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Research Article

Enhanced drought tolerance in Camelina (*Camelina sativa* L.) through foliar application of salicylic acid and putrescine: Physiological and biochemical changes

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Abstract

Water limitation is a major constraint to crop productivity in semi-arid regions, particularly under rainfed agricultural systems where irregular precipitation limits plant growth during critical developmental stages. This study evaluated the interactive effects of foliar application of putrescine (0, 1, 2, and 3 mM) and salicylic acid (0, 1, 2, and 3 mM) on physiological, biochemical, and yield-related traits of camelina (*Camelina sativa* L.) grown under rainfed conditions. Compared with untreated plants, the combined application of putrescine and salicylic acid significantly improved physiological performance under limited soil moisture availability. Total chlorophyll, chlorophyll a, and carotenoid contents increased substantially (up to approximately 60–70%), indicating improved stability of the photosynthetic apparatus. Soluble sugar content increased by about 51%, reflecting enhanced osmotic adjustment and carbon metabolism. Proline accumulation showed a dose-dependent response, with moderate increases (up to 73%) indicating adaptive metabolic regulation rather than stress injury. Antioxidant defense was markedly enhanced, as activities of ascorbate peroxidase, catalase, and peroxidase increased significantly, with ascorbate peroxidase showing the strongest response. Grain yield was significantly enhanced under combined treatments, reflecting improved photosynthetic efficiency, metabolic balance, and assimilate partitioning rather than simple growth stimulation. Overall, the coordinated application of putrescine and salicylic acid effectively enhanced physiological resilience and yield performance of camelina under rainfed conditions. These findings highlight the potential of elicitor-based management strategies to improve crop productivity in semi-arid environments experiencing increasing water limitations.

Keywords: Antioxidant enzymes, Chlorophyll, Elicitor, Proline, Putrescine, Salicylic acid

Introduction

Oilseed crops are essential sources of dietary lipids and industrial raw materials, particularly polyunsaturated fatty acids such as omega-3 and omega-6, which play critical roles in human nutrition and health (Simopoulos and De Meester, 2009). Among oilseed crops, camelina (*Camelina sativa* L.) has gained increasing attention due to its short growth cycle, adaptability to marginal environments, and favorable oil composition, making it a promising crop for sustainable agriculture under water-limited conditions (Berti *et al*., 2011; Mondor and Hernandez-Alvarez, 2022).

Despite its relative adaptability, drought stress remains one of the main constraints limiting camelina productivity, particularly in semi-arid regions characterized by irregular precipitation and high evaporative demand. Water limitation disrupts key physiological processes, including photosynthesis and carbon assimilation, accelerates oxidative damage, and ultimately reduces biomass production, grain yield, and

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oil accumulation (Bukhari *et al*., 2022). Although camelina exhibits moderate drought tolerance, prolonged or severe water deficit significantly restricts its physiological performance and yield stability.

Climate change has further intensified the frequency and severity of water limitation in arid and semi-arid regions, posing major challenges to crop production under rainfed farming systems (Fattahi *et al*., 2023). Under such conditions, crop growth is often constrained by limited and irregular soil moisture availability rather than short-term drought events. In camelina, reduced soil moisture during reproductive stages has been reported to impair photosynthetic efficiency through chlorophyll degradation and reduced photosystem performance, enhance oxidative stress, stimulate the accumulation of compatible solutes such as proline, and activate antioxidant defense mechanisms as part of stress acclimation responses (Canak *et al*., 2020; Bukhari *et al*., 2022; Eskandarzadeh *et al*., 2025). Nevertheless, under severe or prolonged water limitation, these protective mechanisms are often insufficient to fully prevent yield loss, highlighting the need for effective strategies to enhance physiological resilience under rainfed agro systems.

