yield of plants due to its crucial role in photosynthesis, enzyme biosynthesis, and respiratory mechanisms. The availability of this element directly affects the quality and quantity of yield through an increase in the area units and duration of photosynthesis (Sabet and Mortazaeinezhad 2018).

Zn deficiency is the second common deficiency after Fe in the plants (Ghavami et al. 2016). Zn plays a vital role in the physiological performance of plants, such as the biosynthesis of plant growth regulators, e.g., indole acetic acid, and the regulation of stomatal aperture. It also has a catalytic activating role in many plant enzymes. Metabolism and N uptake efficiency are also enhanced by this vital element (Bybordi and Mamedov 1970). Zn deficiency may reduce carbohydrates synthesis, membrane stability, and phytohormones and pigment synthesis in plants (Singh et al. 2005).

Different methods and strategies, including chemical, biological, and organic fertilization, have been used to alleviate nutrient deficiency in plants. Foliar application of nutrients, especially micronutrients, has been reported to increase the nutrients uptake efficiency in calcareous soils, where the solubility of micronutrients is limited (Martín-Fernández et al. 2017). On the other hand, the overuse of chemical fertilizers causes major environmental issues; for instance, changing the soil pH and reducing humic acid and organic matter content of the soil (Gyaneshwar et al. 2002; Suthar 2012).

One potential solution to alleviate the adverse effects of chemical fertilizers is biostimulants, including different microbes and substances. Biostimulants can increase nutrient use and uptake efficiency by stimulating natural processes (Calvo, Nelson, and Kloepper 2014). The chelating agents, such as siderophores, can be one of the efficient ways to relieve nutrient deficiencies (Sabet and Mortazaeinezhad 2018). Siderophores are natural chelating agents synthesized via the plant growth-promoting rhizobacteria (PGPR), especially *Pseudomonas* species, under Fe deficiency conditions. Siderophores, with a low molecular weight (200–2000 Da) and intense combinability with Fe and Zn (Fe^{+3} and Zn^{+2}), stimulate the availability of those elements in the rhizosphere (Schwyn and Neilands 1987). Phytosiderophores, which are extruded from grassroots in response to Fe deficiency, may have a role in absorbing Zn in maize (von Wirén, Marschner, and Romheld 1996; Welch and Shuman 1995). Cotton seeds inoculation by *Pseudomonas* siderophores significantly enhanced the Fe and Zn absorption (Yao et al. 2010). Foliar application of PGPR and their metabolites also led to higher absorption and concentration of Fe and Zn in rice tissues (Sharma et al. 2014). Sabet and Mortazaeinezhad (2018) found that the combined application of Fe and siderophores was more efficient than their separate application and increased the absorption of these elements by the plant. Working on Arabidopsis accessions, Aznar et al. (2014) reported that siderophores could also activate plant defense mechanisms to pathogens and influence the homeostasis of heavy metals.

Given that the soil pH in semi-arid and arid regions like Iran is high, one of the main issues for growing medicinal herbs under such conditions is supplying macro- and micro-nutrients, which is not readily available in calcareous soils (Bostani 2018; Ramzani et al. 2016). Nutrient availability, especially such micronutrient as Fe and Zn, is decreased due to a high pH (Miransari 2013), which adversely affects the growth and development of plants. Despite the efforts that have been made to increase the nutritional values of crops, including corn and wheat (Dimkpa

Table 1. Physicochemical characteristics of the experimental field soil.

pH	EC (dS m^{-1})	Mn	Zn	Cu	Fe	P	K	N	Organic matter	Soil texture
		mg·kg^{-1}						%		
8.12	2.63	7.88	0.47	0.73	1.24	9	391	0.13	0.87	Loam sand

and Bindraban 2016), to our knowledge, little data is available for medicinal plants such as cumin. Therefore, regarding the importance of Fe and Zn for the growth and quality of medicinal plants, we hypothesized that a proper method of siderophores application would improve the availability and absorption of nutrients in cumin. The effects of the application of siderophores on physiological traits, and essential oil, which are essential criteria in spice and medicinal plants such as cumin, were also evaluated. Given that plant genotypes respond differently to the environmental stimuli, we also examined whether there are variations between the cumin ecotypes in response to the treatment. At last, the most effective method of siderophore application to improve cumin growth and grain yield production was evaluated.

