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Impact of different irrigation and fertilization strategies on growth, yield, and physiological traits of camelina

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Abstract

Objective: This research aimed to investigate the effects of irrigation regimes and fertilizer types on growth, yield, and physiological characteristics of camelina (*Camelina sativa*).

Methods: The effects of rainfed and supplementary irrigation (once or twice) on yield and physiochemical traits of camelina were evaluated under two different fertilizer sources (chemical and bio-organic fertilizers) based on a split-plot design with four replications based on a randomized complete block design.

Results: There was a reduction in grain yield by 48.08% and 28.41% under rain-fed and single irrigation conditions, respectively, compared with the double irrigation. Chemical fertilizer treatments increased both harvest index and grain yield, regardless of the irrigation regime. Bio-organic fertilizers enhanced yield by 22.35% under twice irrigation, 8.24% under single irrigation, and 25.49% under rain-fed conditions, compared with the control plots. Antioxidant enzyme activity (superoxide dismutase and peroxidase) increased under drought stress, especially in unfertilized plants, whereas chemical fertilizer application reduced these activities. Water deficit significantly inhibited nutrient uptake; however, fertilizer application, especially the chemical fertilizer, improved these effects, resulting in higher concentrations of N, K, Zn, and Fe in plant tissues. Both chemical and bio-organic fertilizers had almost similar effects on oil content.

Conclusion: Chemical fertilizer outperformed the bio-fertilizer in boosting camelina yield under irrigated conditions, yet they were not significantly different under rainfed conditions. Bio-organic fertilizers thus offer a sustainable alternative for maintaining camelina productivity in the water-scarce environments. These results highlight bio-fertilizers as a viable option for sustainable agriculture under rain-fed systems.

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Introduction

The global population is expected to hit 8.6 billion by the year 2030, increasing the demand for food and other resources greater than ever (Hafez *et al.* 2021). Such population growth creates immense stress on the water and nutrient resources, resulting in a dreadful deficit that can impact the agricultural productivity across the globe (Mohammadi *et al.* 2019). Almost half of the world population is expected to face water shortages by 2050, making access to freshwater one of the major hurdles facing food production (Liu *et al.* 2011; Mohammadi *et al.* 2019). In regions where water is scarce, it is crucial to manage water resources optimally to maintain crop productivity and food security (Ahmed *et al.* 2020; Daneshnia *et al.* 2015). Deficit irrigation and water scarcity negatively impact plants by changing their physiology and metabolism, which lowers their quantity and quality characteristics (Aboodeh *et al.* 2024). Providing adequate soil moisture during critical periods of growth helps in better nutrient absorption and supports important metabolic activities (Rahil and Qanadillo 2015). Farmers frequently modify irrigation intervals to alleviate drought stress, but more effective and sustainable methods for conserving water on farms are critically lacking (Askari *et al.* 2019; Zahedyan *et al.* 2022). Cultivating drought-tolerant crops like camelina, combined with strategic supplemental irrigation, has emerged as a key practice for managing water resources in arid regions (Merajipoor *et al.* 2020).

Camelina is a cold and drought-resistant oilseed crop that could be highly useful for dryland farming systems (Amiri-Darban *et al.* 2020). Regions with arid climates may find value in cultivating this crop, considering its short growth cycle of 90-110 days, adaptability to rainfed farming, and expectation of relatively high yield (Wiwart *et al.* 2019; Agarwal *et al.* 2021). The diverse applications for food, feed, and bio-based industries can be addressed by camelina, as its seeds possess high protein (27-32%) and oil (38-43%) (Ahmed *et al.* 2020; Wang *et al.* 2020). Though it holds potential, there is considerably limited research on camelina's performance under low water conditions.

Appropriately balancing the nutrient management of crops is crucial to improving the plant's tolerance to water deficits while simultaneously improving water use efficiency (WUE). Research indicates that providing nutrients more effectively can enhance crop WUE and yield significantly, even with insufficient rainfall (Srivastava *et al.* 2019; Al-Amri 2021). On the other hand, over-dependence on chemical fertilizers harms the environment by causing water contamination and pollution, the imbalance of nutrients in soil, and excessive emission of greenhouse gases, which consequently threatens sustainable crop production (Smil 1999; Diaz and Rosenberg 2008; Zheng *et al.* 2017; Li *et al.* 2021). Microbial bio-organic fertilizers that promote the release of nutrients through microbes constitute a sustainable solution with many advantages, improving soil physicochemical characteristics and enhancing long-term agricultural productivity (Ning *et al.* 2017; Alinejad *et al.* 2020; Zare Hoseini *et al.* 2021).

The introduction of drought-tolerant oilseed crops such as camelina is important for enhancing resilience and diversifying cropping systems because of the limited number of crops suitable for dryland farming. This study assumes that under drought stress and deficit irrigation, bio-organic fertilizers can enhance the yield and physiological performance of camelina and act as a partial substitute for chemical fertilizers. Therefore, this research aimed to study the impacts of rainfed plus supplemental irrigation alongside bio-organic fertilizers on the grain yield, agro-morphological traits, physiological responses, and WUE of camelina cultivated in arid and semi-arid agro-environments.

Materials and Methods

Experimental site and meteorological data

The cultivar Soheil (Winter camelina), which was supplied by Biston Shafa Company, was sown two consecutive growing seasons (2017-2019) under field conditions at the research farm of Razi University of Kermanshah, Iran. The coordinates of these locations are 34°19′ N and 47°06′ E. Figure 1 shows the average relative humidity, temperature, and monthly precipitation during the study period. To measure the physicochemical characteristics of the soil, a composite sample of the soil (0 to 30 cm deep) was prepared. Soil samples were sent to the Soil and Water Laboratory along with a sample of the cow manure used. The soil physicochemical properties and the references for which the measurement methods are based can be seen as follows: pH= 7.2 (McLean 1983), electrical conductivity= 0.82 dS m^{-1} (Smith and Doran 1997), the soil texture was silt-loam (55% Silt, 21% Clay, and 24% sand) (Klute 1986), total nitrogen= 0.11% (Kjeldahl 1883), organic matter= 1.8% (Walkley and Black 1934), available phosphorus= 7.8 mg kg^{-1} (Olsen *et al.* 1954), available potassium= 329 mg kg^{-1} (McLean and Watson 1985). Also, the amount of zinc and iron in soil was

0.48 and 4.5 mg kg^{-1}, respectively, extracted by TEA, DTPA 0.005 M, and their concentration was determined by atomic absorption (Lindsay and Norvell 1978). The soil moisture content was 29% at the field capacity and 16% at the permanent wilting point (Cassel and Nielsen 1986).
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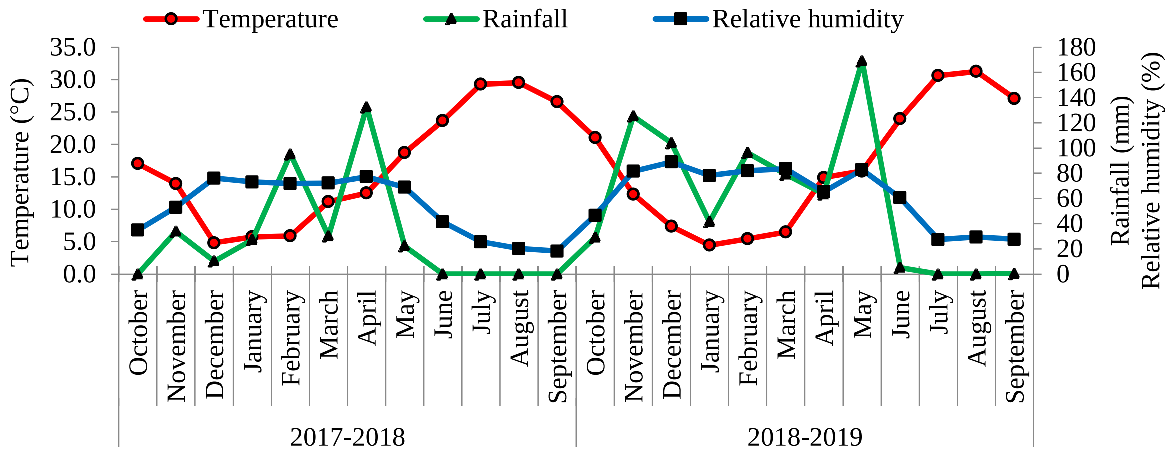

Figure 1. Monthly precipitation, average monthly air temperature, and relative humidity during the 2017-2019 growing seasons in Kermanshah, Iran.

Experimental design and field management

The experiment was a split-plot design based on a randomized complete block design with four replications. The main plots consisted of three types of irrigation: rainfed, single irrigation applied at the flowering stage (BBCH 69), and double irrigation, with the first application at flowering and the second 15 days later. The subplots consisted of a chemical fertilizer (N, P, K, and micronutrients) and a bio-organic fertilizer (cow manure + *Bacillus coagulans*, and *Pseudomonas vancouverensis* strain S19 as potassium and phosphate solubilizers, and *Azotobacter chroococcum* as nitrogen-fixing bacteria), and a control without fertilization. The amount of irrigation water was calculated from the percentage of soil moisture and its delivery to field capacity using the following equation (Benami and Ofen 1984).

$$VN = [(FC - WP) \times BD \times D \times (1 - ASM) \times A] / 100$$

Where FC is the weight percentage of moisture at field capacity, WP is the weight percentage of moisture at the wilting point, BD is soil specific gravity (kg m^{-3}), D is the depth of root development (m), ASM is the field soil moisture before irrigation, and A is the area of each plot (m^2). The WP was determined using the pressure plate method at -1.5 MPa, following the standard soil science protocols (Richards 1948). Root depth was estimated based on the field measurement of camelina root systems on 10 representative plants per plot at the reproductive stage, as determined by excavation at 0.3 m depth. Irrigation was applied to each plot using a volume meter to ensure precise water delivery.

