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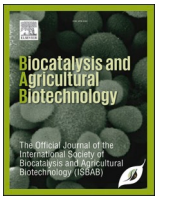

Optimizing camelina performance under drought conditions through the combined action of nanochitosan-encapsulated rosemary oil and arbuscular mycorrhizal fungi

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ABSTRACT

Camelina is recognized for its high oil content and richness in α-linolenic acid, a key precursor for omega-3 fatty acid biosynthesis; however, it is increasingly affected by drought stress associated with climate change. This study evaluated the effects of rosemary essential oil encapsulated in nanochitosan (NPs), applied individually or combined with arbuscular mycorrhizal fungi (AMF), on growth, physiological traits, antioxidant defense, and oil yield and composition of camelina under different irrigation regimes. A two-year field experiment was conducted using a split-plot design based on a randomized complete block with three replications. The main plots included full irrigation throughout the growing season (IR1), limited irrigation from flowering (IR2), and limited irrigation from pod formation (IR3). Subplots comprised no treatment, foliar application of NPs, AMF inoculation, and the combined use of NPs and AMF. Drought stress, particularly when initiated from flowering, markedly impaired photosynthetic pigments, nutrient assimilation, relative water content, seed yield, oil-related traits, and the extent of mycorrhizal colonization. In contrast, the combined application of NPs and AMF, compared to no treatment and individual applications, significantly improved seed and oil yield alongside enhanced chlorophyll fluorescence, nutrient availability, accumulation of antioxidant metabolites including phenolics, flavonoids, ascorbic acid, proline, soluble sugars, and tocopherols. It also increased mycorrhizal colonization, stimulated enzymatic antioxidant defenses, and reduced oxidative stress markers such as malondialdehyde and hydrogen peroxide. Additionally, the oil profile improved through an increased proportion of unsaturated fatty acids accompanied by a decrease in saturated fatty acids. Overall, the results suggest that the co-application of nanochitosan-encapsulated rosemary

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essential oil and AMF may offer a sustainable and potentially effective strategy to enhance drought tolerance and improve seed and oil quality in camelina under water-limited conditions.

1. Introduction

Climate change, reduced rainfall, and rising temperatures have intensified environmental pressures that threaten food security by reducing agricultural productivity (Tabassum et al., 2024; Ullah et al., 2024). Among these stressors, drought is one of the most significant, increasingly constraining plant growth and development (Hamedani et al., 2022; Mabudi Bilasvar et al., 2022). It negatively impacts all aspects of plant physiology by disrupting biochemical and physiological processes, leading to excessive production of reactive oxygen species (ROS) and triggering oxidative stress (Alsherif et al., 2023; Haghaninia et al., 2025b). This oxidative stress causes photoinhibition, degradation of biomacromolecules, lipid peroxidation of membranes, and damage to DNA and proteins (Sharma et al., 2024).

In response to harsh environmental conditions, plants activate defense mechanisms involving enzymatic and non-enzymatic antioxidants (Sayed et al., 2024). Although these systems mitigate oxidative damage, research indicates that they are insufficient to fully protect plants from prolonged and severe stress (Shehzad et al., 2020; Sutulienė et al., 2021). Therefore, effective nutrient management in arid and semi-arid regions is essential for alleviating environmental stress, particularly drought (Ayyaz et al., 2022; Li et al., 2021). However, drought conditions significantly impair nutrient uptake efficiency, especially in regions that depend on chemical fertilizers to maximize crop yields (Haghaninia et al., 2024). Moreover, the extensive use of chemical fertilizers can degrade environmental quality, reduce crop yield quality, promote weed proliferation, and increase pests and diseases susceptibility, highlighting the need for sustainable and alternative management strategies (Begum et al., 2022; Sutulienė et al., 2021).

In recent years, nanoparticles have emerged as an advanced technology in agriculture due to their unique physical and chemical properties, including nanoscale size, high surface-to-volume ratio, and active mobility (Alsherif et al., 2023; Ghiyasi et al., 2023). Among them, chitosan nanoparticles, biocompatible and biodegradable materials derived from natural polysaccharides, have garnered significant attention (Giglou et al., 2022). These nanoparticles, primarily obtained from natural sources such as crustacean shells and fungi, have extensive applications in both agriculture and pharmaceuticals (Fregonezi et al., 2024; Shehzad et al., 2020). Notably, under stress conditions such as drought and salinity, chitosan nanoparticles have demonstrated significant potential in mitigating stress-induced damage and enhancing plant performance (Tabassum et al., 2024). Research indicates that they activate stress-defense enzymes and reduce oxidative damage caused by reactive oxygen species (ROS), thereby alleviating the detrimental effects of environmental stressors (Alenazi et al., 2024; Hassan et al., 2021; Tabassum et al., 2024). Furthermore, chitosan nanoparticles enhance water and nutrient uptake in plants, which is particularly critical under conditions of water scarcity and drought stress (Attaran Dowom et al., 2022; do Carmo et al., 2021).

Chitosan nanoparticles are also recognized as efficient carriers for various bioactive compounds, including plant essential oils (Arabpoor et al., 2021; Sotelo-Boyás et al., 2017). Essential oils, known for their antioxidant, antimicrobial, and anti-inflammatory properties, can assist plants mitigate environmental stresses (Hassan et al., 2021; Roshan et al., 2022; Sindhu et al., 2023). However, a major limitation of essential oils is their instability under environmental conditions, which reduces their effectiveness (Taban et al., 2020). Encapsulation within chitosan nanoparticles has been proposed as an innovative strategy of essential oils while enabling their controlled release (Plati and Paraskevopoulou, 2022; Taban et al., 2020). This approach, not only improves the environmental stability of essential oils, but also enhances nutrient uptake and strengthens plant tolerance to abiotic stresses (Hassan et al., 2021; Upadhyay et al., 2021). The findings of Giglou et al. (2022) have demonstrated that using chitosan nanoparticles as encapsulation carriers significantly enhances plant resistance to drought stress.

The use of biological agents in sustainable agricultural systems enhances crop performance, quality, and stability while preserving environmental health (Gupta et al., 2021). Among these biological agents, arbuscular mycorrhizal fungi (AMF) play a crucial role in supporting plant growth under both normal and stressful conditions (Afshari et al., 2022). AMF improve plant water and nutrient uptake, produce growth-promoting hormones, modify root morphology and architecture, contribute to osmotic balance and turgor pressure maintenance, and solubilize insoluble and fixed phosphate, ultimately enhancing photosynthesis and increasing plant growth and productivity (Igiehon et al., 2021; Mathur et al., 2019; Mohammadi et al., 2022; Ye et al., 2022). The extraradical mycelium of AMF extends into the surrounding soil, forming an extensive absorption network that supplements the plant root system (Nahuelcura et al., 2022). This network allows plants to exploit a larger soil volume than their roots alone could access, improving acquisition and overall plant resilience (Begum et al., 2022; Pavithra and Yapa, 2018).

Oilseeds are a crucial source of calories and energy for human needs, and their global demand is continuously increasing worldwide (Haghaninia et al., 2024). Camelina [*Camelina sativa* (L.) Crantz], a member of the *Brassicaceae* family, is native to the Mediterranean regions of Asia and Europe (Mondor and Hernández-Álvarez, 2022; Sydor et al., 2022). It is also commonly referred to as false flax, wild flax, and German sesame (Veljković et al., 2022). Compared to other oilseed crops, particularly rapeseed, camelina requires lower inputs of water, fertilizers, and pesticides (Drabińska et al., 2024). Additionally, it has a short life cycle of 80–100 days, the ability to alternate with small-seeded grains, simple cultivation requirements, and high tolerance to adverse growing conditions, making it an attractive option for farmers (Ghidoli et al., 2023; Veljković et al., 2022). Camelina seeds are a rich source of oil (29–40 %) characterized by a high content of polyunsaturated fatty acids (PUFAs), low levels of toxic erucic acid, and significant amounts of antioxidants, particularly vitamin E (Amiri-Darban et al., 2020; Mondor et al., 2022; Sainger et al., 2017).

The inefficiency of chemical fertilizers under drought stress, along with their negative environmental impacts, underscores the

need for sustainable alternatives. Nanotechnology and beneficial microorganisms have emerged as promising strategies for enhancing plant resilience under such conditions. However, the potential of rosemary (*Rosmarinus officinalis*) essential oil encapsulated in chitosan nanoparticles, whether applied alone or in combination with AMF inoculation, in mitigating drought stress in camelina and improving oil yield and oil quality remains largely unexplored. This research represents a pioneering effort to investigate these innovative approaches, thereby contributing to the advancement of knowledge in the field. The study hypothesizes that the combined application of foliar-sprayed rosemary essential oil encapsulated in chitosan nanoparticles and AMF inoculation may serve as a sustainable strategy to enhance both the overall performance and oil quality of camelina under drought conditions.

2. Materials and methods

2.1. Experimental site

The study was conducted over two cropping seasons (2022 and 2023) at the research farm of the Faculty of Agriculture, Maragheh University (Latitude 37°24′N, Longitude 46°16′E, and Altitude 1477 m a.s.l.), East Azerbaijan Province, Iran. The region has a semi-arid climate, characterized by cold winters and moderate temperatures. Detailed meteorological for the experimental site collected during the experimental growing seasons are provided in Table 1.

2.2. Experimental design and treatments

The field experiment was conducted over two consecutive growing seasons using a split-plot arrangement based on a randomized complete block design (RCBD) with three replications. The main plot factor consisted of three irrigation regimes: (i) full irrigation throughout the growing season (IR1), (ii) limited irrigation from flowering (BBCH 64; IR2), and (iii) limited irrigation from pod formation (BBCH 71; IR3). The subplot factor included four growth promoter treatments: (i) control (no application), (ii) foliar application of rosemary essential oil encapsulated in nanochitosan (NPs), (iii) inoculation with arbuscular mycorrhizal fungi (AMF), and (iv) a combined application of NPs and AMF (NPs + AMF). A combined analysis of variance (ANOVA) was performed across both years to assess the effects of treatments and their interactions.