Materials and methods

Experimental site and treatments

This experiment was carried out at the research filed of the Vali-e-Asr University of Rafsanjan during the 2018–2019 growing season (55° 55′ N, 30° 22′ W, 1526 m asl). Rafsanjan, with a mean annual precipitation of 75.5 mm, is classified as an arid climate based on the Domarten climatic classification. Four ecotypes of cumin (Sabzevar, Torbat-e Ja'm, Taibad and Shiraz) and four bacterial siderophore treatments (control, seed priming, foliar application, and seed priming + foliar application (combined treatment)) were considered as experimental factors. The siderophore was purchased from the Persian Bonyan Aria Company. Cumin seeds were soaked in the siderophore solution (*v/v* 0.2%) for 24 h as the priming treatment (Adib et al. 2020; Neamatollahi et al. 2009). Distilled water was used for the control treatment. Foliar application of siderophore was applied twice (*v/v* 0.2%) when the seedlings had 7–10 true leaves (36 days after sowing), and two weeks after the first application (50 days after sowing) (Baghizadeh and Shahbazi 2013).

Field practices and sowing

Uniform cumin seeds were hand-sown in early March in 1–1.5 cm soil depth and four rows with 20 cm apart and three meters long, giving 80 plants m^{-2} in plots of 1×3 m. The field was irrigated right after sowing; the second irrigation was done five days after the first irrigation. Then, the plants were irrigated at a 7 day interval to avoid water stress. Weeding was done weekly by hand. Nitrogen as urea (46% N) was applied twice, along with the foliar application of siderophore at the rate of 66 N kg ha^{-1} in each time during the experiment. The physicochemical characteristics of the experimental soil are represented in Table 1.

Sampling

Eight samples were collected (60 days after emergence (DAE) equal to 10 days after the last foliar spaying) from the youngest fully expanded leaves at the inflorescence emergence stage and grains at the physiological maturation from the middle row plants of each plot for measurement. Then, they were immediately frozen in liquid nitrogen and kept at −80 °C for further physiochemical analysis.

Leaf chlorophyll content

Leaf pigments, including chlorophyll a, b, a + b, and carotenoids, were evaluated by homogenizing 100 mg leaf fresh weight in 98% ethanol using a mortar and pestle. The absorbance of the extract was measured at 665 and 649 nm spectrophotometrically (Unico 2100, USA) (Lichthentaler 1987).

Proline determination

The method of Bates, Waldren, and Teare (1973) was used to determine leaf proline content. 50 mg of frozen tissue (leaves) was homogenized with 10 mL of 3% sulfosalicylic acid. The proline content was quantified using the aliquots (20 mL) of the extract by measuring the samples at 520 nm spectrophotometrically using a standard curve.

Leaf carbohydrates and sucrose content

The protocol outlined by Wu, Lou, and Li (2015) was used to determine carbohydrates and sucrose concentration in leaves. Grounded dry leaf samples (50 mg) were homogenized in 4 ml of 80% ethanol and incubated for 40 min and centrifuged at 2500*g* for 5 min. The residues were extracted again as described above, and the mixture of two supernatant was used to measure *carbohydrates* content. A glucose standard curve was then used to assay leaf soluble carbohydrate content. Leaf sucrose content was determined according to the procedure described by Wu, Lou, and Li (2015). 0.15 mL supernatant and 0.15 mL 2 *M* NaOH were mixed and incubated at 100 °C for 5 min. The mixture was then mixed with 2.1 mL 30% HCl together with 0.6 mL 0.1% resorcinol at 80 °C for 10 min. The absorbance of the extract was measured at 480 nm, and sucrose content was assayed using a sucrose standard curve.