Based on soil analysis, urea was applied at 50 kg ha^{-1}, triple superphosphate at 75 kg ha^{-1}, and potassium sulfate at 50 kg ha^{-1} (50% K_2O) as N, P, and K fertilizers. The P and K fertilizers were applied between rows before sowing, and nitrogen fertilizer was applied at the sowing and inflorescence emergence (BBCH 59), described by Martinelli and Galasso (2011). Librel ^{BMX}, a commercial fertilizer containing micro-nutrient fertilizers, was manufactured by the Royal Agro Science Co. (royalagroscience.com/en), and applied on foliar surfaces at three stages: vegetative (BBCH 29), stem elongation (BBCH 39), and pre-flowering (BBCH 59).

Cow manure (pH= 7.47, EC= 5 dS m^{-1}, organic matter= 50.8%, N= 1.2%, P= 0.4%, K= 1.1%, Fe= 150 mg kg^{-1} and Zn=20 mg kg^{-1}) was applied at a dose of 30 t ha^{-1} based on the recommendation for the camelina production. The bio-fertilizer was manufactured by the Green Biotech Co., Ltd, Tehran, Iran. Application of bio-fertilizers was done with seed priming and spraying at the vegetative (BBCH 29), stem elongation (BBCH 39), and pre-flowering (BBCH 59) stages. For inoculation, the seeds were coated with the Arabic gum as an adhesive and rolled into the bacterial suspension until evenly coated (Khalilzadeh *et al.* 2016).

The sowing took place on two different days: November 6 for the first year and November 16 for the second year. The main plots' dimensions were 2.5 × 9 m while the subplots were 2.5 × 2 m. Each subplot consisted of 7 rows, spaced 15 cm apart, with 5 cm between plants within rows, resulting in a planting density of 400 seeds per m². Plants were harvested at maturity from different areas of the field. Weed control was performed manually throughout the growing season.

Morphometric and physiological characteristics

Morphometric traits, including plant height and number of leaves, along with physiological characteristics, were measured before seed ripening at the growth stage of BBCH79. Fresh leaf samples were collected, wrapped in aluminum foil, immediately frozen in liquid nitrogen, and then stored at –80 °C in plastic wraps until analysis.

Yield and yield components

At physiological maturity (BBCH 89), a 2 m² area from each plot was hand-harvested, the above-ground biomass was weighed, and threshed to assess grain yield. The grain yield was determined by a digital scale. Yield components, including the number of pods per plant and seeds per pod, were recorded just before harvest. Harvested seeds were dried and adjusted to 87% dry matter to calculate the 1000-seed weight (Bujnovský 2020). The harvest index (HI) was then calculated as follows:

$$HI = (\text{Grain yield}/\text{Biomass})\times 100$$

Where biomass is the total above-ground dry matter of the plant at harvest.

Seed oil and protein content

To measure the seed protein content, five grams of seeds per plot (on a dry matter basis) were analyzed for nitrogen content using the procedure of Kjeldahl (1883) with the Gerhardt model VaPOXest 20, and protein content was calculated by multiplying the nitrogen content by a conversion factor of 6.25. The oil was extracted according to the method described by Tsaknis *et al.* (1999). Seeds were divided into three portions for cold pressing and solvent extraction with n-hexane. Oil and protein yields (kg ha^{-1}) were obtained by multiplying grain yield by oil and protein percentage (Mohtashami *et al.* 2020).

Leaf chlorophyll and enzymes

The leaf chlorophyll (chlorophyll a, chlorophyll b, and total chlorophyll) was measured based on Arnon (1949). To measure the superoxide dismutase (SOD) activity, 50 µl of protein extract (containing approximately 10 µg of protein) was added to a 3 ml reaction mixture containing distilled H_2O, 13 mM L-methionine, 50 mM phosphate buffer (pH 7.8), 0.1% Triton-X, 75 µM NBT, and 2 µM riboflavin, with the absorption recorded at 560 nm (Giannopolitis and Ries 1977). The catalase (CAT) activity was determined by adding 15 µl of the protein extract (approximately 5 µg of protein) to a 1.015 ml reaction mixture, comprising 2.5 µl of 30% H2O2 and 1 ml of 100 mM potassium phosphate buffer (pH 7.5) in an ice bath, with the absorbance changes monitored at 240 nm over 1 minute against a plant extract-free blank (Chaparro-Giraldo *et al.* 2000). For the POX activity, 50 µl of protein extract (approximately 10 µg of protein) was added to a 2.55 ml reaction mixture containing 100 µM Tris buffer, 10 mM pyrogallol, and 5 mM hydrogen peroxide, with the absorption recorded at 425 nm (Kar and Mishra 1976).

Nutrient content

Total N was determined using the Kjeldahl method (du Preez and Bate 1989). The P was measured by the colorimetric method (vanadate-molybdate) with a spectrophotometer at 470 nm. The K was measured using a standard flame photometer method (Temminghoff and Houba 2004). Harvested plant materials were thoroughly washed in distilled water and oven-dried at 65 °C. Dried plant materials were digested with H_2SO_4 and H_2O_2 and heated to 250 °C (Wolf 1982). The filtered extract was used to determine Zn and Fe with the atomic absorption spectrophotometer (AAnalyst 300 PerkinElmer, Germany).

WUE

WUE was determined by the ratio of grain yield, biomass, and essential oil yield (as WUE_{grain}, $WUE_{biomass}$, and WUE_{oil}, respectively) to the irrigation water (Al-Jamal *et al.* 2001). According to Doorenbos and Pruitt (1977), WUE was calculated as follows:

$$WUE = \text{Grain yield (kg ha}^{-1}\text{)} / \text{(Total water used + total rainfall (m}^{3}\text{))}$$

Statistical analysis

The combined analysis of variance, based on the data from two years, was carried out using SAS software 9.4. The mean values of the experimental treatments were compared with Duncan's multiple range test at a 5% probability level.

Results

Plant height, number of leaves, and yield components

The results of the combined analysis of variance are presented in Table 1. Plant height, number of leaves, and yield components of camelina were significantly affected by the type of irrigation and fertilizer. Results showed that plant height and number of leaves were significantly reduced under rainfed and non-fertilized conditions as compared to the other treatments. Plants under double and single irrigation had the highest plant height when compared with plants under rainfed conditions. Under fertilizer treatments, the tallest plants and the highest number of leaves were recorded for the chemical fertilizer, followed by the bio-organic fertilizer. Double irrigation accounted for 7.8%, 13.3%, and 25.5% more pod number, seed number per pod, and 1000-seed weight, respectively, compared to the single irrigation (Table 2). The highest pod number was obtained in the double irrigation scheme and the chemical fertilizer. Chemical and bio-organic fertilizers showed higher 1000-seed weight (1.01 g and 0.96 g, respectively) and seeds per pod (6.32 and 6.46, respectively), than the unfertilized control, although no significant difference was observed between the two fertilizers (Table 2).

Chlorophyll content

A significant interaction between year and fertilizer application was observed for the chlorophyll content of the leaves of camelina (Table 1). The highest values of chlorophyll a, chlorophyll b, and total chlorophyll content were recorded for plants that had been treated with chemical fertilizer in 2017. In contrast, the lowest values were recorded in 2018, and there was no significant difference among the fertilizer treatments. In 2017, the chemical and bio-organic fertilizers did not differ significantly for the chlorophyll a and chlorophyll b content (Figure 2).

The activity of SOD, CAT, and peroxidase (POX)

There was a significant interaction between fertilizers and irrigation type (Table 1). The highest SOD activity (80.41 U mg^{-1} FW min^{-1}) was recorded in the camelina plants subjected to severe drought stress (rainfed) + no fertilizer application (Table 3). Also, at all irrigation levels, the highest SOD activity was recorded in the control (no fertilizer) treatment, which was significantly higher than that for the fertilizer treatments. Fertilizer treatments also showed a significant effect on the POX activity (Table 1). The POX activity progressively increased with increasing drought intensity (Table 2). Also, the maximum level of POX was detected in unfertilized plants, which was statistically different from the fertilizer treatments (Table 2). Moreover, the application of chemical fertilizer lowered CAT and POX activities by 18.9% and 37.24%, respectively, compared to the control (Table 2).

The chemical fertilizer consistently showed the highest potassium content, followed by bio-organic fertilizers with moderate levels, while no-fertilizer treatments had the lowest in both years (Figure 2d).

Nutrient content

The chemical fertilizer consistently showed the highest potassium content, followed by bio-organic fertilizers with moderate levels, while no-fertilizer treatments had the lowest values in both years (Figure 2d). There was a significant interaction between the fertilizer application and the irrigation level for N, P, K, Zn, and Fe nutrients (Table 3). Significant inhibition of N, P, K, Fe, and Zn levels was noted by imposing the severe water-deficit stress, compared to the mild stress and/or two-times irrigation conditions. This effect was counteracted by fertilization, and among all fertilizers, chemical fertilizers were the most effective (Table 3). The maximum concentrations of N (1.66%), K (1.86%), Zn (54.18 mg kg^{-1}), and Fe (92.11 mg kg^{-1}) were recorded in plants applied with chemical fertilizers under two-times irrigation. Under the applications of chemical fertilizers, N concentrations of the aerial organs increased by 25.3 %, 7.23%, and 12.8% under two-times irrigation, single irrigation, and rainfed conditions, respectively, compared to the unfertilized control. However, under single irrigation, no significant difference occurred in nitrogen concentration between the bio-organic fertilizer treatments and the non-fertilized control (Table 3). Besides that, the mixed bio-organic fertilizer treatment considerably improved the nutrient status in plant leaves compared to the control, except for P, under the single irrigation regime. Furthermore, nitrogen was significantly increased by applying bio-organic fertilizer under two-times irrigation (Table 3). Potassium content ranged from 0.82% in the control to 1.86% in plants treated with chemical fertilizers under twice-irrigation. Application of bio-organic fertilizers increased potassium content by 46.51%, 17.35%, and 10.86%

under twice irrigation, single irrigation, and rainfed conditions, respectively, compared with the control plants (Table 3).