2.3. Field preparation and crop management

The experimental site was initially plowed, followed by additional land preparation operations, including discing and leveling, before the plots were established. Soheil variety seeds were purchased from Shefa Bistun Kermanshah Company and sown manually. In the first year, camelina seed sowing was performed on 15th October, while in the second year, it was conducted on 20th October at a depth of 1–2 cm. The seeding rate was 7 kg per hectare, determined based on the thousand-seed weight. Each plot measured 6 m in length and contained 7 crop rows, with an inter-row spacing of 20 cm and an intra-row spacing of 5 cm. To minimize the potential effects of water movement and treatment interference, a buffer distance of 0.5 m was maintained between plots, and 2 m between blocks. Before applying drought stress treatments, uniform irrigation was carried out across all plots to ensure proper seedling establishment. Thinning was performed at the 4–6 leaf stage to achieve the target plant density. Weed management was conducted manually by hand weeding, no pesticides or herbicides were applied throughout the growing period.

2.4. Irrigation regimes

Irrigation was managed using a drip irrigation system with drip laterals spaced 0.2 m apart and emitters positioned every 0.05 m. To ensure uniform water distribution, emitter pressure was maintained at 1 bar, with a flow rate of 4 L per hour, regulated through control valves and pressure gauges for each irrigation zone. The volume of water applied in each irrigation event was measured using an independent flow meter (Desoky et al., 2021). Three irrigation regimes were implemented: IR1: full irrigation throughout the growing season; IR2: deficit irrigation starting from the flowering stage (BBCH: 64); IR3: deficit irrigation starting from the pod formation stage (BBCH: 71). Irrigation scheduling was based on potential crop evapotranspiration (ETc), calculated using the crop coefficient method (Allen et al., 1998). Since FAO-56 guidelines do not provide specific crop coefficients for the study area, adjustments were made to reflect local conditions. Potential evaporation and transpiration were estimated using the Penman-Monteith method. ETc was determined using the following equation:

$$ETc = ETo \times Kc,$$

Where ETc represents potential crop evapotranspiration, ETo is the daily reference evapotranspiration, and Kc is the crop coefficient.

Meteorological data, including minimum and maximum temperatures, dew point, and wind speed, were obtained from the nearest weather station to calculate ETo. The Kc values for camelina, as recommended by FAO-56, were adjusted based on the local climatic conditions, particularly wind speed and relative humidity. Irrigation was stopped two weeks before camelina harvest.

Table 1
Soil characteristics in the 0–30 cm layer prior to camelina planting at the study site.

Soil texture	Sand (%)	Silt (%)	Clay (%)	Organic matter (%)	EC ($ds \cdot m^{-1}$)	pH	Field capacity (%)	Permanent Wilting point (%)	Exchangeable potassium ($mg \cdot kg^{-1}$)	Cation exchange capacity ($mg \cdot kg^{-1}$)	Available phosphorus ($mg \cdot kg^{-1}$)	Total nitrogen ($g \cdot kg^{-1}$)
sandy clay loam	53	17	30	0.8	1.12	6.8	27.1	12.4	551.35	26.3	8.2	0.75

2.5. Growth promoting agents

2.5.1. Chitosan nanoparticles and characterization

In this study, both neat chitosan nanoparticles and rosemary essential oil-loaded chitosan nanoparticles were prepared following a procedure similar to our previous work on the synthesis of neat and active ingredient-loaded chitosan nanoparticles (Haghaninia et al., 2024; Jafari et al., 2021). Briefly, a 0.1 wt% chitosan solution was prepared by dissolving 1 g of chitosan powder in 1000 mL of distilled water. To facilitate dissolution, 2 mL of acetic acid was added. The solution was vigorously stirred at 2000 rpm using a mechanical stirrer until a clear chitosan solution was obtained. Subsequently, a TPP solution (0.8 g in 10 mL of distilled water) was slowly added while maintaining vigorous stirring (2000 rpm), leading to the formation of chitosan nanoparticles, indicated by a cloudy appearance. The resulting nanoparticle solution was stored at ambient temperature in a sealed bottle. The preparation of rosemary-loaded chitosan nanoparticles followed a similar procedure with slight modifications. A 0.2 wt% chitosan solution (2 L) was prepared, and 5 mL of Tween 80 was added as an emulsifier. Once a clear and homogeneous solution was obtained, 2 mL of rosemary essential oil was introduced and allowed to disperse completely. The TPP solution (0.8 g in 10 mL of distilled water) was then added to induce nanoparticle formation. The rosemary-loaded nanoparticles were stored in a sealed container at ambient temperature. It is important to note that the prepared solutions contained 1000 ppm of chitosan nanoparticles, based on the chitosan content in 1000 mL of water. Solutions with a concentration of 500 ppm were prepared by dilution.

The nanoparticle (NP) solution was prepared at a final concentration of 500 ppm. This concentration was selected for the main experiment based on its demonstrated effectiveness in enhancing plant growth and stress tolerance during preliminary tests. In these initial tests, we assessed a range of concentrations (0, 250, 500, and 1000 ppm), and 500 ppm was chosen for further investigation as it produced the most favorable results. Focusing on a single concentration minimized experimental variability and allowed for a precise assessment of the treatment's effects, particularly in interaction with mycorrhizal fungi, a key objective of this study. Foliar spraying was performed at three critical growth stages: pre-flowering, full flowering, and pod formation. This strategic timing was intended to optimize the impact of nanoparticles during key developmental phases. The foliar application was conducted in the early morning to minimize evaporation losses and maximize absorption. A hand-held sprayer was used to ensure uniform coverage of plant leaves, with the solution applied to both the upper and lower leaf surfaces until runoff was observed.

Rosemary-loaded chitosan nanoparticles characterization was done using TEM (Philips CM10), Scanning Electron Microscopy (SEM, MIRA 3, TESCAN), and Dynamic Light Scattering (DLS, Zetasizer Nano ZS90). The DLS analysis (Fig. 1a) revealed an average nanoparticle diameter of approximately 185 nm, while TEM imaging (Fig. 1b) showed spherical nanoparticles with an average diameter of 165 nm. The increase in size compared to neat chitosan nanoparticles may be attributed to the incorporation of rosemary essential oil during nanoparticle formation, leading to larger structures. Similar findings were reported by Sotelo-Boyás et al. (2017) for thyme essential oil-loaded chitosan nanoparticles, which also exhibited increased size after essential oil loading. The discrepancy between the diameters obtained by DLS and TEM may result from nanoparticle interactions in the solution, as DLS measures the hydrodynamic diameter, which includes the solvation layer. SEM analysis (Fig. 1c) confirmed the spherical morphology of the rosemary-loaded chitosan nanoparticles. The observed nanoparticle aggregation in the SEM image is likely due to interactions

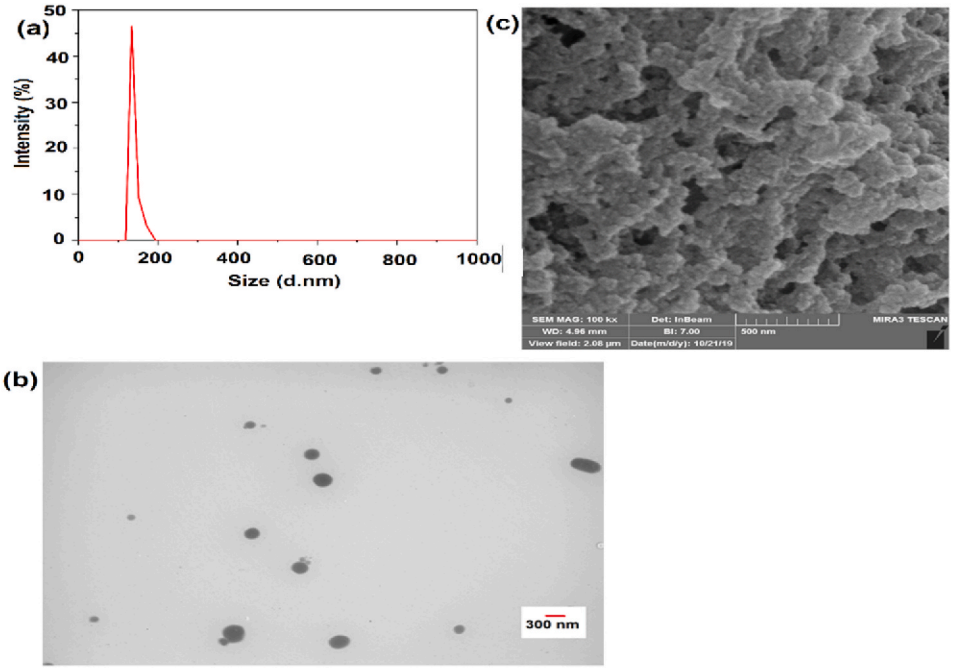

Fig. 1. (a) DLS, (b) TEM, and (c) SEM of rosemary loaded chitosan nanoparticles.

occurring during the drying process.

2.5.2. Arbuscular mycorrhiza Fungus

The arbuscular mycorrhizal fungi (AMF) utilized in this study were supplied by Zist Fanavar Pishtaz Varian Company (Iran) under the commercial name Mycoroot. The inoculum comprised a mixture of 3 a.m. fungal species; *Funneliformis mosseae*, *Claroideoglomus etunicatum*, and *Rhizophagus irregularis*. Each gram of the inoculum contained approximately 100 a.m. spores, including 35 viable spores of F. *mosseae*, 35 viable spores of R. *irregularis*, and 30 viable spores of C. *etunicatum*. The inoculum was applied at a rate of 130 kg ha^{-1} beneath the seedbed immediately after establishing the crop rows and was then covered with soil. The application rate followed the manufacturer's guidelines.

2.6. AMF root colonization

To assess mycorrhizal root colonization, camelina root samples were randomly selected and thoroughly rinsed to remove soil residues (Fig. S1). The cleaned root fragments were cleared by heating in a 10 % potassium hydroxide (KOH) solution for 15 min. The samples were then washed three times with distilled water and acidified with 2 % hydrochloric acid (HCl) for 20 min. Subsequently, the roots were stained by heating in a 0.05 % trypan blue solution for 10 min following the method proposed by Phillips and Hayman (1970). Mycorrhizal colonization was evaluated using the procedure described by Giovannetti and Mosse (1980). The stained roots were sectioned into 1 cm fragments, randomly arranged on a Petri dish, and examined under a microscope at 40 × magnification. A 1 × 1 cm grid plate measuring was placed beneath the Petri dish to facilitate counting. The number of infected and non-infected root segments intersecting the grid's vertical and horizontal lines was recorded. Mycorrhizal colonization was determined by dividing the number of infected root pieces by the total number of root pieces and multiplying by 100 (Fig. S1).