Nutrients measurements

The Kjeldahl method was used for the determination of the N content (Horneck and Miller 1997). Plant leaves and grains were prepared for the quantitative determination of Fe and Zn concentration by the method of the dry ashing using high-temperature dry oxidation of the organic matter and dissolution of the ash by HCl (Baker et al. 1964). Fe and Zn concentrations were determined using the method of atomic absorption (Hanlon 1997). The grains were harvested at the physiological maturation (95 DAE), semi-grinded, and the Clevenger method was used to measure the essential oil content (Clevenger 1928).

Harvesting

Ninety-five DAE, ten plants from the middle row of each plot were harvested, and the grains were collected by hand and weighed, and the mean grain weight was determined. The grain yield per m^2 was also determined by harvesting the plants from the middle rows, considering the side effects.

Statistical analysis

The experiment was arranged as a factorial in a randomized complete block design with three replications (4 ecotypes × 4 siderophore treatments). The collected data were subjected to the analysis of variance using SAS (*v*. 9.1) software (SAS Institute, Cary, NC, USA). The significance of means was determined using the LSD test ($p \leq 0.05$).

Table 2. Ecotype and siderophore effects on the nutrients of leaves and grains of cumin ecotypes.

		Leaf		Grain		
		Fe	N	Fe	Zn	N
Ecotype	Siderophore	mg·kg^{-1}	%	mg·kg^{-1}		%
Sabsevar	Control	604^{cd}	1.78^{f}	192$^{c–e}$	201^{e}	2.79^{e}
	Priming (P)	991^{bc}	1.89^{ef}	247$^{b–d}$	219de	3.00^{de}
	Foliar application (F)	1125^{b}	2.20$^{c–e}$	279^{bc}	239$^{b–d}$	3.29^{ab}
	P + F	1566^{a}	2.30$^{c–e}$	404^{a}	303^{a}	3.29^{ab}
Torbet-e-Ja'm	Control	548^{d}	1.88^{ef}	203$^{c–e}$	226$^{c–e}$	2.90^{de}
	Priming (P)	915^{bc}	1.87^{ef}	20$^{c–e}$	230^{cd}	3.10^{b-d}
	Foliar application (F)	974^{b}	2.09^{cd}	279^{bc}	238$^{b–d}$	3.10^{b-d}
	P + F	1062^{b}	2.20^{c-e}	309^{b}	258^{b}	3.40^{a}
Taibad	Control	543^{d}	2.00^{ef}	147^{ef}	229^{cd}	3.10$^{b–d}$
	Priming (P)	1175^{b}	2.20$^{c–e}$	153$^{d–f}$	242$^{b–d}$	3.10$^{b–d}$
	Foliar application (F)	1315^{ab}	2.48^{ab}	162$^{d–f}$	250^{bc}	3.19$^{b–d}$
	P + F	1563^{a}	2.70^{a}	238$^{b–e}$	259^{b}	3.30^{c}
Shiraz	Control	598^{cd}	1.90^{ef}	94^{f}	226$^{c–e}$	3.09^{b-d}
	Priming (P)	894^{c}	1.90^{ef}	155$^{d–f}$	232$^{b–d}$	3.19$^{b–d}$
	Foliar application (F)	981^{bc}	2.49^{ab}	157$^{d–f}$	241$^{b–d}$	3.18$^{b–d}$
	P + F	1008^{b}	2.50^{ab}	230$^{b–e}$	253^{bc}	3.29^{c}

Means with a similar letter(s) in each column are not significantly different (LSD, $p \le 0.05$).

Results

Leaf and grain Fe and Zn concentration

Leaf Fe concentration was affected by siderophore treatment, ecotype, and their interactions; however, leaf Zn concentration was only affected by siderophore treatments. The most significant leaf Fe concentration was found in Sabzevar and Taibad ecotypes when the combined (seed priming + foliar application) treatment was applied (Table 2). The combined application of siderophore increased the Zn concentration of leaves by 47% compared with the control (Figure 1).