Table 1. Combined analysis of variance for agronomic, physiological, and biochemical traits of camelina under different irrigation regimes and applications of fertilizers.

Source of variation	df	Mean squares								
		PH	**LN**	**PN**	**SNPP**	**TSW**	**Chl-a**	**Chl-b**	**Total Chl**	**CAT**
Year (Y)	1	20.04^{ns}	193.3^{ns}	11.41^{ns}	0.20^{ns}	0.002^{ns}	6.27**	3.28**	18.66*	50.40^{ns}
Block (Y)	6	47.78**	104.3*	6.69^{ns}	0.85*	0.050^{ns}	0.17^{ns}	0.061^{ns}	0.25^{ns}	23.63**
Irrigation (I)	2	806.2**	538.5**	269.3**	20.9**	0.64**	0.031^{ns}	0.10^{ns}	0.22^{ns}	3.20^{ns}
I × Y	2	20.22^{ns}	33.5^{ns}	5.80^{ns}	0.06^{ns}	0.054^{ns}	0.11^{ns}	0.05^{ns}	0.32^{ns}	0.58^{ns}
Error I	12	28.28	51.66	8.94	0.41	0.03	0.03	0.04	0.06	6.07
Fertilizer (F)	2	396.9**	676.8**	160.8**	1.76**	0.143**	0.03^{ns}	0.05^{ns}	0.17^{ns}	99.21**
F × Y	2	0.06^{ns}	39.8^{ns}	0.155^{ns}	0.23^{ns}	0.066^{ns}	0.68**	0.21*	1.62**	21.82^{ns}
F × I	4	8.4^{ns}	46.3^{ns}	4.17^{ns}	0.19^{ns}	0.023^{ns}	0.07^{ns}	0.03^{ns}	0.13^{ns}	8.62^{ns}
F × I × Y	4	4.01^{ns}	1.22^{ns}	0.48^{ns}	0.15^{ns}	0.025^{ns}	0.02^{ns}	0.03^{ns}	0.09^{ns}	0.98^{ns}
Error Π	36	12.07	33.32	5.73	0.26	0.02	0.11	0.05	0.22	4.32
CV (%)	-	5.65	14.84	5.87	8.30	17.07	17.04	25.37	16.13	10.99

Table 1 continued

Source of variation	df	Mean squares							
		POX	**SOD**	**N**	**P**	**K**	**Zn**	**Fe**	**GY**
Year (Y)	1	2.35^{ns}	0.4^{ns}	0.0029^{ns}	0.00061^{ns}	0.015^{ns}	0.26^{ns}	0.40^{ns}	112759^{ns}
Block (Y)	6	16.55**	558.1**	0.0045^{ns}	0.010^{ns}	0.0031^{ns}	0.25^{ns}	2.98^{ns}	41031ns
Irrigation (I)	2	32.72**	196.2^{ns}	0.75**	0.19**	1.95**	554.7**	428.12**	4344670**
I × Y	2	1.65^{ns}	145.3^{ns}	0.004^{ns}	0.007^{ns}	0.0078^{ns}	0.25^{ns}	0.78^{ns}	22534^{ns}
Error I	12	1.19	140.3	0.003	0.0079	0.0081	0.15	1.98	10696
Fertilizer (F)	2	210.06**	8253.8**	0.33**	0.26**	2.39**	538.5**	19.14**	98755**
F × Y	2	0.70^{ns}	294.1^{ns}	0.022^{ns}	0.014^{ns}	0.019*	0.10^{ns}	2.77^{ns}	15220^{ns}
F × I	4	30.00^{ns}	569.8**	0.087**	0.086**	0.396**	28.33**	388.99**	187190.82**
F × I × Y	4	1.99^{ns}	177.5^{ns}	0.016^{ns}	0.0071^{ns}	0.003^{ns}	0.29^{ns}	0.91^{ns}	6019.04^{ns}
Error Π	36	3.47	107.5	0.009	0.011	0.0048	0.17	2.29	29887.5
CV (%)	-	14.30	20.12	7.22	18.85	5.59	0.95	1.97	15.12

Table 1 continued

Source of variation	df	Mean squares							
		Bio	**OY**	**HI**	**SO**	**SP**	**WUE-GY**	**WUE-Bio**	**WUE-OY**
Year (Y)	1	99235^{ns}	10665^{ns}	139.1*	1.52^{ns}	0.33^{ns}	0.44*	20.18**	0.015^{ns}
Block/Y	6	556486^{ns}	5832^{ns}	63.8^{ns}	39.46**	4.56^{ns}	0.11^{ns}	1.32^{ns}	0.016^{ns}
Irrigation (I)	2	2324437**	318360**	1785.9**	18.38^{ns}	1.47^{ns}	10.96**	5.90**	0.79**
I × Y	2	30112^{ns}	439^{ns}	10.0^{ns}	0.97^{ns}	1.95^{ns}	0.23^{ns}	0.21^{ns}	0.008^{ns}
Error I	12	265511	1739	19.8	3.84	3.40	0.02	0.69	0.0048
Fertilizer (F)	2	1887424**	127938**	210.8**	113.09**	42.27*	2.51**	4.69**	0.32**
F × Y	2	253830^{ns}	381.05^{ns}	12.61^{ns}	1.29^{ns}	1.79^{ns}	0.09^{ns}	0.07^{ns}	0.003^{ns}
F × I	4	140742^{ns}	24229.5**	105.84*	2.30^{ns}	2.89^{ns}	0.45**	0.36^{ns}	0.059**
F × I × Y	4	35699^{ns}	1394.8^{ns}	10.34^{ns}	3.20^{ns}	1.29^{ns}	0.01^{ns}	0.10^{ns}	0.001^{ns}
Error Π	36	253706	3557.05	31.55	8.66	8.22	0.077	0.65	0.009
CV (%)	-	13.16	21.59	18.88	12.39	17.30	15.47	13.35	21.96

Ns,*,**: Not significant, and Significant at p≤ 0.05 and p≤ 0.01, respectively; PH: plant height, LN: Leaf number, PN: Pod number SNPP: Seed number per pod, TSW: 1000-seed Weight, Chl-a: Chlorophyll-a, Chl-b: Chlorophyll-b, Total Chl: Total Chlorophyll, CAT: Catalase, POX: Peroxidase, SOD: Superoxide dismutase, GY: grain yield, Bio: Biomass, OY; Oil yield, HI: Harvest index, SO; Seed oil, SP: Seed Protein, WUE-GY: WUE of grain yield, WUE-Bio: WUE of biomass, WUE-OY: WUE of oil yield.

Table 2. Mean comparison of the effects of year, irrigation, and fertilizer on the agronomic, physiological, and biochemical traits of camelina.

Factor	PH (cm)	LN	PN	SNPP	TSW (g)	Chl-a (mg g^{-1} FW)	Chl-b (mg g^{-1} FW)	Total Chl (mg g^{-1} FW)	CAT (μmol H_2O_2 min^{-1} g^{-1} FW)
Year									
2017	60.94±1.11^{a}	40.52±1.63^{a}	41.13±0.7^{a}	6.19±0.17^{a}	0.94±0.02^{a}	2.30±0.05^{a}	1.13±0.03^{a}	3.43±0.07^{a}	18.08±0.41^{b}
2018	62.00±1.25^{a}	37.25±1.2^{a}	40.34±0.7^{a}	6.29±0.15^{a}	0.95±0. 04^{a}	1.71±0.05^{b}	0.70±0.04^{b}	2.42±0.08^{b}	19.75±0.56^{a}
Irrigation									
Twice irrigation	66.87±1.2^{a}	43.00±1.82^{a}	44.04±0.75^{a}	7.14±0.13^{a}	1.13±0.036^{a}	2.01±0.09^{a}	0.98±0.07^{a}	2.99±0.15^{a}	18.60±0.53^{a}
Once irrigation	62.19±1.18^{b}	39.95±1.75^{a}	40.83±0.56^{b}	6.30±0.11^{b}	0.90±0.039^{b}	2.04±0.1^{a}	0.93±0.06^{a}	2.97±0.15^{a}	19.32±0.52^{a}
Rainfed	55.35±0.84^{c}	33.70±1.2^{b}	37.34±0.64^{c}	5.28±0.12^{c}	0.80±0.038^{b}	1.97±0.07^{a}	0.84±0.05^{a}	2.81±0.11^{b}	18.83±0.80^{a}
Fertilizers									
Chemical	65.27±1.35^{a}	43.58±1.18^{a}	43.05±0.81^{a}	6.32±0.21^{a}	1.01±0.05^{a}	2.05±0.12^{a}	0.97±0.07^{a}	3.02±0.18^{a}	17.13±0.58^{c}
Bio-organic	61.97±1.37^{b}	39.95±1.58^{b}	41.21±0.67^{b}	6.46±0.18^{a}	0.96±0.04^{a}	1.98±0.07^{a}	0.87±0.06^{a}	2.85±0.12^{a}	18.49±0.57^{b}
No-fertilization	57.18±1.14^{c}	33.12±1.23^{c}	37.94±0.76^{c}	5.94±0.18^{b}	0.86±0.03^{b}	1.98±0.05^{a}	0.91±0.05^{a}	2.90±0.10^{a}	21.13±0.43^{a}