2.7. Soil sampling and analysis

Before initiating the experiment, soil samples were collected from the field at a depth of 0–30 cm and transported to the laboratory for physicl and chemical analysis. The results indicated that the soil had sandy-clay-loam texture, an electrical conductivity of 1.2 dS. m^{-1}, an organic matter content of 0.8 %, and a pH of 6.8. Additional soil properties are detailed in Table 2.

2.8. Observations, measurements, and data analysis

After drought stress treatments and foliar applications, leaves were harvested separately from each plot. The leaves were thoroughly washed with tap water to remove any contaminants, then immediately frozen in liquid nitrogen and stored at −20 °C to prevent enzymatic degradation until biochemical analysis.

2.8.1. Chlorophylls and carotenoids

Chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), and carotenoid (CARs) levels in camelina leaves were determined using a standardized method. Fresh leaf samples (0.5 g) were finely ground in liquid nitrogen and extracted with 10 mL of 80 % acetone. The extracts were centrifuged at 10,000 rpm for 10 min, and the absorbance of the supernatant was measured at 645 nm, 663 nm, and 470 nm using a UV-1800 spectrophotometer (Shimadzu, Japan). Photosynthetic pigment concentrations were calculated using the equations described by Armon (1949).

2.8.2. Measurement of chlorophyll fluorescence parameters

Chlorophyll fluorescence parameters were measured on fully expanded leaves of camelina plants using a PAM fluorometer (Effeltrich, Germany). Prior to measurement, plants were dark-adapted for 20 min to ensure full oxidation of PSII reaction centers. During this period, the minimal fluorescence yield (Fo) was recorded. Subsequently, a saturating light pulse was applied to determine the maximum fluorescence (Fm). The variable fluorescence (Fv) was calculated as the difference between Fm and Fo, and the maximum quantum efficiency of PSII (Fv/Fm) was determined as Fv divided by Fm. All fluorescence data were analyzed using

Table 2
Monthly averages of precipitation and temperature (minimum and maximum) during the growing seasons of the first and second experimental years.

	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
First growing season: 2021/2022												
Average rainfall (mm)	0.1	0.2	1.9	3.6	4.2	65.9	22.8	17.5	6.0	16.7	21.7	2.2
Minimum temperature (°C)	21.8	22.5	15.4	7.1	3.7	−0.9	−4.4	0.2	0.7	9.2	11.0	18.4
Maximum temperature (°C)	33.7	36.8	29.7	25.4	15.7	7.9	6.0	10.3	11.5	22.8	24.3	33.5
Second growing season: 2022/2023												
Average rainfall (mm)	0.1	0.1	2.3	11.6	19.5	4.2	29.5	8.0	27.4	24.4	30.6	0.4
Minimum temperature (°C)	20.3	19.9	14.3	6.8	4.7	0.6	−3.7	−2.9	5.8	7.3	11.6	17.2
Maximum temperature (°C)	32.8	35.6	27.8	22.3	16.0	8.9	4.7	7.6	17.3	20.1	25.2	31.5

PamWin-3 software (Walz GmbH, Germany).

2.8.3. Relative water content (RWC)

The relative water content of leaves was determined according to the method of Barrs and Weatherley (1962). Fresh leaf discs were weighed immediately to determine fresh weight (FW), then floated in distilled water in Petri dishes for 4 h under low light at room temperature to obtain the turgid weight (TW). After blotting the surface moisture, the samples were reweighed. Subsequently, the samples were oven-dried at 70 °C for 48 h to record the dry weight (DW). The RWC was calculated using the following formula:

$$RWC\ (\%) = [(FW - DW) / (TW - DW)] \times 100$$

2.8.4. Measurement of total phenolics content (TPC)

The total phenolic content was quantified using the Folin-Ciocalteu method, as described by Singleton and Rossi (1965). A 20 μL aliquot of plant extract (1 % acidic methanol solution) was mixed with 100 μL of 10 % Folin-Ciocalteu reagent and 1590 μL of distilled water. The mixture was incubated in the dark for 10 min. Subsequently, 2000 μL of 7.5 % sodium carbonate was added, and the solution was further incubated in darkness for 2 h. After incubation, absorbance was measured at 765 nm using a UV–VIS spectrophotometer.

2.8.5. Determination of total flavonoid content (TFC)

Total flavonoid content in fresh camelina leaf tissue was determined using the aluminum chloride colorimetric method (Chang et al., 2002).One gram of leaf tissue was ground in liquid nitrogen and extracted with 4 mL of 96 % ethanol. The extract was centrifuged, and 500 μL of the supernatant was mixed with 100 μL of 1 M potassium acetate and 100 μL of 10 % aluminum chloride. Then, 1500 μL of methanol and 2800 μL of distilled water were added. The mixture was incubated at 25 °C for 30 min. Adsorbance was measured at 415 nm using a spectrophotometer to quantify total flavonoid content.

2.8.6. Determination of ascorbic acid aontent

Ascorbic acid content in camelina leaves was determined according to the method described by Kampfenkel et al. (1995) with slight modifications. Fresh leaf tissue (0.2 g) was homogenized in 6 mL of 5 % (w/v) trichloroacetic acid (TCA) using a chilled mortar and pestle and centrifuged at 12,000 rpm for 15 min at 4 °C. The supernatant (1 mL) was mixed with 0.5 mL of 150 mM phosphate buffer (pH 7.4) and 0.5 mL of 0.5 % (w/v) bathophenanthroline, followed by 0.5 mL of 10 % (w/v) TCA and 0.2 mL of 0.03 % (w/v) $FeCl_3$. The mixture was incubated at 37 °C for 90 min, and the absorbance was measured at 534 nm using a UV–Vis spectrophotometer. Ascorbic acid content was calculated using a standard curve prepared with known concentrations of L-ascorbic acid and expressed as mg g^{-1} fresh weight (FW).

2.8.7. Measurement of proline content

To determine proline content, 0.25 g of leaf tissue was homogenized in 5 mL of 3 % (w/v) sulfosalicylic acid. The filtrate (2 mL) was mixed with 2 mL of ninhydrin reagent and incubated at 95 °C for 60 min. After cooling, 4 mL of toluene was added, and the chromophore was separated. The absorbance of the toluene phase was measured at 520 nm using a UV–Vis spectrophotometer. Proline content was calculated using a standard proline curve (Bates et al., 1973). For total soluble sugars, 0.3 g of leaf tissue was homogenized in 5 mL of 80 % ethanol and heated at 90 °C for 40 min. The mixture was centrifuged, and the supernatant volume was adjusted to 8 ml with ethanol. 0.5 mL of the supernatant was mixed with 1.5 mL of anthrone reagent and heated at 90 °C for 10 min. Absorbance was measured at 490 nm using a UV–Vis spectrophotometer. Total soluble sugar content was determined using a standard glucose curve (Yemm and Willis, 1954).

2.8.8. Measuring the percentage of tocopherols

The levels of α-, β-, and γ-tocopherols in camelina seed oil were quantified using high-performance liquid chromatography (HPLC). Initially, oil was extracted from the seeds using the Soxhlet method with n-hexane as the solvent. Following extraction, the oil samples were diluted at a ratio of 1:10 (v/v) with HPLC-grade n-hexane to reduce the viscosity and facilitate smooth injection. The diluted oil samples were then filtered through a 0.45 μm PTFE syringe filter to remove any particulate matter before analysis. For chromatographic analysis, 10 μL of the filtered, diluted oil sample was injected into a Kinetex C18 column (Phenomenex, 250 mm length × 4.6 mm internal diameter, 5 μm particle size, 100 Å pore size). The mobile phase consisted of 95 % methanol (HPLC grade), delivered isocratically at a flow rate of 1.5 mL/min. The column temperature was maintained at 25 °C. Tocopherols were detected using a Diode Array Detector (DAD) set at 280 nm. Quantification was carried out by comparing peak areas with those obtained from external standards of α-, β-, and γ-tocopherols. Final concentrations were expressed in ppm (Ebrahimi et al., 2025).

2.8.9. Measuring the activity of antioxidant enzymes

The activity of antioxidant enzymes was determined as follows: (i) ascorbate peroxidase (APX) activity was assessed using a reaction mixture containing 0.1 mM H_2O_2, 50 mM potassium phosphate buffer (pH 7), 0.5 mM ascorbic acid, and 0.1 mM EDTA. A 150 μL aliquot of enzyme extract was added to the reaction solution, and absorbance was measured at 290 nm. An extinction coefficient of 2.8 $mmol^{-1}$ cm^{-1} was used for calculations (Nakano and Asada, 1981). (ii) Superoxide dismutase (SOD) activity was measured based

on its ability to inhibit the photoreduction of nitroblue tetrazolium (NBT). The reaction mixture contained 3 mL of 50 mM phosphate buffer (pH 7.8), 13 mM methionine, 75 μL of NBT, 2 μM EDTA, and 50 μL of protein extract. The mixture was placed in microtubes and exposed to a 15 W fluorescent lamp at a 30 cm distance for 10 min while being shaken. A control sample without enzyme extract was included. Absorbance at 560 nm was measured using a spectrophotometer, and SOD activity was expressed in units per minute per milligram of protein (Dhindsa et al., 1981). (iii) Guaiacol peroxidase (GPX) activity was measured according to the method described by Upadhyaya et al. (1985). The enzymatic reaction was monitored at 470 nm using a UV–VIS spectrophotometer.

2.8.10. Malondialdehyde (MDA) content assessment

MDA content, an indicator of lipid peroxidation, was determined following the method described by Heath and Packer (1968). Fresh leaf samples (0.5 g) were homogenized with 1500 μL of 0.1 % trichloroacetic acid (TCA) in an ice bath. The homogenate was then centrifuged at 10,000 rpm for 4 min at 4 °C. A 0.5 mL aliquot of the supernatant was mixed with 1000 μL of 0.5 % thiobarbituric acid solution and heated at 95 °C for 95 min. After heating, the samples were rapidly cooled in an ice bath to halt the reaction. Absorbance was measured at 532 nm and 600 nm using a spectrophotometer.