The grain Fe and Zn concentrations were influenced by ecotype × siderophore interactions. Combined application of siderophore increased the grain Fe and Zn concentrations by 110 and 50%, respectively, over the control in Sabzevar, which was the highest concentrations among the treatments (Table 2).

Leaf and grain nitrogen concentration

The interaction of ecotype and siderophore significantly affected the leaf and grain N content. The highest leaf N content was observed in the combined siderophore treatment in Taibad. In contrast, the highest concentration of the grain N content was observed in Torbat-e-Ja'm and the combined application of siderophore (Table 2).

Leaf chlorophyll content

The leaf chlorophyll a, total chlorophyll, and carotenoids content were influenced by ecotype and siderophore interaction. The results showed that the highest leaf chlorophyll a, total chlorophyll, and carotenoid content were observed in Taibad when the combined application of siderophore was applied (Table 3).

Leaf proline content

Leaf proline content was significantly increased in all ecotypes when siderophore applied. In the combined application on siderophore, however, the highest increase, 43% over control, was

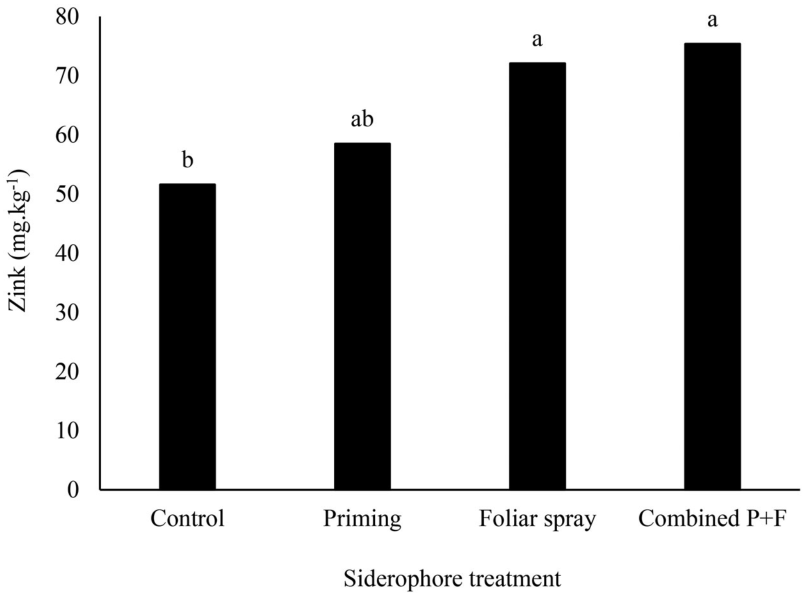

Figure 1. Changes in cumin leaf Zn concentration induced by siderophore treatments as seed priming (P), foliar spray (F), and combined priming + foliar application (*v/v*: 0.2%). Means with a similar letter(s) are not significantly different (LSD, $p \leq 0.05$).

Table 3. Ecotype and siderophore interaction effects on the leaf physiological traits and grain yield in cumin.