Table 2 continued

Factor	POX (U mg^{-1} FW min^{-1})	SOD (U mg^{-1} FW min^{-1})	N (%)	P (%)	K (%)	Zn (mg kg^{-1})	Fe (mg kg^{-1})	GY (kg ha^{-1})
Year								
2017	13.21±0.59^{a}	51.45±3.57^{a}	1.38±0.03^{a}	0.55±0.02^{a}	1.26±0.06^{a}	44.26±0.96^{a}	76.77±1.61^{a}	1103.31±77.17^{b}
2018	12.85±0.49^{a}	51.60±3.07^{a}	1.37±0.03^{a}	0.56±0.02^{a}	1.23±0.06^{a}	44.14±0.94^{a}	76.92±1.56^{a}	1182.46±65.81^{a}
Irrigation								
Twice irrigation	11.85±0.58^{c}	48.30±4.56^{a}	1.50±0.04^{a}	0.60±0.03^{a}	1.50±0.08^{a}	47.23±1.08^{a}	77.40±2.7^{b}	1617.36±72.55^{a}
Once irrigation	13.05±0.61^{b}	52.55±3.79^{a}	1.44±0.01^{b}	0.61±0.02^{a}	1.30±0.08^{b}	46.71±0.78^{b}	80.76±1.42^{a}	1016.01±40.82^{b}
Rainfed	14.18±0.72^{a}	53.73±4.22^{a}	1.17±0.01^{c}	0.45±0.02^{b}	0.94±0.02^{c}	38.65±0.63^{c}	72.37±0.63^{c}	795.28±29.48^{c}
Fertilizers								
Chemical	9.94±0.55^{c}	34.71±2.95^{c}	1.48±0.03^{a}	0.66±0.03^{a}	1.54±0.07^{a}	48.95±1.14^{a}	85.52±1.57^{a}	1353.84±102.6^{a}
Bio-organic	13.31±0.42^{b}	48.45±2.87^{b}	1.40±0.04^{b}	0.55±0.02^{b}	1.28±0.07^{b}	44.17±0.61^{b}	77.33±0.9^{b}	1125.53±70.63^{b}
No-fertilization	15.84±0.33^{a}	71.42±2.61^{a}	1.24±0.03^{c}	0.45±0.03^{c}	0.91±0.01^{c}	39.48±0.74^{c}	67.68±1.14^{c}	949.27±61.37^{c}

Table 2 continued

Factor	Bio (kg ha^{-1})	OY (kg ha^{-1})	HI (%)	SO (%)	SP (%)	WUE-SY (kg m^{-3})	WUE-Bio (kg m^{-3})	WUE-OY (kg m^{-3})
Year								
2017	3863.2±104.2^{a}	264.05±21.85^{b}	28.34±1.7^{b}	23.60±062.^{a}	16.50±0.42^{a}	1.87±013.^{a}	6.58±0.17^{a}	0.45±0.03^{a}
2018	3789.0±94.35^{a}	288.39±21.43^{a}	31.12±1.43^{a}	23.89±0.55^{a}	16.63±0.44^{a}	1.72±0.09^{b}	5.52±0.13^{b}	0.42±0.03^{a}
Irrigation								
Twice irrigation	4118.6±114.4^{a}	405.68±27.86^{a}	39.51±1.71^{a}	24.75±0.87^{a}	16.67±0.52^{a}	2.55±0.12^{a}	6.51±0.23^{a}	0.64±0.04^{a}
Once irrigation	3860.7±95.66^{a}	237.89±11.86^{b}	26.52±1.04^{b}	23.31±0.81^{b}	16.74±0.59^{a}	1.59±0.06^{b}	6.10±0.18^{a}	0.37±0.01^{b}
Rainfed	3499.0±121.17^{b}	185.12±9.05^{c}	23.18±1.05^{c}	23.17±0.63^{b}	16.28±0.48^{a}	1.25±0.04^{c}	5.53±0.21^{b}	0.29±0.01^{c}
Fertilizers								
Chemical	4119.2±96.96^{a}	349.84±33.53^{a}	32.82±2.47^{a}	25.62±0.91^{a}	15.23±0.55^{b}	2.13±0.17^{a}	6.51±0.19^{a}	0.55±0.05^{a}
Bio-organic	3798.8±105/98^{b}	275.01±19.44^{b}	29.47±1.43^{b}	24.24±0.55^{a}	16.58±0.42^{ab}	1.77±0.11^{b}	6.00±0.19^{b}	0.43±0.03^{b}
No-fertilization	3560.4±133.46^{b}	203.83±13.85^{c}	26.91±1.62^{b}	21.360±0.19^{b}	17.88±0.47^{a}	1.49±0.09^{c}	5.63±0.24^{b}	0.32±0.02^{c}

Values are Mean ± Standard Error; In each column and each factor, the means with different letters are significantly different at $p \leq 0.05$, based on Duncan's multiple range test. PH: plant height, LN: Leaf number, PN: Pod number SNPP: Seed number per pod, TSW: 1000-seed weight, Chl-a: Chlorophyll-a, Chl-b: Chlorophyll-b, Total Chl: Total Chlorophyll, CAT: Catalase, POX: Peroxidase, SOD: Superoxide dismutase, GY: grain yield, Bio: Biomass, OY; Oil yield, HI: Harvest index, SO; Seed oil, SP: Seed Protein, WUE-GY: WUE of grain yield, WUE-Bio: WUE of biomass, WUE-OY: WUE of oil yield.

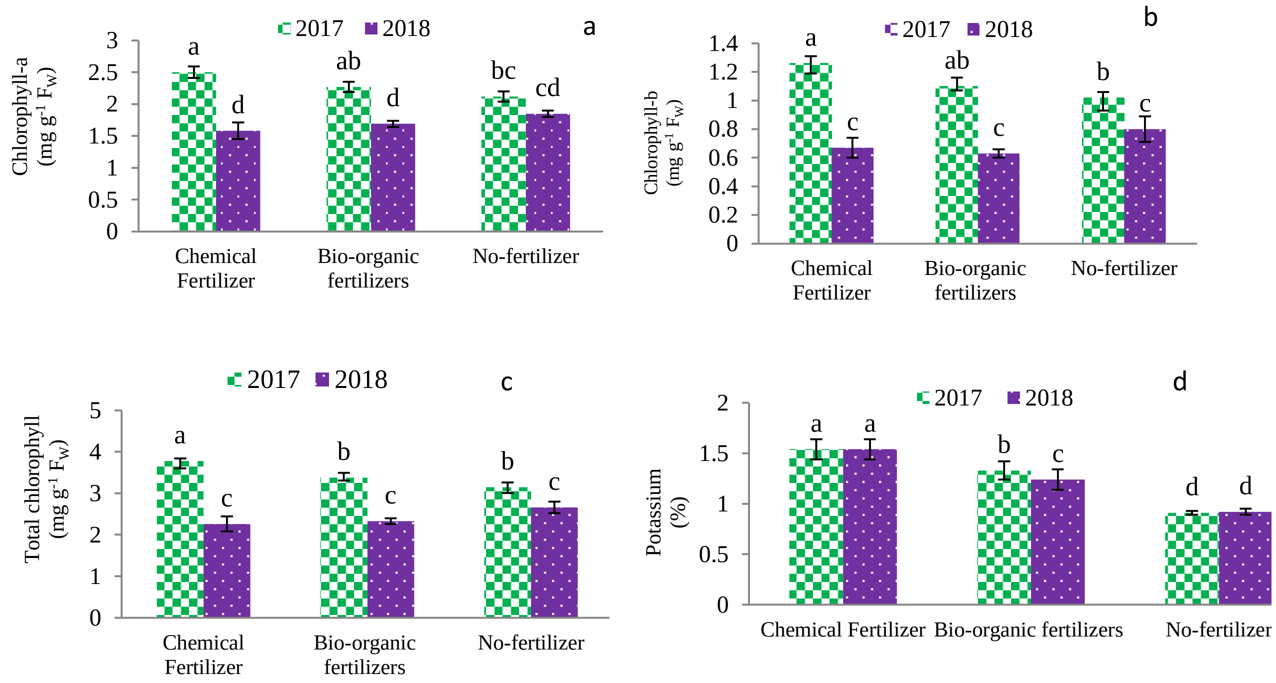

Figure 2. Concentration of chlorophyll-a (a), chlorophyll-b (b), total chlorophyll (c), and potassium concentration (d) of camelina affected by various fertilizer treatments and year; Error bars show standard error (SE); In each figure, the means with different letters are significantly different at $p \leq 0.05$, based on Duncan's multiple range test.

Biomass, grain, and oil yield

Grain and oil yields were influenced significantly due to the interaction between irrigation regime and fertilizer application (Table 1). Grain yield was the highest (2018.90 kg ha^{-1}) under the twice-irrigation treatment combined with the chemical fertilizer. For the single irrigation, grain yield was 14.04% higher when the chemical fertilizer was applied than that for the bio-organic fertilizer (Table 3). The use of bio-organic fertilizer led to a 29.21% oil yield boost under twice irrigation, a 7.61% rise under single irrigation, and a 20.31% increase in the rainfed plots compared to unfertilized plots (Table 3). The research revealed that the biomass of camelina increased significantly under twice-irrigation, followed by single-irrigation, while rainfed treatments produced the lowest yields. The chemical and bio-organic fertilizers increased the biomass of camelina by 13.56% and 6.27% when compared to the control that did not receive any fertilizer (Table 2).

Oil and protein content

The research data showed camelina seeds contained 21.36% to 25.62% oil content on a whole-seed basis. Camelina seeds had a protein content range of 15.23% to 17.88%. The protein content of camelina seeds decreased because of fertilizer application, while their oil content increased (Table 2).