2.8.11. Assessment of hydrogen peroxide content

Hydrogen Peroxide (H_2O_2) content was quantified based on its reaction with potassium iodide (KI). Fresh leaf tissue (0.5 g) was homogenized in 0.1 % TCA and the extract was centrifuged at 12,000 rpm for 15 min. A 500 μL aliquot of the supernatant was mixed with 500 μL of 100 mM potassium phosphate buffer (pH 7) and 2 mL of 1 M potassium iodide. The reaction mixture was incubated in the dark at room temperature for 1 h. Absorbance was then measured at 390 nm using a spectrophotometer, following the method described by Alexieva et al. (2001).

2.8.12. Mineral content

Phosphorus content was determined colorimetrically using molybdate vanadate yellow methods, with adsorbance at 470 nm (Tandon et al., 1968). Potassium content was analyzed using flame photometry (Jones, 1972), while nitrogen content was quantified via the Kjeldahl method.

Table 3
Interaction effects of irrigation regimes and growth-promoting agents on mycorrhizal colonization, photosynthetic pigments, chlorophyll fluorescence parameters, and relative water content in *Camelina sativa*.

Treatments		Colonization (%)	Chlorophyll *a* (mg g^{-1})	Chlorophyll *b* (mg g^{-1})	Carotenoids (mg g^{-1})	RWC (%)	F_O	F_m	F_v/F_m	F_v	F_o/F_v
IR1	C	4.8e	7.48c	5.45c	1.44h	75.53d	1.01ef	4.17de	0.756d	3.16e	1.34gh
	NPs	3.7e	7.65bc	5.64b	1.92gh	82.89c	0.975 fg	4.52c	0.784c	3.53c	1.24gh
	AMF	81.1a	7.77 ab	5.47bc	2.96 fg	86.48b	0.887h	4.67b	0.809b	3.78b	1.09ij
	NPs + AMF	79.2a	7.92a	6.03a	2.59g	90.81a	0.824i	5.02a	0.836a	4.19a	0.987j
IR2	C	2.3e	3.14j	3.39i	3.87ef	44.14k	1.29a	3.71h	0.652h	2.42i	1.99a
	NPs	2.6e	3.78i	4.97e	4.39de	58.97h	1.24 ab	3.79gh	0.671g	2.54hi	1.87 ab
	AMF	33.3d	3.89i	3.79h	4.77de	50.26j	1.22b	3.87 fg	0.684 fg	2.64gh	1.81bc
	NPs + AMF	40.8c	4.34h	4.53f	5.09cd	61.84gh	1.12d	4.14e	0.728e	3.01f	1.54de
IR3	C	3.3e	4.87g	4.15g	5.16cd	54.84i	1.17c	3.90 fg	0.698f	2.72g	1.68cd
	NPs	2.8e	5.88e	5.05de	5.91bc	66.55f	1.08d	3.99f	0.727e	2.91f	1.49ef
	AMF	58.6b	5.47f	5.17d	6.48 ab	64.96 fg	1.03e	4.23de	0.754d	3.19e	1.37 fg
	NPs + AMF	55.5b	6.16d	5.19d	7.11a	70.96e	0.956g	4.29d	0.776c	3.33d	1.22hi

Source of variation	Significance levels									
Year (Y)	ns	*	ns	ns	ns	ns	ns	ns	*	ns
Irrigation (IR)	**	**	**	*	**	**	*	*	**	*
Y × IR	ns	ns	ns	*	ns	ns	ns	*	ns	ns
Growth Promoting Agents (G)	**	**	*	**	**	**	**	*	**	**
IR × G	**	*	**	*	**	*	**	*	**	*
Y × G	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Y × IR × G	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

C: Control; NPs: rosemary essential oil coated with nanochitosan; AMF: arbuscular mycorrhizal fungi; NPs + AMF: rosemary essential oil coated with nanochitosan + arbuscular mycorrhizal fungi. IR1: full irrigation throughout the growing season; IR2: deficit irrigation starting from the flowering stage; IR3: deficit irrigation starting from the pod formation stage. Different letters indicate significant differences at the 5 % level according to the LSD test. Ns, * and ** indicated no significant difference, significant at 5 % probability level, and significant at 1 % probability level, respectively.

2.8.13. Agronomic traits measurements

Camelina seed yield was assessed at the physiological maturity stage (BBCH: 89), excluding marginal effects. A two-square-meter area was harvested from each plot and transported to the laboratory, where seeds were manually separated from the harvested plants.

2.8.14. Oil extraction and analysis

To determine the oil content of camelina seeds, seed samples from each treatment were separately ground. Oil extraction was performed on 5 g of the ground seed samples using a Soxhlet apparatus with hexane as a solvent. The extraction process lasted 11 h at 60 °C. The extracted oil content was expressed as a percentage of seed weight and stored at a 4 °C until further chemical analysis. Oil yield was calculated by multiplying grain yield by oil content and expressed in kilograms per hectare. Additionally, the fatty acid profile was analyzed using chromatography-mass spectrometry (GC-MS) and chromatography-flame ionization detection (GC-FID), following the methodology modified by Haghaninia et al. (2024).

2.9. Statistical analysis

The experiment was conducted using a split-plot design within a randomized complete block design (RCBD) framework, consisting of 12 treatments with three replications. Data were subjected to analysis of variance (ANOVA) using SAS software version 9.4 (SAS Institute, Cary, NC, USA). Prior to combined ANOVA, Hartley's Fmax test was employed to assess the homogeneity of variances. The test results confirmed variance homogeneity across years, permitting combined analysis. In the ANOVA model, irrigation levels and growth promoters were treated as fixed effects, while blocks and years were considered random effects. Mean comparisons were performed using the least significant difference (LSD) test at the 0.05 significance level. Graphical illustrations were prepared using Microsoft Excel.

3. Results

3.1. Arbuscular mycorrhizal fungi colonization

AMF colonization was significantly influenced by irrigation regimes, growth promoter treatments, and their interaction (Table 3). The highest root colonization percentage was observed under IR1 conditions with AMF application, while the lowest was recorded under IR2 conditions without growth promoters (Table 3). Arbuscular mycorrhizal fungi colonization exhibited a significant decline in response to irrigation restriction imposed at different reproductive stages, with a 57 % reduction under IR2 (deficit irrigation starting from the flowering stage) and a pronounced 31 % reduction under IR3 (deficit irrigation starting from the pod formation stage), as compared to full irrigation (IR1). The application of nanoparticles (NPs) in combination with AMF (NPs + AMF) enhanced AMF colonization across all irrigation conditions (Table 3). Under IR1, AMF application increased colonization by 33-fold compared to the no growth promoters condition in IR2. Notably, under IR2 conditions, NPs + AMF increased AMF colonization by 14-fold compared to no growth promoters and by 27 % compared to AMF alone (Table 3).

3.2. Photosynthetic pigments

Analysis of variance revealed significant effects of irrigation regimes, growth promoter treatments, and their interactions on chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), and carotenoid (CAR) content in camelina (Table 3). Notably, Chl *a* and Chl *b* levels declined with increasing drought stress, while carotenoid content increased under IR3 compared to normal irrigation (Table 3). The lowest levels of Chl *a* and Chl *b* were recorded under IR2 conditions without growth promoters, whereas the highest levels were observed under IR1 with the combined NPs + AMF treatment. Carotenoid content peaked under IR3 with the application of NPs + AMF (Table 3). Furthermore, under IR1, Chl *a* and Chl *b* contents increased by 103 % and 36 % compared to IR2, and by 90 % and 16 % compared to IR3, respectively. Similarly, carotenoid content was 35 % and 177 % higher under IR2 and IR3, respectively (Table 3). In addition, under IR1, the combined NPs + AMF treatment increased Chl *a* and Chl *b* contents by 153 % and 80 %, respectively, compared to IR2 conditions without growth promoters (Table 3).

3.3. Chlorophyll fluorescence

The analysis of variance (Table 3) revealed that chlorophyll fluorescence parameters (Fo, Fm, Fv/Fm, Fv, and Fo/Fv) in camelina were significantly influenced by irrigation regimes, growth-promoting agents, and their interaction. The highest values of Fo and Fo/Fv were recorded under IR2 without any growth stimulants, showing increases of 24 % and 63 %, respectively, compared to IR1 (Table 3). Conversely, the application of growth-promoting agents under IR1 reduced Fo and Fo/Fv by 24 % and 62 %, respectively. Furthermore, under IR2, the combined treatment of NPs + AMF decreased Fo and Fo/Fv by 13.17 % and 22.61 % relative to the untreated control (Table 3). In contrast, the maximum values of Fm, Fv/Fm, and Fv were observed under IR1 with the co-application of NPs and AMF. These values increased by 35.03 %, 27.22 %, and 73.17 %, respectively, compared to the untreated plants under IR2.

3.4. Relative water content

According to the analysis of variance (Table 3), irrigation regimes, growth-promoting agents, and their interaction significantly

affected the relative water content (RWC) in Camelina sativa. The highest RWC was observed under full irrigation conditions (IR1) combined with the application of both AMF and NPs, whereas the lowest value was recorded under deficit irrigation starting from the flowering stage (IR2) without any growth-promoting treatments (Table 3). Compared with IR1, RWC declined by 36.89 % and 23.35 % under IR2 and deficit irrigation starting from the pod formation stage (IR3), respectively. Nevertheless, the application of biostimulants led to notable improvements in RWC across all irrigation regimes, with the combined application of NPs and AMF being the most effective. Specifically, under IR1, the co-application of NPs + AMF enhanced RWC by 105.73 % relative to the untreated control under IR2 (Table 3). Moreover, compared to the separate application of AMF and NPs, the combined treatment improved RWC by 11.86 % and 8.81 %, respectively (Table 3).

3.5. Total phenolics and flavonoid content

The variance analysis (Table 4) revealed significant effects of irrigation regimes, growth promoter treatments, and their interactions on the total phenolic content (TPC) and total flavonoid content (TFC) in camelina plants. The highest levels of TPC and TFC were observed under IR3 conditions with the NPs + AMF treatment, while the lowest values occurred under IR1 conditions without any growth promoter application (Table 4). Comparing irrigation regimes, TPC under IR3 was, on average, 45 % higher than under IR1 and 18 % higher than under IR2. Similarly, TFC was 30 % and 14 % higher under IR3 compared to IR1 and IR2, respectively. Furthermore, the combined application of NPs + AMF under IR3 led to a substantial increase of 91 % in TPC and 67 % in TFC compared to IR1 without growth promoters. Additionally, NPs + AMF application resulted in significant increases of 34 % in TPC and 25 % in TFC compared to the control (Table 4).