Ecotype	Siderophore	Chlorophyll a	Total chlorophyll	Carotenoids	Proline	Sucrose
		mg·g·FW^{-1}			µM·g FW^{-1}	mg·g FW^{-1}
Sabsevar	Control	0.98^{l}	1.18$^{f\text{-}h}$	4.98$^{b–d}$	5.07^{fg}	1.39^{l}
	Priming (P)	1.97^{h}	2.94^{bc}	5.05$^{b–d}$	6.03^{de}	2.66^{g}
	Foliar application (F)	2.19^{g}	2.82$^{b–d}$	5.33$^{a–c}$	6.72$^{b–d}$	2.90^{f}
	P + F	3.42^{b}	4.01^{ab}	5.56$^{a\text{-}c}$	7.18^{ab}	3.45^{e}
Torbat-e-Ja'm	Control	0.55^{m}	0.85^{gh}	4.31^{d}	4.90^{g}	2.46^{h}
	Priming (P)	1.8^{l}	2.07$^{c–f}$	4.73^{cd}	5.91$^{d–f}$	2.99^{f}
	Foliar application (F)	2.04^{h}	2.30$^{c–e}$	5.25$^{b–d}$	6.72$^{b–d}$	3.49^{de}
	P + F	3.26^{c}	3.51^{ab}	5.79^{ab}	**7.67^{a}**	3.85^{c}
Taibad	Control	0.97^{l}	1.24$^{e–h}$	4.33^{d}	6.04^{de}	2.58^{gh}
	Priming (P)	2.47^{f}	2.75$^{c–f}$	5.67$^{a–c}$	6.67$^{b–d}$	3.51^{de}
	Foliar application (F)	2.62^{e}	2.87$^{b–d}$	5.91^{ab}	7.12$^{a–c}$	3.81^{c}
	P + F	4.44^{a}	4.58^{a}	6.21^{a}	7.31^{ab}	4.18^{ab}
Shiraz	Control	0.34^{n}	0.55^{h}	3.32^{e}	5.42$^{e–g}$	3.03^{f}
	Priming (P)	1.36^{k}	1.72$^{d–g}$	4.75^{cd}	6.31^{cd}	3.63^{d}
	Foliar application (F)	1.61^{j}	1.78$^{d–g}$	5.41$^{a–c}$	7.18$^{a–c}$	4.03^{b}
	P + F	3.09^{d}	3.42^{ab}	5.80^{ab}	**7.75^{a}**	4.32^{a}

Means with the same letters in each column are not significantly different, LSD test, $p \leq 0.05$.

observed in Shiraz. Nevertheless, no significant difference was found between the ecotypes (Table 3).

Leaf soluble carbohydrates and sucrose content

The soluble carbohydrates content of the leaf was not affected by the experimental factors. However, leaf sucrose content was significantly affected by ecotype, siderophore treatments, and their interactions. The greatest leaf sucrose content was observed in Shiraz in the combined application of siderophore by a 43% increase over the control. However, the most significant increase in leaf sucrose content was recorded in Sabzevar by 140% compared with the control when the combined treatment was applied (Table 3).

Table 4. Ecotype and siderophore interaction effects on the grain yield, mean grain weight, and essential oil yield in cumin.

Ecotype	Siderophore	Grain yield ($g \cdot m^{-2}$)	Mean grain weight (g)	Essential oil ($g \cdot m^{-2}$)
Sabsevar	Control	56.4^{j}	2.89^{fg}	1.50^{ef}
	Priming (P)	74.5^{i}	$3.21^{d\text{–}f}$	1.86^{de}
	Foliar application (F)	$84.9^{g\text{–}i}$	$3.52^{b\text{–}d}$	$2.25^{a\text{–}d}$
	P + F	$91.7^{e\text{–}h}$	3.81^{ab}	2.42^{ab}
Torbat-e-Ja'm	Control	42.8^{k}	2.76^{g}	1.01^{f}
	Priming (P)	$93.5^{d\text{–}g}$	$2.97^{e\text{–}g}$	$2.36^{a\text{–}d}$
	Foliar application (F)	106^{cd}	$3.32^{c\text{–}e}$	$2.35^{a\text{–}d}$
	P + F	121^{ab}	4.01^{a}	2.73^{a}
Taibad	Control	97.1^{hi}	2.72^{g}	$1.91^{b\text{–}e}$
	Priming (P)	$98.4^{c\text{–}f}$	$3.01^{e\text{–}g}$	2.45^{a}
	Foliar application (F)	$103^{c\text{–}e}$	3.58^{bc}	$2.36^{a\text{–}d}$
	P + F	124^{a}	3.80^{ab}	2.74^{a}
Shiraz	Control	$80.5^{g\text{–}i}$	2.93^{fg}	$1.88^{c\text{–}e}$
	Priming (P)	$88.6^{f\text{–}h}$	$3.18^{d\text{–}f}$	$2.30^{a\text{–}d}$
	Foliar application (F)	$103^{c\text{–}e}$	$3.32^{c\text{–}e}$	$2.39^{a\text{–}c}$
	P + F	109^{bc}	3.82^{ab}	2.70^{a}

Means with the same letters in each column are not significantly different, LSD test, $p \leq 0.05$.