Table 3. Mean comparison of the interaction effects of different irrigation and fertilizer treatments on some studied traits of camelina

Irrigation	Fertilizer	SOD (UA mg^{-1} FW min^{-1})	N (%)	P (%)	K (%)	Zn (mg Kg^{-1})
Twice irrigation	Chemical	24.99±2.9^{e}	1.66±0.02^{a}	0.77±0.01^{a}	1.86±0.01^{a}	54.18±0.42^{a}
	Bio-organic	54.15±6.59^{c}	1.61±0.06^{ab}	0.64±0.04^{bc}	1.72±0.02^{b}	45.60±0.06^{d}
	No- fertilizers	65.76±5.2^{b}	1.24±0.03^{d}	0.40±0.02^{ef}	0.92±0.02^{f}	41.90±0.01^{e}
Once irrigation	Chemical	41.97±6.54^{d}	1.52±0.03^{b}	0.73±0.02^{ab}	1.69±0.04^{b}	51.25±0.11^{b}
	Bio-organic	47.60±4.88^{cd}	1.41±0.01^{c}	0.51±0.03^{de}	1.21±0.03^{c}	46.81±0.04^{c}
	No- fertilizers	68.08±4.63^{b}	1.41±0.02^{c}	0.60±0.05^{cd}	1.00±0.01^{e}	42.07±0.11^{e}
Rainfed	Chemical	37.18±3.59^{d}	1.25±0.02^{d}	0.48±0.04^{de}	1.07±0.01^{d}	41.42±0.05^{f}
	Bio-organic	43.61±2.46^{cd}	1.17±0.02^{de}	0.52±0.01^{d}	0.92±0.02^{f}	40.09±0.02^{g}
	No- fertilizers	80.41±1.06^{a}	1.09±0.01^{e}	0.35±0.01^{f}	0.82±0.02^{g}	34.45±0.03^{h}

Table 3 continued

Irrigation	Fertilizer	Fe (mg kg^{-1})	Yield (kg ha^{-1})		HI	WUE (kg m^{-3})	
			Grain	Oil		Grain yield	Oil yield
Twice irrigation	Chemical	92.11±0.004^{a}	2018.90±67.15^{a}	547.57±44.74^{a}	46.99±2.94^{a}	3.19±0.14^{a}	0.86±0.07^{a}
	Bio-organic	80.00±0.001^{c}	1559.03±66.45^{b}	392.0±16.19^{b}	37.97±0.99^{b}	2.46±0.12^{b}	0.61±0.03^{b}
	No- fertilizers	60.10±0.002^{g}	1274.16±63.7^{c}	277.49±13.93^{cd}	33.55±2.43^{bc}	2.01±0.11^{c}	0.43±0.02^{cd}
Once irrigation	Chemical	89.51±0.33^{b}	1148.57±81.82^{cd}	284.58±15.38^{c}	28.39±1.76^{cd}	1.81±0.14^{cd}	0.45±0.02^{c}
	Bio-organic	79.83±0.35^{c}	987.34±48.84^{de}	235.29±19.57^{cde}	25.41±1.65^{de}	1.55±0.06^{de}	0.37±0.02^{cde}
	No- fertilizers	72.95±0.003^{e}	912.11±56.4^{e}	193.78±13.28^{ef}	25.76±2.01^{de}	1.42±0.06^{e}	0.30±0.01^{ef}
Rainfed	Chemical	74.96±0.005^{d}	894.09±36.28^{e}	217.38±12.13^{de}	23.08±1. 83de	1.41±0.05^{e}	0.34±0.02^{de}
	Bio-organic	72.16±1.47^{e}	830.21±18.5^{ef}	197.74±6.98^{ef}	25.02±1.07^{de}	1.31±0.03^{ef}	0.31±0.01^{ef}
	No- fertilizers	69.99±0.001^{f}	661.54±52.79^{f}	140.23±12.35^{f}	21.43±2.31^{e}	1.03±0.07^{f}	0.22±0.01^{f}

Table 2 showed that no statistical differences occurred between the effects of chemical and bio-organic fertilizers on the oil content.

Harvest index

There was a significant interaction between the fertilizer application and irrigation conditions for the harvest index (Table 1). The camelina harvest index ranged from 21.43% to 46.99% across different irrigation and fertilizer treatments (Table 3). Compared to the twice-irrigation condition, the harvest index decreased by 39.58% under once-irrigation and 50.87% under rainfed conditions, when chemical fertilizer was used.

WUE (grain, biomass, and oil)

A significant interaction was observed between fertilizer application and irrigation conditions for

WUEgrain and WUEoil (Table 1). Also, there was a significant difference among the fertilizer treatments and among irrigation conditions for WUE-biomass. The WUEgrain under the twice-irrigation regime was estimated as 3.19, 2.46, and 2.01 kg m^{-3} for the chemical fertilizer, the bio-organic fertilizer, and the control (no fertilizer) treatments, respectively. Meanwhile, the WUEoil under the same irrigation regime was 0.86, 0.61, and 0.43 kg m^{-3} for the chemical fertilizer, the bio-organic fertilizer, and the control (no fertilizer), respectively (Table 3). Camelina plants treated with the chemical fertilizer under twice-irrigation had significantly higher WUEs for grain and oil yield than those treated with the bio-organic fertilizer and without fertilizer application. However, under one-irrigation scheme, there were no significant differences in WUE between chemical and bio-organic fertilized plants for both grain and oil (Table 3). The biomass and grain yield WUE differed significantly between years (Table 1), with higher values in 2017 than in 2018 (Table 2). The highest biomass WUE values recorded were 6.51 and 6.10 kg m^{-3} for twice- and once-irrigation treatments, respectively. The application of chemical fertilizers consistently resulted in a significantly higher biomass WUE compared to the bio-organic fertilizer (Table 2).

Discussion

Double irrigation increased the plant height and the number of leaves of camelina in comparison with the rainfed conditions (Table 2). The improvement in plant height and leaf number under optimum irrigation, may be attributed to the adequate water supply provided to the plants. The highest yield components were recorded in the plots treated with chemical fertilizers. The absence of moisture in the soil may have prevented the roots from absorbing nutrients, such as phosphorus and potassium which are the building requirements for growth and, eventually, the grain yield of camelina (Jahanzad *et al.* 2013; Daneshnia *et al.* 2015). Yield and vegetative responses occur due to the uniformity of water distribution across the root zone under twice irrigation that promotes nutrient uptake, photosynthesis, and physiological activity (Rahil and Qanadillo 2015). This can be interpreted as an increase in yield components, that is, a greater number of pods, more seeds per pod, and a higher 1000-seed weight, which were observed in this study. These results were in agreement with findings reported by Agarwal *et al.* (2021), which stated that irrigation during the flowering stage and at 15-day intervals was conducive to better plant growth, flower, and pod development, and finally brought about a greater grain yield in camelina.

The statistical analysis demonstrated that the camelina growth characteristics and the yield components were significantly higher in the plots that were treated with the bio-organic fertilizers than in those from the control treatment (Table 2). This result is also consistent with the data from

Anwar *et al.* (2005) and Bajeli *et al.* (2016), from which we could infer that organic manures, a rich source of essential nutrients such as C, N, P, and K, had a positive effect on the plant growth cycle. What is more, biofertilizers are good not only for the environment, but they also have an effect on the phytohormones secretion, e.g., auxin, cytokinin, and gibberellin, which are the best accompanying substances for plants to grow and yield (Lucy *et al.* 2004).

The chlorophyll a and chlorophyll b content elicited by the chemical fertilizer application were significantly higher than those of the control, especially in the 2017 growing season. Better availability of nutrients increased the number of leaves and plant height, which, in turn, improved the photo-assimilate production and physiological activity, thus improving the vegetative growth and chlorophyll content (Latt *et al.* 2009). It is most likely that the increased amount of chlorophyll under chemical and bio-organic fertilizers is caused by the biosynthesis of chlorophyll molecules and by the action of enzymes taking part in the chlorophyll turning process (Najm *et al.* 2012; Khajeeyan *et al.* 2019). Another example can be found in Janmohammadi *et al.* (2014) who also came to the same conclusion that the availability of higher nutrient concentrations in the organic manure stimulates the photosynthetic apparatus, leading to not only an increase in growth but also in grain yield. Also, Zhaoxiang *et al.* (2020) went ahead to prove that chemical fertilizers ensure the speedy supply of nitrogen, thus allowing rapid chlorophyll biosynthesis. In a different context, the decrease in chlorophyll content observed under organic manure in 2018 was assigned to the fact that the nutrient uptake by roots was diminished, and that it in turn, limited the synthesis of chlorophyll precursors (Mohasseli *et al.* 2020).

Water deficit significantly increased the POX and SOD enzyme activities in camelina, which was consistent with the findings of Zahedyan *et al.* (2022). Under environmental stress conditions, an increase in reactive oxygen species (ROS) is detrimental to cellular membranes. Plants respond to oxidative stress with enzymatic antioxidant defenses, including SOD, CAT, and POX, which limit lipid peroxidation and inhibit ROS chain reactions and protein damage (Khalilzadeh *et al.* 2016). More specifically, the key ROS detoxifying enzyme SOD catalyzes the dismutation of superoxide radicals (O^{2-} −) into hydrogen peroxide (H_2O_2), and the reduction in the SOD activity of the plant likely leads to higher H_2O_2 and greater oxidative stress. After production of H_2O_2, the CAT and POX enzymes convert H_2O_2 to water (Pourya *et al.* 2021). On the contrary, fertilizer application increased camelina's resistance to the water-deficit stress, and thus, the antioxidant enzyme activity was lower in the fertilized plants (Table 2), thus indicating lesser oxidative stress. The protective effect of the fertilizer may have been based on maintaining sufficient iron (Fe) in the aerial tissues; Fe contributes to stress tolerance because it limits the need for higher antioxidant enzyme activity when plants experience drought (Mohasseli *et al.* 2020). Iron can aid ROS scavenging and improve photosynthetic efficiency (Hänsch and Mendel 2009).