3.6. Ascorbic acid content

The analysis of variance (Table 4) demonstrated that irrigation regimes, growth-promoting agents, and their interaction had significant effects on the ascorbic acid content in camelina sativa. The highest ascorbic acid concentration was observed under the combined application of NPs and AMF in the IR3, while the lowest content was found in the untreated control group (Table 4). Furthermore, ascorbic acid content increased by 38.5 % and 13.46 % under IR3 compared to IR1 and IR2, respectively. Notably, the combined treatment of NPs + AMF under IR3 enhanced ascorbic acid content by 67.38 % relative to the control. Moreover, NPs + AMF increased ascorbic acid levels by 6.3 % and 4.5 % compared to the sole application of AMF and NPs, respectively (Table 4). These findings underscore the positive synergistic effect of NPs and AMF on enhancing antioxidant capacity under water deficit conditions.

Table 4
Mean comparisons of the interactive effects of irrigation regimes and growth-promoting factors on phenolic compounds, flavonoids, ascorbic acid, tocopherols (α, β, and γ), proline, and total soluble sugar in *Camelina sativa*.

Treatments		Flavonoid (mg g^{-1})	Phenolic (mg g^{-1})	Ascorbic acid (mg g^{-1})	α-Tocopherol (ppm)	β-Tocopherol (ppm)	γ-Tocopherol (ppm)	Proline (μg g^{-1})	Total soluble sugar (mg g^{-1})
IR1	C	22.15j	40.47k	237.93j	14.41i	1.20i	722.69g	10.69j	23.02i
	NPs	26.72 fg	49.12i	293.21h	15.43gh	1.68h	749.28ef	13.64gh	28.07g
	AMF	25.29h	47.53j	269.84i	15.34h	1.57h	742.26f	12.10i	26.35h
	NPs + AMF	26.15gh	54.52g	275.78i	15.84g	1.94g	756.47e	13.04h	29.59 fg
IR2	C	23.79i	50.86h	310.38g	21.74c	2.29f	641.75k	17.45c	30.16f
	NPs	27.52ef	60.64e	324.26f	22.29b	2.86d	661.09j	18.44b	30.96ef
	AMF	32.27c	57.64f	316.59 fg	21.90bc	2.60e	670.02i	17.97bc	31.99e
	NPs + AMF	30.56d	66.97d	353.80d	22.91a	3.09cd	687.38h	19.38a	34.01d
IR3	C	28.54e	58.41f	336.37e	18.37f	2.57e	774.15d	14.29 fg	34.58cd
	NPs	33.95b	70.99c	365.62c	18.98e	3.35b	796.42b	15.02ef	38.05b
	AMF	31.14cd	72.02b	380.52b	19.56d	3.28bc	787.48c	15.50de	35.71c
	NPs + AMF	37.16a	77.34a	398.22a	19.38de	3.64a	811.04a	16.11d	43.02a

Source of variation	Significance levels							
Year (Y)	ns	*	ns	ns	ns	ns	ns	ns
Irrigation (IR)	*	**		*	**	*	**	**
Y × IR	ns	ns	ns	ns	ns	ns	ns	ns
Growth Promoting Agents (G)	*	**	**	**	**	**	**	*
IR × G	*	**	**	*	*	*	**	**
Y × G	ns	ns	ns	ns	ns	ns	ns	ns
Y × IR × G	ns	ns	ns	ns	ns	ns	ns	ns

C: Control; NPs: rosemary essential oil coated with nanochitosan; AMF: arbuscular mycorrhizal fungi; NPs + AMF: rosemary essential oil coated with nanochitosan + arbuscular mycorrhizal fungi. IR1: full irrigation throughout the growing season; IR2: deficit irrigation starting from the flowering stage; IR3: deficit irrigation starting from the pod formation stage. Different letters indicate significant differences at the 5 % level according to the LSD test. Ns, * and ** indicated no significant difference, significant at 5 % probability level, and significant at 1 % probability level, respectively.

3.7. Proline and total soluble sugars content

The data from the ANOVA (Table 4) demonstrated that both proline and total soluble sugar levels in camelina sativa were significantly modulated by the irrigation regimes, the application of biostimulants, and their interactive effects. Proline content reached its peak under IR2 when treated with the combination of NPs and AMF, whereas the greatest accumulation of total soluble sugars occurred under IR3 under the same combined treatment. The lowest levels for both parameters were consistently recorded in the untreated control plants (Table 4). Interestingly, the imposed water deficits independently triggered a marked rise in osmoprotectants, with proline increasing by 50.1 % under IR2 and soluble sugars by 39.4 % under IR3, both relative to IR1. Application of biostimulants further enhanced these traits. Under IR2, the use of NPs + AMF boosted proline by 81.3 % over the control, while in IR3, the same treatment enhanced soluble sugars by 87.8 % (Table 4). These findings suggest that the integrative application of NPs and AMF reinforces osmotic balance under limited irrigation through enhanced biosynthesis and accumulation of key compatible solutes.

3.8. Tocopherol content

According to the analysis of variance (Table 4), α-, β-, and γ-tocopherol contents were significantly influenced by irrigation regimes, growth-promoting agents, and their interaction. The highest α-tocopherol concentration was recorded under IR2 combined with the application of NPs + AMF, whereas the maximum levels of β- and γ-tocopherols were observed under IR3 with the same treatment. Conversely, the lowest γ-tocopherol content was detected in IR2 without growth stimulants, while the minimum α- and β-tocopherol values were found in the untreated control (Table 4). Notably, α-tocopherol under IR2 increased by 45.5 % and 16.4 % compared to IR1 and IR3, respectively. Similarly, β- and γ-tocopherol levels in IR3 were elevated by 100.9 % and 6.7 %, respectively, in comparison with IR1. The growth-promoting agents positively modulated tocopherol biosynthesis. Specifically, under IR2, the combined application of NPs + AMF led to a 58.8 % enhancement in α-tocopherol content relative to the control. Moreover, β- and γ-tocopherol concentrations under IR3 increased by 203.2 % and 12.4 %, respectively, following the application of NPs + AMF compared to the control (Table 4).

3.9. Antioxidant anzymes activity

The analysis of variance results (Table 5) revealed significant effects of irrigation regimes, growth promoter treatments, and their

Table 5
Mean comparisons of the interactive effects of irrigation regimes and growth-promoting factors on the activities of ascorbate peroxidase (APX), superoxide dismutase (SOD), guaiacol peroxidase (GPX), and the contents of hydrogen peroxide (H_2O_2) and malondialdehyde (MDA) in *Camelina sativa*.

Treatments		Ascorbate Peroxidase (μmol min^{-1} mg^{-1} protein)	Superoxide Dismutase (U g^{-1} FW)	Guaiacol Peroxidase (μmol min^{-1} mg^{-1} protein)	Hydrogen Peroxide (μmol.g^{-1} FW)	Malondialdehyde (mg. g^{-1} FW)
IR1	C	0.354j	3.09i	1.45i	2.04h	6.96fgh
	NPs	0.537gh	3.24hi	1.81h	2.01h	6.47gh
	AMF	0.465i	3.63hi	2.46 fg	1.93i	6.04hi
	NPs + AMF	0.511hi	3.92 fg	2.21g	1.65j	4.92i
IR2	C	0.579 fg	4.01 fg	2.63ef	3.34a	14.21a
	NPs	0.612ef	4.25ef	2.95de	2.69c	13.79 ab
	AMF	0.589efg	4.26ef	2.92e	2.37de	12.68b
	NPs + AMF	0.796c	4.51de	3.26d	2.39d	9.67cd
IR3	C	0.702d	4.86cd	3.98c	2.81b	10.82c
	NPs	0.648de	5.27bc	4.51b	2.31ef	8.31def
	AMF	0.869b	5.41 ab	4.84b	2.14g	8.84de
	NPs + AMF	0.937a	5.81a	5.52a	2.28f	7.71efg

Source of variation	Significance levels				
Year (Y)	ns	ns	*	ns	ns
Irrigation (IR)	*	**	**	**	**
Y × IR	ns	ns	*	ns	ns
Growth Promoting Agents (G)	**	**	**	**	**
IR × G	*	**	**	**	**
Y × G	ns	ns	ns	ns	ns
Y × IR × G	ns	ns	ns	ns	ns

C: Control; NPs: rosemary essential oil coated with nanochitosan; AMF: arbuscular mycorrhizal fungi; NPs + AMF: rosemary essential oil coated with nanochitosan + arbuscular mycorrhizal fungi. IR1: full irrigation throughout the growing season; IR2: deficit irrigation starting from the flowering stage; IR3: deficit irrigation starting from the pod formation stage. Different letters indicate significant differences at the 5 % level according to the LSD test. ns, * and ** indicated no significant difference, significant at 5 % probability level, and significant at 1 % probability level, respectively.

interactions on the activity of antioxidant enzymes (APX, SOD, and GPX) in camelina plants. The highest APX, SOD, and GPX activities were recorded under IR3 conditions with the NPs + AMF treatment, while the lowest activities were observed under IR1 conditions without any growth promoter application (Table 5). Across irrigation regimes, APX, SOD, and GPX activities increased by 164 %, 89 %, and 280 %, respectively, with NPs + AMF application under IR3 conditions compared to IR1 without growth promoter (Table 5). Furthermore, the NPs + AMF treatment significantly enhanced APX, SOD, and GPX activities by 40 %, 19 %, and 34 %, respectively, compared to the control (Table 5).

3.10. Malondialdehyde and hydrogen peroxide levels

The results presented in Table 5 indicate significant effects of irrigation regimes, growth promoter treatments, and their interaction on Hydrogen Peroxide (H_2O_2) and Malondialdehyde (MDA) levels in camelina. The highest concentrations of H_2O_2 and MDA were recorded under IR2 conditions without growth promoter application, whereas the lowest levels were observed under IR1 conditions with the NPs + AMF treatment (Table 5). Under IR2 conditions without growth promoter, H_2O_2 and MDA content increased by 102 % and 189 %, respectively, compared to IR1 with NPs + AMF application (Table 5). Additionally, H_2O_2 levels in IR2 were 40 % higher than in IR3 and 107 % higher than in IR1. Similarly, MDA content increased by 14 % and 42 % in IR2 compared to IR3 and IR1, respectively. Conversely, the combined application of NPs + AMF effectively reduced oxidative stress markers, as shown in Table 5. This treatment led to significant reductions of 19 % in H_2O_2 and 33 % in MDA compared to the control, highlighting its potential in mitigating oxidative damage under stress conditions.