Grain yield and mean grain weight

Cumin grain yield was significantly affected by either the main effects or the interaction effect of ecotype × siderophore. The greatest grain yield was obtained from Taibad when siderophore was applied as a combined treatment by a 28% increase over the control, which was not different from Torbat-e-Ja'm (Table 4). Amongst the ecotypes, Torbat-e-Ja'm was affected most by the siderophore application; the grain yield of which was almost twice as high as the control. Foliar application of siderophore and priming interacted to affect the mean grain weight. The highest mean grain weight was obtained from Torbat-e-Ja'm when the combined treatment was applied by a 48% increase over the control (Table 4).

Essential oil

The percentage of grain essential oil was affected by siderophore treatments. The combined siderophore treatment increased the essential oil percentage of the grains by 22% compared with the control (Figure 2). Seed priming and foliar spray with siderophore interacted to influence essential oil yield per land area unit (m^2). Taibad showed the greatest essential oil yield when the combined siderophore treatment was applied. However, no significant difference was observed between the ecotypes (Table 4).

Discussion

The results of the present study showed that Fe and Zn concentration of the plant leaf and grain were significantly affected by the siderophore treatments. The chelating ability of siderophores by forming complexes with Fe and Zn in the rhizosphere increased the absorption and concentration of the elements in canola and maize plants (Ghavami et al. 2016). Comparing basic Fe and Zn concentration (control treatment) of ecotypes reveals that Taibad had a higher potential to absorb Fe. Sarathambal et al. (2010) reported that for higher solubilization of micronutrients, such as Fe and Zn, in the soil solution, low pH plays a key role. The great combinability of siderophore with such micronutrients as Zn and Cu makes them more available for plants to absorb (Hernlem, Vane, and Sayles 1996).

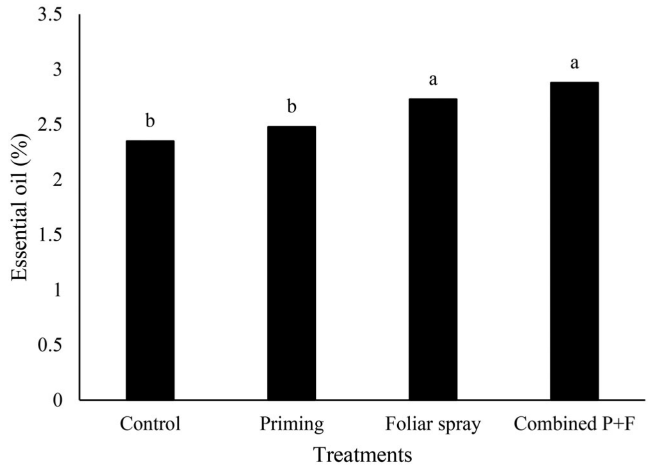

Figure 2. Changes in the essential oil percentage of cumin grains induced by siderophore treatments as seed priming (P), foliar spray (F), and combined priming + foliar application (*v/v*: 0.2%). Means with a similar letter(s) are not significantly different (LSD, $p \leq 0.05$).

An increase in the grain Fe content can be due to the improvement of plant nutritional status by applying siderophore. Siderophores can either increase the Fe availability for cellular use or regulate Fe homeostasis in the plant, which might subsequently affect the utilization of which by the plant cells (Ellermann and Arthur 2017). A positive correlation between the concentration of Fe in the leaf and grain ($r = 0.50^{**}$) might indicate an increase in the leaf Fe concentration increased its translocation toward the grains. It has been reported that the grain microelement content is depended on the uptake and remobilization of Zn and Fe by plants (Garnett and Graham 2005).