Water deficit reduced the leaf nutrient content, regardless of the fertilizer treatments. However, nutrient concentrations were higher in the fertilized plants than in the unfertilized control (Table 2). The extent of nutrient accumulation in aerial organs, was primarily related to soil uptake (Negi *et al.* 2021), and it has been well documented that reduced transpiration when soil moisture is limited, reduces nutrient uptake by roots, and as well, affects the translocation of ions from roots to shoots (Jahanzad *et al.* 2013), leading to a decline in yield components and vegetative growth during the reduced deficit irrigation. As a result, additional nutrient supply through fertilization is important during drought for sustainable plant growth (Amiri-Darban *et al.* 2020). Indirectly, where fertilizers were applied with adequate irrigation, optimal conditions for photosynthetic performance and root growth are provided, which results in improved nutrient uptake *(*Sheshbahreh *et al.* 2019). Furthermore, increased K concentration may enhance plant tolerance to environmental stresses (Cakmak 2005).

With the application of bio-fertilizers under both sufficient and deficient water conditions, greater nitrogen uptake by aerial organs likely occurred because of the molecular fixation of atmospheric nitrogen via the activity of bio-fertilizers. This also improved WUE (Merajipoor *et al.* 2020). By providing a slow nutrient release, manure also enhances soil physical properties, which in turn improves nutrient bioavailability and root uptake efficiency (Nadeem *et al.* 2017). Furthermore, the observed higher P and K levels in the bio-fertilizer-treated plants, especially under rainfed conditions, were likely due to bio-fertilizer-mediated strategies such as rhizosphere acidification, and the production of soluble root exudates, which release available nutrients and then solubilize nutrients for uptake. That would likely have occurred only with well-established nitrifying and denitrifying bacterial populations were present under bio-fertilized conditions, as described by Sheshbahreh *et al.* (2019). The reduction in P availability under rainfed conditions could have been a result of strong adsorption of P to clay particles, limiting mobility and the feasibility of plant root uptake (Sheshbahreh *et al.* 2019).

In the current study, bio-fertilizer inoculum + cow manure decreased the concentration of Zn in plants as compared to the chemical fertilizer, possibly due to antagonistic interactions affecting Zn uptake. Importantly, nutrients released from organic matter mineralized by our bio-fertilizers persisted in soil longer than with inorganic fertilizers, and which directly benefit future crops (Negi *et al.* 2021). It has also been shown that bio-fertilizer impacts plant growth (Attarzadeh *et al.* 2019) by facilitating the uptake of nutrients and enhancing photosynthesis. As nutrients are gradually released from organic amendments, this improves the physical and chemical properties of soil, and promotes retained nutrient availability and uptake.

It became apparent from Table 3 that the *Camelina sativa* grain production was highly associated with the application of chemical fertilizer, and the top yield of 2018.9 kg ha^{-1} was reached when this fertilizer was used. This result is in accordance with the findings by Stolarski *et al.* (2019) and Sintim *et al.* (2015) in *C. sativa.* On the other hand, water deficit put a severe limitation on the grain yield of *camelina*, as found to be true again by Amiri-Darban *et al.* (2020) in camelina, Abhari and Gholinezhad (2019) in chickpea, Ghazian Tafrihi *et al.* (2013) in sweet corn and Khalilzadeh *et al.* (2016) in wheat. However, our observation showed that both bio-organic and chemical fertilizers helped reduce yield loss under deficit irrigation and also under rainfed conditions. These findings not only are in accordance with the results of Alinejad *et al.* (2020) but also confirm the better preservation of yield through the slow nutrient release function of organic fertilizers as a response to the dry soil caused by conventional treatment.

It was noticeable from Table 3 that camelina oil content and oil yield were markedly less in the case of water shortage compared to optimal irrigation. This result was also consistent with the study of Singh and Sinha (2005), who investigated the drops in the change of polyunsaturated fatty acids, one of the main reasons for which the oil content witnessed a decrease under water stress conditions in *Brassica juncea*. However, application of fertilizers had a major impact on the oil yield under all irrigation conditions, which was consistent with findings reported for *Mentha arvensis* L. by Bajeli *et al.* (2016).

Amtmann *et al.* (2005) determined that K, supplied by both chemical fertilizers and bio-fertilizers, was very important for enzymatic processes and photosynthetic metabolism regulation and, in turn, for the translocation of photosynthates into oil. Besides affecting nutrient availability, bio-organic fertilizers containing PGPRs influence plant growth through multiple mechanisms. This dual action is important since the application of the bio-organic fertilizer not only enhances camelina growth and grain yield but also reduces the application of chemical micronutrients and N–P–K fertilizers, thus conferring both economic and environmental benefits, especially under rainfed conditions. Al-Amri (2021) reported that beneficial bacteria primarily protected against stress, thus improving environmental resilience and plant development.

The non-irrigated conditions led to modifications in plant development, which caused biomass reduction. The growth rate in plants reduces as an adaptive response during stress periods, not merely because resources are insufficient (Daneshnia *et al.* 2015). Plants experiencing water shortages reduce their water loss by shutting down stomatal openings. This process reduces the availability of CO_2

essential for photosynthesis and dry matter formation (Khalilzadeh *et al.* 2016). However, the application of chemical fertilizer with proper irrigation resulted in a substantial increase in biomass (Table 2). The present study measured camelina's harvest index, which ranged from 21.43% to 46.99%, exceeding previously reported values by Gesch and Cermak (2011) and Sintim *et al.* (2015) for the Midwestern United States.

Application of the chemical fertilizer reduced the protein content of the camelina as compared to the control (without fertilizer application). However, simultaneous seed inoculation with microorganisms together with manure application led to an increase in the protein content to a value that was not significantly different from the control. The quantity of plant protein directly corresponded to the nitrogen levels present in the plant. According to Lal *et al.* (2020), organic manure application caused enhanced nutrient absorption, which resulted in increased amino acids and phosphorus content that supported the increased protein synthesis in forage crops.

The results in Table 3 emphasize the importance of the chemical fertilizer in enhancing the WUE for grain and oil production in camelina under all irrigation conditions. The combined effects of irrigation and fertilizer application increased grain production, thereby improving WUE in well-watered plants. The studies by Sonntag *et al.* (2019) and Daoud *et al.* (2020) demonstrated that yield and WUE, assessed via biomass and grain yield, were strongly influenced by K fertilization, with significant improvements observed under adequate K supply. In the present study, the bio-fertilizer had no significant effect on the WUE of grain yield, as compared to the control under drought stress. Adequate moisture during the flowering and capsule-development stages is essential for maintaining photosynthetic activity, such that WUE of grain yield declined under drought conditions.

Conclusion

Chemical fertilizers proved superior for maximizing camelina grain yield, oil yield, and WUE under twice supplemental irrigation. However, under water-limited conditions (rainfed and single irrigation), bio-organic fertilizers demonstrated a remarkable ability to sustain productivity, showing comparable yield improvements to chemical fertilizers. The application of fertilizers, particularly chemical ones, mitigated the adverse effects of drought stress on nutrient uptake (N, K, Zn, and Fe) and reduced antioxidant enzyme activity (SOD, POD), indicating lower oxidative stress in the fertilized plants. While chemical fertilizer is optimal for productivity under sufficient water supply, bio-organic fertilizers present a viable and sustainable alternative for maintaining stable camelina yield and oil content in rainfed and water-scarce agroecosystems, supporting ecological sustainability.

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Data Availability

The data analyzed in the current study are available from the corresponding author upon reasonable request.

Conflict of Interest

The authors have no relevant financial or non-financial interests with any individual or organization.

References

Abhari A, Gholinezhad E. 2019. Effect of humic acid on grain yield and yield components in chickpea under different irrigation levels. J Plant Physiol Breed. 9(2): 19–29. https://doi.org/10.22034/jppb.2019.10441

Aboodeh H, Bakhshandeh A, Moradi Telavat MR, Siadat SA, Moosavi SA, Alami Saeid K. 2024. The physiological response of rapeseed (*Brassica napus* L.) genotypes to drought stress. Agrotech Ind Crops. 4: 38–47. https://doi.org/10.22126/atic.2024.9989.1127

Agarwal A, Prakash O, Bala M. 2021. Effect of irrigation schedule on growth and seed yield of camelina (*Camelina sativa* L.) in Tarai region of central Himalaya. Oil Crop Sci. 6: 8–11. https://doi.org/10.1016/j.ocsci.2021.01.004

Ahmed Z, Liu J, Waraich EA, Yan Y, Qi Z, Gui D, Zeng F, Tariq A, Shareef M, Iqbal H, *et al.* 2020. Differential physio-biochemical and yield responses of *Camelina sativa* L. under varying irrigation water regimes in semi-arid climatic conditions. PLoS One. 15: e0242441. https://doi.org/10.1371/journal.pone.0242441

Al-Amri SM. 2021. Application of bio-fertilizers for enhancing growth and yield of common bean plants grown under water stress conditions. Saudi J Biol Sci. 28: 3901–3908. https://doi.org/10.1016/j.sjbs.2021.03.064

Al-Jamal MS, Ball S, Sammis TW. 2001. Comparison of sprinkler, trickle and furrow irrigation efficiencies for onion production. Agric Water Manag. 46: 253–266. https://doi.org/10.1016/S0378-3774(00)00089-5