3.11. Nutrient elements

Analysis of variance revealed significant effects of irrigation regimes, growth promoter treatments, and their interactions on nitrogen (N), phosphorus (P), and potassium (K) content in camelina seeds (Table 6). Drought stress led to a reduction in these macronutrients, with the lowest levels observed under IR2 conditions without growth promoter application. In contrast, the highest N (Fig. 2a), P (Fig. 2b), and K (Fig. 2c) contents were recorded under IR1 conditions with the combined NPs + AMF treatment. Compared to IR2, N, P, and K contents under IR1 increased by 48 %, 59 %, and 36 %, respectively, while compared to IR3, these increases were 19 %, 45 %, and 21 % (Fig. 2). Furthermore, applying NPs + AMF under IR1 conditions resulted in significant increases of 112 % (N), 209 % (P), and 103 % (K) compared to IR2 without growth promoters. On average, the NPs + AMF treatment enhanced N, P, and K contents by 49 %, 89 %, and 56 %, respectively, compared to the control (Fig. 2).

3.12. Seed yield

Camelina seed yield varied significantly in response to irrigation regimes, growth promoter treatments, and their interactions (Table 6). The highest seed yield was recorded under IR1 conditions with the application of NPs + AMF, whereas the lowest yield was observed under IR2 conditions without growth promoter application (Fig. 3a). Compared to IR2 (deficit irrigation starting from the flowering stage) and IR3 (deficit irrigation starting from the pod formation stage), IR1 (full irrigation throughout the growing season) resulted in 49 % and 27 % higher grain yield, respectively (Fig. 3a). The application of growth promoter treatments significantly enhanced seed yield across all irrigation regimes, with the highest increase observed under the combined NPs + AMF treatment. Specifically, NPs + AMF application improved seed yield by 36 %, 51 %, and 47 % under IR1, IR2, and IR3 conditions, respectively, compared to no growth promoter application. Notably, the use of NPs + AMF under IR1 conditions led to a remarkable 125 % increase in seed yield compared to the absence of growth promoter under IR2 conditions. Furthermore, the combined application of NPs + AMF resulted in an average 17 % increase in seed yield compared to NPs alone and a 12 % increase compared to AMF alone (Fig. 3a).

3.13. Oil content and yield

The oil content and oil yield of camelina were significantly influenced by irrigation regimes, growth promoter treatments, and their interactions (Table 6). The highest oil content (Fig. 3b) and oil yield (Fig. 3c) were achieved with the application of NPs + AMF under IR1 conditions, whereas the lowest values were recorded under IR2 conditions without growth promoter application. Notably, the application of NPs + AMF under IR1 conditions resulted in an 80 % increase in oil content and a 307 % increase in oil yield compared to

Table 6
The ANOVA results of nitrogen, phosphorus, potassium, seed yield, oil content, and oil yield of *Camelina sativa* affected by experimental factors.

Source of Variation	Nitrogen	Phosphorus	Potassium	Seed Yield	Oil Content	Oil Yield
Year (Y)	ns	ns	ns	ns	ns	ns
Irrigation (IR)	*	**	*	**	**	**
Y × IR	ns	ns	*	ns	ns	ns
Growth Promoting Agents (G)	*	**	**	**	**	**
IR × G	**	**	*	**	**	**
Y × G	ns	ns	ns	ns	ns	ns
Y × IR × G	ns	ns	ns	ns	ns	ns

ns, * and ** indicated no significant difference, significant at 5 % probability level, and significant at 1 % probability level, respectively.

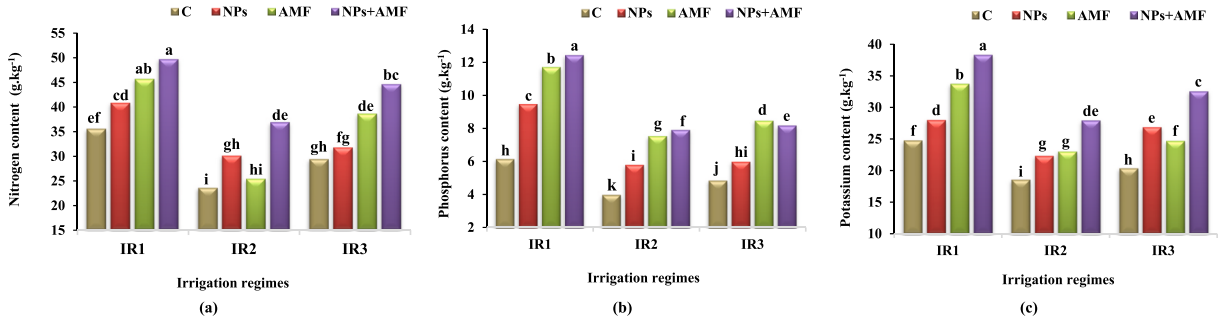

Fig. 2. Nitrogen (a), Phosphorus (b), and Potassium (c) content of *Camelina sativa* L. under growth-promoting agents and Irrigation Levels. C: Control; NPs: rosemary essential oil coated with nanochitosan; AMF: arbuscular mycorrhizal fungi; NPs + AMF: rosemary essential oil coated with nanochitosan + arbuscular mycorrhizal fungi. IR1: full irrigation throughout the growing season; IR2: deficit irrigation starting from the flowering stage; IR3: deficit irrigation starting from the pod formation stage. Different letters indicate significant differences at the 5 % level according to the LSD test.

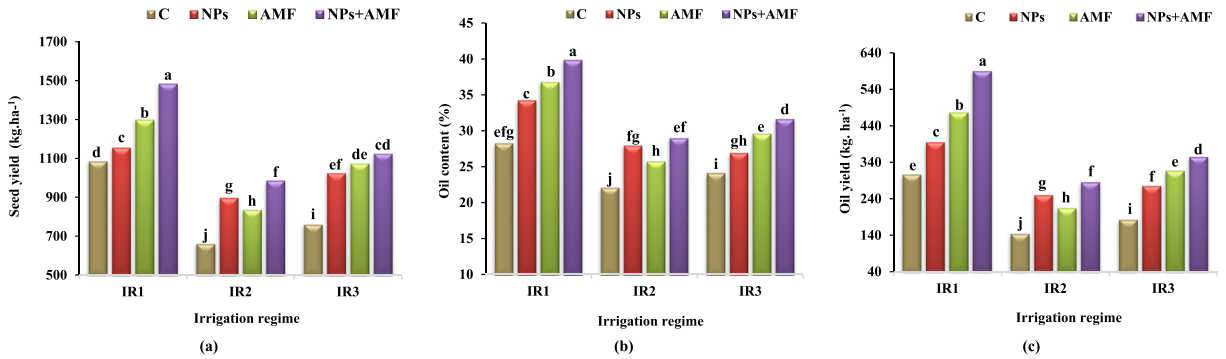

Fig. 3. Seed Yield (a), Oil Content (b), and Oil Yield (c) of *Camelina sativa* L. under growth-promoting agents and irrigation levels. C: Control; NPs: rosemary essential oil coated with nanochitosan; AMF: arbuscular mycorrhizal fungi; NPs + AMF: rosemary essential oil coated with nanochitosan + arbuscular mycorrhizal fungi. IR1: full irrigation throughout the growing season; IR2: deficit irrigation starting from the flowering stage; IR3: deficit irrigation starting from the pod formation stage. Different letters indicate significant differences at the 5 % level according to the LSD test.

the absence of growth promoter application under IR2 conditions (Fig. 3). Across irrigation regimes, oil content was 35 % higher in IR1 than in IR2 and 24 % higher than in IR3. Similarly, oil yield under IR1 conditions increased by 98 % and 57 % compared to IR2 and IR3, respectively. Furthermore, the combined application of NPs + AMF significantly enhanced oil content and yield, leading to increases of 32 % and 92 %, respectively, compared to the control. Notably, the NPs + AMF treatment outperformed the separate applications of NPs and AMF, with oil yield increasing by up to 35 % compared to NPs alone and up to 22 % compared to AMF alone (Fig. 3).

3.14. Oil composition

The analysis of variance (Table 7) revealed significant effects of irrigation regimes, growth promoter treatments, and their interactions on the composition of camelina oil. The analyzed compounds included saturated fatty acids, such as palmitic and stearic acids, as well as unsaturated fatty acids, including oleic, linoleic, linolenic, eicosenoic, and erucic acids. The highest palmitic acid content was recorded under IR2 conditions, whereas stearic acid levels peaked under IR3 conditions without growth promoter application (Table 7). In contrast, the lowest concentrations of both palmitic and stearic acids were observed with the application of NPs + AMF under IR1 conditions. The combined treatment of NPs + AMF under IR1 conditions resulted in the highest content of oleic, linoleic, and linolenic acids, while the lowest levels were detected under IR2 conditions without growth promoter application (Table 7). Additionally, the maximum eicosenoic acid content was recorded with AMF under IR3 conditions, whereas the highest erucic acid content was obtained with AMF under IR1 conditions. Conversely, the lowest levels of eicosenoic and erucic acids were observed without growth promoter application under IR2 conditions (Table 7).

4. Discussion

The study findings revealed a significant decline in AMF inoculation rates under deficit irrigation regimes. This reduction in colonization is attributed to decreased carbon availability in host plants, diminished soil microbial activity, and limitations in AMF colonization capacity, hyphal extension, and spore germination and development under water deficit conditions (Afshari et al., 2022;

Table 7
Mean comparisons of the interactive effects of irrigation regimes and plant growth-promoting treatments on seed fatty acid profiles in *Camelina sativa*.