The absorption of microelement and their translocation toward the grains were stimulated by the combined application of siderophore. However, lower Fe concentration of the grains than that of the leaves probably indicated the limited capacity of grains to absorb and store this element and the lower mobility of Fe in the plant. Despite lower Zn concentration of leaves than the grains, the translocation of this element toward the grains was more than Fe. Meanwhile, the siderophore application increased Zn translocation toward the grains due to the greater absorption of Zn from the soil. The positive effects of Zn on the formation, growth, fertility, and quality of grains has also previously been reported (Alloway 2008). It can be explained through the role of Zn in the accumulation of photoassimilates in the grains and a better translocation of proteins toward them during the final growth stages, which result in the formation of larger and heavier grains (Alloway 2008).

Since Fe, Zn, and N play important roles in the chlorophyll structure, the increase in the content of the pigments by the application of siderophore can enhance the concentrations of these elements. As a constituent of chlorophyll, Fe can increase plant growth by improving the photosynthetic ability of plant cells (Sabet and Mortazaeinezhad 2018). Positive correlations coefficients were observed between leaf chlorophyll a content and Zn ($r = 0.42^{**}$), Fe ($r = 0.46^{**}$), and N ($r = 0.54^{**}$) concentrations. Furthermore, due to the increased content of carotenoids, it can be concluded that these pigments are likely to prevent chlorophyll degradation due to their protective and complementary role (Akbarian et al. 2013).

Essential oil biosynthesis depends on the availability of micronutrients because both secreting glands and secondary metabolites biosynthesis are related to the availability of these elements (Kanwal et al. 2016). Regarding the increased accumulation of N, Fe, and Zn in the grains, which is the main organ for the production of essential oil, the higher essential oil percentage of the grains could be due to the positive effects of these nutrients on increasing the number of secreting glands and the production of secondary metabolites (Heidari et al. 2008). Since the essential oil yield results from the essential oil percentage and grain yield, the increase of these two components by the siderophore treatments enhanced the essential oil yield. This finding was confirmed by the correlation between essential oil yield and grain yield ($r = 0.86^{**}$) and essential oil percentage ($r = 0.45^{*}$). The longer interval between the seed priming and grain formation probably had a less pronounced effect on the production of essential oil in comparison with that of the foliar spray, either independently or in combination with seed priming.

Cumin is a tolerant species to adverse environmental conditions (Mortazavian et al. 2018) and is mainly cultivated in arid and semi-arid regains (Hashemian et al. 2013). Besides having a diverse role in plants such as a structural component of proteins, proline is one of the most critical compatible solutes that plays a vital role under stress conditions and can protect cellular structures from dehydration (Lehmann et al. 2010). The plant genotype can influence changes in the proline content. Hence, higher leaf proline content could help plant protection from being damaged by adverse environmental conditions. Seed priming, combined with foliar application of siderophore, increased the proline content of leaves. Lehmann et al. (2010) found that a greater concentration of proline using siderophore was due to higher leaf nutrient elements (Lehmann et al. 2010). It is also possible that the plant converts the higher leaf nitrogen concentration to proline, a storage and non-poisoning form. A positive correlation between leaf Zn and N content with proline concentration ($r = 0.40^{*}$ and $r = 0.60^{**}$, respectively) could be related to the contribution of these elements to the absorption and metabolisms of N and greater proline concentration. Amirinejad et al. (2016) have also reported that foliar application of Fe and Zn increased the concentration of proline in leaves of cumin. They concluded that these elements could play a role as a cofactor in the proline biosynthetic pathways.