Alinejad S, Sarabi V, Bakhtvari ARS, Hashempour H. 2020. Variation in physiological traits, yield and secondary metabolites of jimsonweed (*Datura stramonium* L.) under different irrigation regimes and nutrition systems. Ind Crops Prod. 143: 111916. https://doi.org/10.1016/j.indcrop.2019.111916

Amiri-Darban N, Nourmohammadi G, Rad AHS, Mirhadi SMJ, Heravan IM. 2020. Potassium sulfate and ammonium sulfate affect quality and quantity of camelina oil grown with different irrigation regimes. Ind Crops Prod. 148: 112308. https://doi.org/10.1016/j.indcrop.2020.112308

Amtmann A, Hammond JP, Armengaud P, White PJ. 2005. Nutrient sensing and signaling in plants: potassium and phosphorus. In: Advances in Botanical Research. London: Elsevier. 43: 209–257. https://doi.org/10.1016/S0065-2296(05)43005-0

Anwar M, Patra DD, Chand S, Alpesh K, Naqvi AA, Khanuja SPS. 2005. Effect of organic manures and inorganic fertilizer on growth, herb and oil yield, nutrient accumulation, and oil quality of French basil. Commun Soil Sci Plant Anal. 36: 1737–1746. https://doi.org/10.1081/CSS-200062434

Arnon DI. 1949. Copper enzymes in isolated chloroplasts. Polyphenoloxidase in *Beta vulgaris*. Plant Physiol. 24: 1–15. https://doi.org/10.1104/pp.24.1.1

Askari A, Ardakani MR, Paknejad F, Hosseini Y. 2019. Effects of mycorrhizal symbiosis and seed priming on yield and water use efficiency of sesame under drought stress condition. Sci Hortic. 257: 108749. https://doi.org/10.1016/j.scienta.2019.108749

Attarzadeh M, Balouchi H, Rajaie M, Movahhedi Dehnavi M, Salehi A. 2019. Growth and nutrient content of Echinacea purpurea as affected by the combination of phosphorus with arbuscular mycorrhizal fungus and Pseudomonas fluorescens under different irrigation regimes. J Environ Manage. 231: 182–188. https://doi.org/10.1016/j.jenvman.2018.10.040

Bajeli J, Tripathi S, Kumar A, Tripathi A, Upadhyay RK. 2016. Organic manures a convincing source for quality production of Japanese mint (*Mentha arvensis* L.). Ind Crops Prod. 83: 603–606. https://doi.org/10.1016/j.indcrop.2015.12.064

Benami A, Ofen A. 1984. Irrigation engineering: sprinkler, trickle, surface irrigation; principles, design and agricultural practices. Second edition. Irrigation Engineering Scientific Publications.

Bujnovský R, Holíčková M, Ondrejíčková P. 2020a. Spring *Camelina sativa* – Perspective cultivation as biofuel feedstock in Slovakia. Ind Crops Prod. 154: 112634. https://doi.org/10.1016/j.indcrop.2020.112634

Cakmak I. 2005. The role of potassium in alleviating detrimental effects of abiotic stresses in plants. J Plant Nutr Soil Sci. 168: 521–530. https://doi.org/10.1002/jpln.200420485

Cassel DK, Nielsen DR. 1986. Field capacity and available water capacity. In: Klute A (ed). Methods of Soil Analysis. Part 1 Physical and Mineralogical Methods. Agronomy Monograph No 9. Madison: Soil Science Society of America, pp. 901–926.

Chaparro-Giraldo A, Barata RM, Chabregas SM, Azevedo RA, Silva-Filho MC. 2000. Soybean leghemoglobin targeted to potato chloroplasts influences growth and development of transgenic plants. Plant Cell Rep. 19: 961–965. https://doi.org/10.1007/s002990000254

Daneshnia F, Amini A, Chaichi MR. 2015. Surfactant effect on forage yield and water use efficiency for berseem clover and basil in intercropping and limited irrigation treatments. Agric Water Manag. 160: 57–63. https://doi.org/10.1016/j.agwat.2015.06.024

Daoud B, Pawelzik E, Naumann M. 2020. Different potassium fertilization levels influence water-use efficiency, yield, and fruit quality attributes of cocktail tomato- a comparative study of deficient-to-excessive supply. Sci Hortic. 272: 109562. https://doi.org/10.1016/j.scienta.2020.109562

Darakeh SASS, Weisany W, Diyanat M, Ebrahimi R. 2021. Bio-organic fertilizers induce biochemical changes and affect seed oil fatty acids composition in black cumin (*Nigella sativa* Linn). Ind Crops Prod. 164: 113383. https://doi.org/10.1016/j.indcrop.2021.113383

Diaz RJ, Rosenberg R. 2008. Spreading dead zones and consequences for marine ecosystems. Science. 321: 926–929. https://doi.org/10.1126/science.1156401

Doorenbos J, Pruitt WD. 1977. Guidelines for predicting crop water requirements. FAO Irrigation and Drainage Paper No. 24 (revised). FAO, Rome, Italy.

du Preez DR, Bate GC. 1989. A simple method for the quantitative recovery of nitrate-N during Kjeldahl analysis of dry soil and plant samples. Commun Soil Sci Plant Anal. 20: 345–357. https://doi.org/10.1080/00103628909368087

Gesch RW, Cermak SC. 2011. Sowing date and tillage effects on fall-seeded camelina in the northern corn belt. Agron J. 103: 980–987. https://doi.org/10.2134/agronj2010.0485

Ghazian Tafrihi S, Ayenehband A, Tavakoli H, Khavari Khorasani S, Joleini M. 2013. Impacts of drought stress and planting methods on sweet corn yield and water use efficiency. J Plant Physiol Breed. 3(2): 23–31.

Giannopolitis CN, Ries SK. 1977. Superoxide dismutases. Plant Physiol. 59: 309–314. https://doi.org/10.1104/pp.59.2.309

Hafez M, Popov AI, Rashad M. 2021. Integrated use of bio-organic fertilizers for enhancing soil fertility–plant nutrition, germination status and initial growth of corn (*Zea mays* L.). Environ Technol Innov. 21: 101329. https://doi.org/10.1016/j.eti.2020.101329

Hänsch R, Mendel RR. 2009. Physiological functions of mineral micronutrients (Cu, Zn, Mn, Fe, Ni, Mo, B, Cl). Curr Opin Plant Biol. 12: 259–266. https://doi.org/10.1016/j.pbi.2009.05.006

Jahanzad E, Jorat M, Moghadam H, Sadeghpour A, Chaichi MR, Dashtaki M. 2013. Response of a new and a commonly grown forage sorghum cultivar to limited irrigation and planting density. Agric Water Manag. 117: 62–69. https://doi.org/10.1016/j.agwat.2012.11.001

Janmohammadi M, Sufi-Mahmoudi Z, Ahadnezhad A, Yousefzadeh S, Sabaghnia N. 2014. Influence of chemical and organic fertilizer on growth, yield and essential oil of dragonhead (*Dracocephalum moldavica* L.) plant. Acta Agric Slov. 103(1): 73–81. https://doi.org/10.14720/aas.2014.103.1.08

Kar M, Mishra D. 1976. Catalase, peroxidase, and polyphenol oxidase activities during rice leaf senescence. Plant Physiol. 57(2): 315–319. https://doi.org/10.1104/pp.57.2.315

Khajeeyan R, Salehi A, Movahhedi Dehnavi M, Farajee H, Kohanmoo MA. 2019. Physiological and yield responses of *Aloe vera* plant to biofertilizers under different irrigation regimes. Agric Water Manag. 225: 105768. https://doi.org/10.1016/j.agwat.2019.105768

Khalilzadeh R, Seyed Sharifi R, Jalilian J. 2016. Antioxidant status and physiological responses of wheat (*Triticum aestivum* L.) to cycocel application and bio fertilizers under water limitation condition. J Plant Interact. 11: https://doi.org/10.1080/17429145.2016.1221150

Kjeldahl J. 1883. Neue Methode zur Bestimmung des Stickstoffs in organischen Körpern. Fresenius Z Anal Chem. 22: 366–382. https://doi.org/10.1007/BF01338151

Klute A. 1986. Methods of soil analysis. Part 1: Physical and mineralogical methods. 2nd Edition, Madison, USA: American Society of Agronomy and Soil Science Society of America.

Lal B, Sharma SC, Meena RL, Sarkar S, Sahoo A, Balai RC, Gautam P, Meena BP. 2020. Utilization of byproducts of sheep farming as organic fertilizer for improving soil health and productivity of barley forage. J Environ Manage. 269: 110765. https://doi.org/10.1016/j.jenvman.2020.110765

Latt YK, Myint AK, Yamakawa T, Ogata K. 2009. The effects of green manure (*Sesbania rostrata*) on the growth and yield of rice. J Fac Agric Kyushu Univ. 54(2): 313–319. https://doi.org/10.5109/16109

Li J, Yang Q, Shi Z, Zang Z, Liu X. 2021. Effects of deficit irrigation and organic fertilizer on yield, saponin and disease incidence in *Panax notoginseng* under shaded conditions. Agric Water Manag. 256: 107056. https://doi.org/10.1016/j.agwat.2021.107056

Lindsay WL, Norvell WA. 1978. Development of a DTPA soil test for zinc, iron, manganese, and copper. Soil Sci Soc Am J. 42(3): 421–428. https://doi.org/10.2136/sssaj1978.03615995004200030009x

Liu K, Zhang TQ, Tan CS, Astatkie T. 2011. Responses of fruit yield and quality of processing tomato to drip-irrigation and fertilizers phosphorus and potassium. Agron J. 103: 1339–1345. https://doi.org/10.2134/agronj2011.0111

Lucy M, Reed E, Glick BR. 2004. Applications of free-living plant growth-promoting rhizobacteria. Antonie Van Leeuwenhoek. 86(1): 1–25. https://doi.org/10.1023/B:ANTO.0000024903.10757.6e