Treatments		Palmitic acid (%)	Stearic acid (%)	Oleic acid (%)	Linoleic acid (%)	Linolenic acid (%)	Eicosenoic acid (%)	Erucic acid (%)
IR1	C	4.31f	2.62h	10.62f	19.03d	30.87cde	11.48e	0.98d
	NPs	4.04g	2.07j	12.07de	20.68c	33.16bc	11.88de	1.21bc
	AMF	3.65h	2.42i	12.58cd	21.79b	35.34b	12.06d	1.48a
	NPs + AMF	3.43i	1.84k	17.08a	22.76a	38.69a	14.40b	1.32b
IR2	C	6.93a	3.29e	4.79i	12.18k	20.37i	9.19i	0.53h
	NPs	5.93b	3.04f	9.93 fg	14.82i	23.75h	9.69gh	0.67 fg
	AMF	5.14d	2.67gh	6.59h	13.61j	25.32gh	9.59hi	0.62gh
	NPs + AMF	5.49c	2.81g	10.01 fg	15.54hi	26.91gh	10.09	0.77ef
IR3	C	5.27d	4.44a	9.18g	15.72gh	28.67ef	10.87f	0.72 fg
	NPs	5.57c	3.83c	13.64bc	16.84f	32.10cd	13.94c	0.87de
	AMF	4.85e	4.14b	10.91ef	16.31 fg	30.44de	14.88a	1.27b
	NPs + AMF	4.96e	3.58d	14.83b	17.67e	28.54ef	14.65 ab	1.12c

Source of variation	Significance levels						
Year (Y)	ns	*	ns	ns	ns	ns	ns
Irrigation (IR)	*	**	**	**	**	*	**
Y × IR	ns	*	ns	ns	ns	ns	ns
Growth Promoting Agents (G)	**	*	*	**	**	*	*
IR × G	**	**	**	*	**	*	**
Y × G	ns	ns	ns	ns	ns	ns	ns
Y × IR × G	ns	ns	ns	ns	ns	ns	ns

C: Control; NPs: rosemary essential oil coated with nanochitosan; AMF: arbuscular mycorrhizal fungi; NPs + AMF: rosemary essential oil coated with nanochitosan + arbuscular mycorrhizal fungi. IR1: full irrigation throughout the growing season; IR2: deficit irrigation starting from the flowering stage; IR3: deficit irrigation starting from the pod formation stage. Different letters indicate significant differences at the 5 % level according to the LSD test. ns, * and ** indicated no significant difference, significant at 5 % probability level, and significant at 1 % probability level, respectively.

Mathur et al., 2019). Additionally, research suggests that a decline in photosynthetic activity plays a crucial role in reducing colonization, mycorrhizal dependency, and mycorrhizal growth response (Gupta et al., 2021). A decrease in photosynthetic efficiency can hinder the provision of essential carbohydrates required for spore growth and germination (Zhang et al., 2024). Consequently, reduced carbohydrate accumulation in the host plant's leaves weakens the symbiotic relationship between mycorrhizal fungi and plant roots (Afshari et al., 2022; Gupta et al., 2021). Afshari et al. (2024) reported that severe drought stress significantly reduces AMF root colonization. However, the synergistic application of nanoparticles (NPs) and AMF has been shown to enhance colonization rates and promote greater cooperation under drought stress conditions. This combined approach mitigates the adverse effects of drought on root systems and mycorrhizal activity by improving material binding and transfer, optimizing soil properties, and enhancing biological activity (Alsherif et al., 2023; Zhang et al., 2024). Similarly, Sayed et al. (2024) demonstrated that nanoparticles enhance mycorrhizal fungi colonization and their symbiotic interaction with plants under drought conditions.

Chlorophylls play a vital role in light absorption, energy transfer, and electron transport during photosynthesis. However, under water dficit conditions, chlorophyll content tends to decrease due to the accumulation of ROS (Pirbalouti et al., 2017). ROS induce lipid peroxidation in cell membranes, leading to chloroplast damage and a reduction in chlorophyllase activity, ultimately resulting in the degradation of chlorophyll precursors (Sharma et al., 2024; Ye et al., 2022). Nevertheless, our findings indicate that the combined application of AMF and NPs can alleviate the negative effects of water stress on chlorophyll content. The observed increase in chlorophyll content may be attributed to the improved nutrient availability associated with the integrated application of AMF and NPs (Haghaninia et al., 2024; Mathur et al., 2019). Additionally, NPs have been found to stimulate the expression of genes involved in chlorophyll biosynthesis while repressing those associated with the chlorophyll degradation (Attaran Dowom et al., 2022; Tabassum et al., 2024). These findings align with studies conducted by Pirbalouti et al. (2017) and Safikhan et al. (2018).

The decline in maximum fluorescence yield (Fm) and the Fv/Fm ratio under deficit irrigation regimes reflects the disruption of photosystem II (PSII) efficiency and a reduction in its quantum yield (Fregonezi et al., 2024; Giglou et al., 2022). A decrease in Fv further confirms the diminished photosynthetic capacity due to drought-induced stress, which is commonly accompanied by an increase in FO and Fo/Fv values (Mathur et al., 2019). These alterations suggest structural or functional damage to the PSII reaction center and impaired energy transfer within the photosynthetic apparatus (Begum et al., 2022; Ye et al., 2022). In the present study, the combined application of AMF and NPs demonstrated a significant ameliorative effect on chlorophyll fluorescence parameters under water-limited conditions (Mathur et al., 2019). This improvement may be attributed to enhanced nutrient uptake, better water status, and mitigation of oxidative stress through reduced accumulation of ROS, collectively protecting PSII from drought-induced damage (Begum et al., 2022; Zhang et al., 2024). The observed reduction in FO in plants treated with biostimulants suggests a lower degree of injury to the PSII core and possibly the recovery or preservation of its photochemical integrity (Ye et al., 2022; Giglou et al., 2022). Consistent with our results, Saleh et al. (2023) reported that applying chitosan particles with AMF in wheat significantly enhanced PSII photochemical efficiency, stomatal conductance, and photosynthetic rates.

Relative water content (RWC) is a critical physiological indicator of plant water status under drought conditions (Desoky et al., 2021). The reduction of RWC during flowering (IR2) and pod formation (IR3) stages underscores the sensitivity of camelina to water deficit during key reproductive phases, where water demand is elevated for cellular growth and reproductive development (Farooq et al., 2014; Afshari et al., 2022; Sutulienė et al., 2021). Water limitation at these stages disrupts root water uptake and osmotic balance (Igiehon et al., 2021). The combined application of AMF and NPs significantly improved plant water status. AMF increases water and nutrient uptake by expanding root surface area (Begum et al., 2022), while NPs may enhance osmotic adjustment and physiological resilience (Sheikhalipour et al., 2021). These results corroborate previous studies Igiehon et al. (2021) reported increased RWC in AMF-inoculated plants under drought, and do Carmo et al. (2021) showed chitosan NPs improved osmotic balance and reduced transpiration, enhancing RWC in wheat. Together, these findings support the synergistic use of biostimulants and nanomaterials to mitigate drought stress in plants.

The significant increase in ascorbic acid, proline, and soluble sugar contents under deficit irrigation regimes and growth stimulant treatments highlights the essential role of these metabolites in camelina adaptive response to water deficit (Attaran Dowom et al., 2022; Tabassum et al., 2024). The highest level of ascorbic acid observed under IR3 with the combined application of NPs and AMF reflects the enhancement of the plant's antioxidant defense system, contributing to redox homeostasis and attenuation of oxidative damage (Sharma et al., 2024). This is consistent with the findings of Sayed et al. (2024), who emphasized the pivotal role of ascorbic acid as a key antioxidant in mitigating environmental stress. Moreover, the accumulation of proline and soluble sugars, particularly in the combined NPs + AMF treatments, suggests the activation of osmotic adjustment mechanisms (Alsherif et al., 2023; Sayed et al., 2024). The underlying mechanisms behind these improvements can be attributed to the complementary functions of AMF and NPs (Haghaninia et al., 2025b; Saleh et al., 2023). AMF enhance nutrient uptake—especially phosphorus—and stimulate the synthesis of protective metabolites (Gholinezhad and Darvishzadeh, 2021), whereas NPs are known to activate defense signaling pathways, improve ion homeostasis, and upregulate antioxidant enzymes (Alenazi et al., 2024; Tabassum et al., 2024). These combined effects lead to elevated levels of stress-related metabolites such as ascorbic acid, proline, and soluble sugars (Joel et al., 2023). These findings are corroborated by previous studies, including those by Safikhan et al. (2018) and Attaran Dowom et al. (2022), who demonstrated that nanoparticle treatments—such as chitosan NPs—significantly increased antioxidant capacity, soluble sugars, proline accumulation, and osmotic regulation under drought stress. Overall, our results indicate that the synergistic application of AMF and nanoparticles can effectively activate multiple plant defense mechanisms, thereby improving drought resilience and sustaining physiological performance under water-limited conditions.

Tocopherols, as lipid-soluble antioxidants, protect cellular membranes from oxidative damage and are essential for maintaining the stability of membrane structures, particularly within chloroplasts (Ebrahimi et al., 2025). The increased content of α-, β-, and γ-tocopherols in combined treatments of NPs and AMF under drought stress highlights the crucial role of these compounds in enhancing the defense system of camelina (Ali et al., 2020). The application of AMF improves the nutritional status and facilitates the uptake of essential micronutrients, thereby providing a conducive environment for enhanced tocopherol biosynthesis (Baslam et al., 2013). Concurrently, NPs enhance photosynthetic efficiency and overall physiological status, supplying the necessary precursors for the synthesis of these compounds (Sedghi et al., 2021; Rezayian and Niknam, 2025). The synergistic effect of these two biostimulants activates plant defense pathways, leading to elevated tocopherol accumulation in response to drought stress. These findings are consistent with those reported by Saleh et al. (2023), which demonstrated that growth-promoting agents can increase antioxidant levels under water deficit conditions, thereby contributing to improved plant resilience against oxidative stress.

Our research confirms that camelina plants exhibit increased levels of phenols and flavonoids under water scarcity. These compounds perform multiple protective functions, including preventing lipid peroxidation caused by reactive oxygen species (ROS) and maintaining membrane fluidity by integrating into the lipid bilayer (Ullah et al., 2024; Haghaninia et al., 2025b). Additionally, they act as efficient ROS scavengers by donating electrons to guaiacol peroxidases and polyphenol oxidases (Gharibi et al., 2016). However, excessive drought stress can negatively impact antioxidant properties, leading to a decline in phenolic content (Mohammadi et al., 2022). This reduction compromises the plant's antioxidant capacity, thereby weaking its ability to tolerate stress. In our study, we investigated the combined application of AMF + NPs as a strategy to enhance phenolic and flavonoid accumulation in camelina plants under drought conditions. Our results demonstrated that this integrated approach significantly increased the levels of these bioactive compounds. This enhancement can be attributed to improved nutrient availability facilitated by AMF + NPs, which, in turn, boosted the enzymatic activity involved in phenol and flavonoid biosynthesis (Begum et al., 2022; Nahuelcura et al., 2022; Tabassum et al., 2024). These findings suggest that AMF + NPs can effectively improve plant resilience to drought stress by promoting the accumulation of phenolic and flavonoid compounds, thereby enhancing antioxidant capacity and overall stress tolerance (Ullah et al., 2024).