Siderophore treatments increased the leaf and grain nitrogen content. Positive correlations were found between N and Zn concentrations of the leaves ($r = 0.40^{*}$) and the grain and leaf N concentration ($r = 0.75^{**}$). Furthermore, the grain N concentration was positively correlated with the Zn concentration of the leaves and grains ($r = 0.55^{**}$ and $r = 0.63^{**}$, respectively). This finding indicates the vital role of Zn in the metabolism and accumulation of N in the grains. Karimian and Yasrebi (2005) also observed a positive correlation between the concentration of Zn and N in wheat grains. They found an increase in the concentration of N through increasing the concentration of Zn in the grains. Besides affecting the fundamental processes of plants, it has been elucidated that Zn plays an essential role in the increasing nitrogen uptake efficiency and metabolism, which elevates the nitrogen concentration in the plant tissues (Bybordi and Mamedov 1970).

There were positive correlations between cumin grain yield and the leaf chlorophyll a, total chlorophyll, and sucrose content ($r = 0.66^{**}$, $r = 0.56^{**}$, and $r = 0.75^{**}$, respectively). Since sucrose is mainly produced through the photosynthetic pathway, any factor that improves the photosynthetic process will also affect the sucrose content. Ahmadi-Lahijani et al. (2018) also found that an increase in the leaf chlorophyll content of potato plants resulted in a stimulation of net photosynthetic rate and an increase in leaf soluble carbohydrates content. They also observed a positive correlation between leaf carbohydrates content and the tuber yield of the potato plants. It has been reported that foliar application of sucrose positively (either directly or indirectly) affected photoassimilates content, through which sucrose content of leaves was increased (Mashayekhi and Atashi 2012). We also observed positive correlations between the leaf sucrose concentration and chlorophyll a and total chlorophyll content ($r = 0.63^{**}$ and $r = 0.54^{**}$, respectively). Higher photosynthetic rate and greater leaf chlorophyll content resulted in more available photoassimilates allocating to different parts of plants (Ahmadi-Lahijani et al. 2018). Positive correlations between leaf pigments and carbohydrates, sucrose, and glucose content were also observed (Mashayekhi and Atashi 2012). Therefore, it seems that the positive effects of siderophore treatment on leaf chlorophyll and sucrose content increased available assimilates to enhance cumin grain yield.

The grain yield and mean grain weight were positively correlated ($r = 0.46^*$). Greater mean grain weight could represent the availability of higher photosynthates during the grain filling period of plants. The positive effect of siderophore on the availability of nutrients and phytohormones in the developing grains stimulates cell growth and produces stronger sinks to accumulate more photoassimilates to improve the grain weight (Sulochana et al. 2014). Indole acetic acid has been reported to delay leaf senescence and extend leaf duration leading to longer photosynthetic duration (Awan et al. 1999). A higher photosynthetic rate due to the siderophore application probably increased photoassimilate production and its allocation toward the developing grains leading to greater mean grain weight. Consequently, it seems that favorable plant access to micronutrients indirectly increased the grain yield by improving the photosynthetic capacity and source strength. On the other hand, an increased sink strength also enhanced the ability to store more dry matter. Hence, a simultaneously enhance in source and sink resulted in an improvement in the grain yield of plants.

Conclusion

Siderophore application had positive effects on cumin ecotypes. This chelating agent increased the plant nitrogen metabolism and nutrient uptake by increasing the availability of Fe and Zn in the soil. The grain yield was enhanced through the positive effect of these elements on the leaf pigments, proline, and sucrose content. The ecotypes were differently affected by the siderophore treatments, which could be due to their genetic variations. However, Taibad responded more prominently to the application of siderophore. Comparing the siderophore application methods revealed that the combined treatment (foliar spray + seed priming) was more efficient compared to the other treatments following by the foliar application. Finally, it can be concluded that the application of siderophore is an efficient way to improve the nutrient uptake by cumin plants to enhance the nutritional status, growth, and productivity of the cumin plants in an arid region.

Conflict of interest

No conflict of interest was reported by the authors.

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