Martinelli T, Galasso I. 2011. Phenological growth stages of *Camelina sativa* according to the extended BBCH scale. Ann Appl Biol. 158: 87–94. https://doi.org/10.1111/j.1744-7348.2010.00444.x

McLean EO. 1983. Soil pH and lime requirement. In: Page AL (ed.) Methods of soil analysis part 2: chemical and microbiological properties. Second edition. 9: 199–224. Madison: ASA, CSSA, SSSA. https://doi.org/10.2134/agronmonogr9.2.2ed.c12

McLean EO, Watson ME. 1985. Soil measurements of plant-available potassium. In: Munson RD (ed.) Potassium in agriculture. Madison: ASA, CSSA, SSSA, pp. 277–308. https://doi.org/10.2134/1985.potassium.c10

Merajipoor M, Movahhedi Dehnavi M, Salehi A, Yadavi A. 2020. Improving grain yield, water and nitrogen use efficiency of *Nigella sativa* with biological and chemical nitrogen under different irrigation regimes. Sci Hortic. 260: 108869. https://doi.org/10.1016/j.scienta.2019.108869

Mohammadi M, Modarres-Sanavy SAM, Pirdashti H, Zand B, Tahmasebi-Sarvestani Z. 2019. Arbuscular mycorrhizae alleviate water deficit stress and improve antioxidant response, more than nitrogen fixing bacteria or chemical fertilizer in the evening primrose. Rhizosphere. 9: 76–89. https://doi.org/10.1016/j.rhisph.2018.11.008

Mohasseli V, Farbood F, Moradi A. 2020. Antioxidant defense and metabolic responses of lemon balm (*Melissa officinalis* L.) to Fe-nano-particles under reduced irrigation regimes. Ind Crops Prod. 149: 112338. https://doi.org/10.1016/j.indcrop.2020.112338

Mohtashami R, Movahhedi Dehnavi M, Balouchi H, Faraji H. 2020. Improving yield, oil content and water productivity of dryland canola by supplementary irrigation and selenium spraying. Agric Water Manag. 232: 106046. https://doi.org/10.1016/j.agwat.2020.106046

Nadeem SM, Imran M, Naveed M, Khan MY, Ahmad M, Zahir ZA, Crowley DE. 2017. Synergistic use of biochar, compost and plant growth-promoting rhizobacteria for enhancing cucumber growth under water deficit conditions. J Sci Food Agric. 97(15): 5139–5145. https://doi.org/10.1002/jsfa.8393

Najm AA, Hadi HSMR, Fazeli F, Darzi MT, Rahi A. 2012. Effect of integrated management of nitrogen fertilizer and cattle manure on the leaf chlorophyll, yield, and tuber glycoalkaloids of agria potato. Commun Soil Sci Plant Anal. 43: 912–923. https://doi.org/10.1080/00103624.2012.653027

Negi YK, Sajwan P, Uniyal S, Mishra AC. 2021. Enhancement in yield and nutritive qualities of strawberry fruits by the application of organic manures and biofertilizers. Sci Hortic. 283: 110038. https://doi.org/10.1016/j.scienta.2021.110038

Ning Cd, Gao PD, Wang BQ, Lin WP, Jiang NH, Cai KZ. 2017. Impacts of chemical fertilizer reduction and organic amendments supplementation on soil nutrient, enzyme activity and heavy metal content. J Integr Agric. 16: 1819–1831. https://doi.org/10.1016/S2095-3119(16)61476-4

Olsen SR, Cole CV, Watanabe FS. 1954. Estimation of available phosphorus in soils by extraction with sodium bicarbonate. Washington DC: USDA Circular No. 939, US Government Printing Office.

Pourya M, Shakarami J, Mardani-Talaee M, Sadeghi A, Serrão JE. 2021. Bio-fertilizers and micronutrients affect the digestibility, detoxification, and intermediary metabolisms of English grain aphid, *Sitobion avenae*, in greenhouse. J Asia Pac Entomol. 24(3): 704–710. https://doi.org/10.1016/j.aspen.2021.06.003

Rahil MH, Qanadillo A. 2015. Effects of different irrigation regimes on yield and water use efficiency of cucumber crop. Agric Water Manag. 148: 10–15. https://doi.org/10.1016/j.agwat.2014.09.005

Richards LA. 1941. A pressure-membrane extraction apparatus for soil solution. Soil Sci. 51: 377-386. https://doi.org/10.1097/00010694-194105000-00005

Sheshbahreh MJ, Movahhedi Dehnavi M, Salehi A, Bahreininejad B. 2019. Effect of irrigation regimes and nitrogen sources on biomass production, water and nitrogen use efficiency and nutrients uptake in coneflower (*Echinacea purpurea* L.). Agric Water Manag. 213: 358–367. https://doi.org/10.1016/j.agwat.2018.10.011

Singh S, Sinha S. 2005. Accumulation of metals and its effects in *Brassica juncea* (L.) Czern. (cv. Rohini) grown on various amendments of tannery waste. Ecotoxicol Environ Saf. 62(1): 118–127.

Sintim HY, Zheljazkov VD, Obour AK, Garcia y Garcia A, Foulke TK. 2015. Influence of nitrogen and sulfur application on camelina performance under dryland conditions. Ind Crops Prod. 70: 253–259. https://doi.org/10.1016/j.indcrop.2015.03.062

Smil V. 1999. Nitrogen in crop production: an account of global flows. Global Biogeochem Cycles. 13: 647–662. https://doi.org/10.1029/1999GB900015

Smith JL, Doran JW. 1996. Measurement and use of pH and electrical conductivity for soil quality analysis. In: Doran JW, Jones AJ (eds.) Methods for assessing soil quality. Madison: SSSA Special Publication No 49, pp. 169-185 .https://doi.org/10.2136/sssaspecpub49.c10

Sonntag F, Naumann M, Pawelzik E, Smit I. 2019. Improvement of cocktail tomato yield and consumer-oriented quality traits by potassium fertilization is driven by the cultivar. J Sci Food Agric. 99(7): 3350–3358. https://doi.org/10.1002/jsfa.9552

Srivastava AK, Mboh CM, Gaiser T, Kuhn A, Ermias E, Ewert F. 2019. Effect of mineral fertilizer on rain water and radiation use efficiencies for maize yield and stover biomass productivity in Ethiopia. Agric Syst. 168: 88–100. https://doi.org/10.1016/j.agsy.2018.10.010

Stolarski MJ, Krzyżaniak M, Tworkowski J, Załuski D, Kwiatkowski J, Szczukowski S. 2019. Camelina and crambe production-energy efficiency indices depending on nitrogen fertilizer application. Ind Crops Prod. 137: 386–395. https://doi.org/10.1016/j.indcrop.2019.05.047

Temminghoff E, Houba VJG. 2004. Plant analysis procedures. Dordrecht Netherlands: Springer. https://doi.org/10.1007/978-1-4020-2976-9

Tsaknis J, Spiliotis V, Lalas S, Gergis V, Dourtoglou V. 1999. Quality changes of *Moringa oleífera*, variety Mbololo of Kenya, seed oil during frying. Grasas y Aceites. 50(1): 37–48. https://doi.org/10.3989/gya.1999.v50.i1.634

Walkley A, Black IA. 1934. An examination of the degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. Soil Sci. 37: 29–38. https://doi.org/10.1097/00010694-193401000-00003

Wang S, Guo P, Li X, Wu M, Overmyer K, Liu S, Cui F. 2020. Altered redox processes, defense responses, and flowering time are associated with survival of the temperate Camelina sativa under subtropical conditions. Environ Exp Bot. 177: 104132. https://doi.org/10.1016/j.envexpbot.2020.104132

Wiwart M, Kurasiak-Popowska D, Suchowilska E, Wachowska U, Stuper-Szablewska K. 2019. Variation in the morphometric parameters of seeds of spring and winter genotypes of *Camelina sativa* (L.) Crantz. Ind Crops Prod. 139: 111571. https://doi.org/10.1016/j.indcrop.2019.111571

Wolf B. 1982. A comprehensive system of leaf analyses and its use for diagnosing crop nutrient status. Commun Soil Sci Plant Anal. 13: 1035–1059. https://doi.org/10.1080/00103628209367332

Zahedyan A, Aboutalebi Jahromi Jahromi A, Zakerin A, Abdossi V, Mohammadi Torkashvand A. 2022. Nitroxin bio-fertilizer improves growth parameters, physiological and biochemical attributes of cantaloupe (*Cucumis melo* L.) under water stress conditions. J Saudi Soc Agric Sci. 21(1): 8–20. https://doi.org/10.1016/j.jssas.2021.06.017

Zare Hoseini R, Mohammadi Goltapeh E, Modarres-Sanavy SAM, Heidarzadeh A. 2021. Effect of the bio-fertilizers on the steviol glycosides (SGs) content and biomass in *Stevia rebaudiana* (Bert.) Bertoni at vegetative and flowering stages. Sci Hortic. 275: 109658. https://doi.org/10.1016/j.scienta.2020.109658

Zhaoxiang W, Huihu L, Qiaoli L, Changyan Y, Faxin Y. 2020. Application of bio-organic fertilizer, not biochar, in degraded red soil improves soil nutrients and plant growth. Rhizosphere. 16: 100264. https://doi.org/10.1016/j.rhisph.2020.100264

Zheng J, Han J, Liu Z, Xia W, Zhang X, Li L, Liu X, Bian R, Cheng K, Zheng J, *et al.* 2017. Biochar compound fertilizer increases nitrogen productivity and economic benefits but decreases carbon emission of maize production. Agric Ecosyst Environ. 241: 70–78. https://doi.org/10.1016/j.agee.2017.02.034