Our study provides evidence that water stress conditions upregulate antioxidant enzyme activity in plants, a crucial adaptation since water deficit can reduce plant productivity by triggering lipid peroxidation in cellular membranes. Increased enzymatic activity helps stabilize cellular structures and supports plant growth (Begum et al., 2022; Ullah et al., 2024). Moreover, antioxidant enzymes play a vital role in detoxifying superoxide anion radicals (O_2^-) by converting them into H_2O_2, which is subsequently broken down by catalase and peroxidase (Sharma et al., 2024; Sutulienė et al., 2021). Notably, we observed a significant increase in antioxidant enzyme activity in drought-stressed plants, particularly when treated with NPs + AMF. This suggests that this combined treatment effectively enhances the plant's antioxidant defense system. Since enzymes are protein compounds, their activity can be improved with increased nutrient availability (Pirbalouti et al., 2017; Ayyaz et al., 2022; Haghaninia et al., 2025a). The combined application of NPs + AMF enhances nutrient uptake, leading to higher amino acid and enzyme synthesis, and, consequently, greater enzymatic activity (Safikhan et al., 2018; Joel et al., 2023). These findings align with previous studies showing increased antioxidant enzyme activity following the application of NPs and AMF (Begum et al., 2020; Mohammadi et al., 2022; Nahuelcura et al., 2022).

The research findings also indicate that soil water scarcity induces oxidative stress in camelina plants, resulting in elevated levels of

malondialdehyde (MDA) and H_2O_2. Environmental stresses, including drought, promote ROS accumulation, which can damage DNA, proteins, and membrane lipids, as well as lead to excessive hydrogen peroxide accumulation and cellular damage (Sutulienė et al., 2021; Ullah et al., 2024). However, our research demonstrated that the combined application of AMF + NPs effectively reduced H_2O_2 and MDA levels, enhancing the plants' antioxidant defense mechanisms by increasing enzymatic and non-enzymatic antioxidant activity (Begum et al., 2020; Tabassum et al., 2024). This protective effect reduces oxidative stress, preserves cellular integrity, and mitigates drought-induced damage (Joel et al., 2023).

Drought conditions can negatively impact nutrient concentration in plants by reducing nutrient supply via mineralization, mass flow, and diffusion (Ayyaz et al., 2022; Hamedani et al., 2022). Sharma et al. (2024) reported that drought stress lowers nutrient availability by decreasing soil microbial activity, inhibiting root nutrient uptake, and disrupting nutrient transport within the plant. However, a promising strategy to counteract these effects is the combined application of AMF and NPs, which has been shown to enhance the uptake of essential elements such as nitrogen, phosphorus, and potassium. The improved nutrient concentration in plants associated with AMF under drought stress conditions can be attributed to several factors (Pavithra and Yapa, 2018). Firstly, AMF enhances root hydraulic conductivity, thereby facilitating improved nutrient uptake (do Carmo et al., 2021). Additionally, AMF hyphae efficiently transport nutrients from nutrient-depleted zones to the root cortex, further supporting plant nutrition (Begum et al., 2020). The application of NPs as nano-fertilizers also plays a crucial role in enhancing nutrient availability. This is due to the high surface area-to-volume ratio of nanoparticles, which improves nutrient absorption capacity (Giglou et al., 2022; Haghaninia et al., 2025a). Furthermore, the slower diffusion of NPs enables better nutrient retention and uptake. These findings are consistent with the observations by Ayyaz et al. (2022) who reported improved nutrient levels in *Brassica napus* under drought stress conditions following NPs application.

Drought stress significantly affects crop growth and productivity, with its impact varying depending on timing, duration, and severity (Hamedani et al., 2022; Ghiyasi et al., 2023). This study revealed the greatest yield losses under limited irrigation, deficit irrigation starting from the flowering stage in the absence of fertilization. Water scarcity at this stage disrupts flowering and grain filling stages, impairing camelina's ability to recover or escape drought stress (Alsherif et al., 2023). Additionally, drought accelerates leaf shedding and early maturity during reproductive phases, reducing seed yield (Farooq et al., 2014). It can also hinder flowering, pod formation, and induce pod abortion. Amiri Darban et al. (2020) examined camelina seed yield under different irrigation regimes and found that drought stress during flowering significantly reduced grain yield by 51 % compared to well-watered conditions. However, as hypothesized, the combined application of AMF + NPs mitigated these adverse effects. NPs regulate transpiration, enhance photosynthesis, improve plant water status, alter leaf organelle ultrastructure, activate defense mechanisms, and optimize nutrient uptake (Sheikhalipour et al., 2021). Additionally, AMF colonization enhances water and nutrient uptake while stimulating the production of plant hormones (Shehzad et al., 2020; Tabassum et al., 2024). The extension of mycorrhizal hyphae into root inner tissues further improves phosphorus absorption by expanding the effective soil volume for nutrient uptake (Joel et al., 2023; Mathur et al., 2019). These combined effects strengthen camelina enzymatic and non-enzymatic antioxidant systems, reducing free radical damage, alleviating drought stress, and ultimately improving seed yield (Giglou et al., 2022; Sayed et al., 2024; Zhang et al., 2024).

Under drought conditions, camelina plants may experience reduced oil content due to the oxidation of polyunsaturated fatty acids and limited carbohydrate conversion into oil (Mabudi Bilasvar et al., 2022; Zafari et al., 2020). This decline is associated with decreased activity of key enzymes involved in fatty acid biosynthesis, such as acetyl-CoA carboxylase and 3-ketosyl reductase (Akbari et al., 2020; Ghiyasi et al., 2023; Nazari et al., 2017). The flowering stage is particularly vulnerable to drought, leading to decreased oil concentration and yield (Fatemi et al., 2022). However, NP application enhances dehydration tolerance by reducing transpiration, mantaining relative water content, and boosting antioxidant activity (Chen and Kattab, 2024; Fatemi et al., 2022). This mitigates ROS-induced damage, thereby improving oil percentage and yield (Chen and Kattab, 2024; Haghaninia et al., 2024). Additionally, AMF symbiosis enhances nutrient solubility and water uptake (Haghaninia et al., 2025b), with hyphal penetration into root tissues facilitating phosphorus adsorption, further increasing oil content (Gholinezhad and Darvishzadeh, 2021).

Drought stress typically increases saturated fatty acid levels while reducing unsaturated fatty acid content. Linoleic and linolenic acid synthesis is particularly affected due to impaired desaturation activity (Feizabadi et al., 2021; Kalantar Ahmadi and Eyni-Nargeseh, 2023). Shortened growth periods and reduced sink capacity further constrain unsaturated fatty acid production (Amiri-Darban et al., 2020; Nazari et al., 2017). However, AMF + NPs application can enhance unsaturated fatty acid levels, including oleic and linoleic acid, by stabilizing membranes, reducing oxidative stress, and improving nutrient uptake (Amiri-Darban et al., 2020; Chen and Kattab, 2024; Zafari et al., 2020). NPs are known to bolster membrane stability and mitigate oxidative stress in plants experiencing drought, thereby safeguarding cellular integrity and vital metabolic processes involved in fatty acid synthesis (Amiri-Darban et al., 2020; Chen and Kattab, 2024; Zafari et al., 2020). Additionally, AMF enhance the availability of essential nutrients such as nitrogen and phosphorus, which serve as precursors in the biosynthesis pathways of fatty acids (Ghiyasi et al., 2023; Gholinezhad and Darvishzadeh, 2021; Igiehon et al., 2021).

5. Conclusion

This study investigated the effects of irrigation regimes and chitosan nanoparticles loaded with rosemary essential oil (NPs), with or without arbuscular mycorrhizal fungi (AMF), inoculation, on camelina seed performance. Drought stress, particularly when imposed from the flowering stage, disrupted photosynthetic pigments, nutrient uptake, and water balance, while increasing oxidative stress (H_2O_2, MDA), ultimately reducing seed oil yield and quality. The application of chitosan nanoparticles loaded with rosemary essential oil or AMF, individually or combined, effectively mitigated these negative effects. While AMF inoculation alone enhanced plant performance under non-stress and mild stress conditions, its efficacy declined under severe stress due to reduced symbiotic efficiency.

Conversely, the combined treatment (NPs + AMF) significantly enhanced mycorrhizal colonization under stress and outperformed single treatments in improving plant performance. The synergistic effect of combined NPs + AMF application led to the greatest improvements in growth traits, physiological indices such as photosynthetic pigments, chlorophyll fluorescence, nutrient uptake, relative water content, antioxidant compounds (phenols, flavonoids, ascorbic acid, proline, soluble sugars, and tocopherol isomers α, β, and γ), and antioxidant enzyme activities (ascorbate peroxidase, superoxide dismutase, guaiacol peroxidase), while ROS levels (H_2O_2 and MDA) were reduced, thereby preserving membrane stability and enhancing cellular resilience. Importantly, the combined treatment increased oil yield by approximately 35 % and 22 % compared to separate AMF and nanoparticle applications, respectively, indicating a strong synergistic interaction. Moreover, the oil quality improved, as reflected by increased proportions of essential unsaturated fatty acids—including α-linolenic acid, linoleic acid, and oleic acid—and a significant reduction in saturated fatty acids such as palmitic and stearic acids. These findings emphasize the potential of integrating nanoparticle and AMF treatments to mitigate drought stress impacts on camelina, thereby contributing to improved crop productivity and oil quality. Given the implications for food security and sustainable agriculture, further biochemical and molecular studies are recommended to elucidate the underlying mechanisms and optimize the practical application of these synergistic treatments.

CRediT authorship contribution statement

Mohammad Haghaninia: Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Abdollah Javanmard:** Writing – original draft, Visualization, Validation, Methodology, Investigation, Data curation, Conceptualization. **Farzad Rasouli:** Writing – original draft, Visualization, Validation, Methodology, Investigation, Data curation, Conceptualization. **Emanuele Radicetti:** Writing – review & editing, Validation, Supervision, Methodology, Data curation. **Samaneh Memarzadeh Mashhouri:** Data curation, Methodology, Validation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.bcab.2025.103682.

Data availability

Data will be made available on request.

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