Plants respond to water limitation through a complex network of physiological and biochemical mechanisms, including osmotic adjustment, antioxidant defense, and hormonal regulation. Among these strategies, exogenous application of signaling molecules has emerged as an effective approach to enhance stress tolerance. Salicylic acid plays a central role in regulating redox signaling, photosynthetic activity, and antioxidant responses, while polyamines such as putrescine contribute to membrane stabilization, osmolyte accumulation, and modulation of stress-responsive metabolism (Miura and Tada, 2014; Wasaya *et al*., 2023).

Although the individual effects of salicylic acid or polyamines on drought tolerance have been documented in various crops, information regarding their combined application and potential synergistic effects in camelina remains limited, particularly under rainfed field conditions. Moreover, integrated evaluations linking physiological and biochemical responses with yield performance under water-limited environments are still scarce. Therefore, the present study aimed to evaluate the interactive effects of foliar-applied putrescine and salicylic acid on physiological performance, antioxidant capacity, and grain yield of camelina grown under rainfed, water-limited conditions. This approach provides insight into physiological mechanisms contributing to crop resilience under limited soil moisture availability.

Materials and methods

The experiment was conducted during the 2022–2023 growing season at the Gonbad Kavous Agricultural Research Station with a mean annual precipitation of approximately 328 mm. The experimental site is characterized by rainfed farming conditions and frequent seasonal water limitation. The experiment was arranged as a factorial based on a randomized complete block design (RCBD) with three replications. Treatments consisted of four levels of putrescine (0, 1, 2, and 3 mM) and four levels of salicylic acid (0, 1, 2, and 3 mM). Each experimental plot consisted of four rows, 3 m in length, with 25 cm row spacing and 1 m spacing between plots. Seeds of the camelina cultivar Soheil were sown manually in December 2022 at a depth of approximately 2 cm under rainfed conditions. Table 1 showed the monthly meteorological data for the growing season of camelina.

Fertilizer application was performed based on soil test recommendations (Table 2). Due to a severe deficit in rainfall during critical growth stages, two supplemental irrigations were applied during the flowering and grain-filling stages to prevent crop failure and ensure plant establishment.

Foliar application of putrescine and salicylic acid was performed at the onset of flowering, a critical developmental stage highly sensitive to water limitation under rainfed conditions, and repeated 14 days later to ensure adequate exposure during the reproductive phase. Solutions were freshly prepared using analytical-grade chemicals (≥99% purity; Merck, Germany) and applied using a hand-held backpack sprayer. Spraying was carried out in the late afternoon (after 17:00 h) to minimize evaporation losses. Sprays were applied until full wetting of the leaf surfaces was achieved, ensuring uniform coverage of all aboveground plant parts. Control plants were sprayed with distilled water following the same procedure. All treatments were applied under calm weather conditions to ensure uniform deposition of the solutions. Leaf samples were collected two weeks after the second foliar application. Fully expanded, healthy leaves from the upper canopy were harvested, immediately frozen in liquid nitrogen, and stored at −80°C until analysis.

Photosynthetic pigments were determined according to Arnon (1975), soluble sugars according to Dubois *et al.* (1956), and soluble protein following the method of Bradford (1976). Proline content was quantified using the method of Bates *et al.* (1973). Catalase and peroxidase activities were measured following the method described by Aebi (1984), while ascorbate peroxidase activity was determined according to Nakano and Asada (1981). Grain yield was measured at physiological maturity by harvesting the two central rows of each plot, excluding 0.5 m from both ends to avoid border effects.

Data were analyzed using SAS (version 9.4), and means were compared by LSD at 5% and 1% probability levels. Graphs were prepared with Microsoft Excel.

Results and discussion

Foliar putrescine application significantly increased total chlorophyll content, proline levels, and ascorbate

Table 1. Meteorological statistics of Gonbad Kavous Research Station in the experimental year (2022-2023)

2022-2023 months	Temperature mean (°C)	Precipitation (mm)	Humidity mean (%)	Evaporation rate (mm)
December 2022	11.6	27.2	72	50.1
January 2022	7.4	8	63	30.4
February 2023	7.6	19.7	65	33.7
March 2023	14.9	9.3	64	80.4
April 2023	16.9	26.6	65	122.5
May 2023	21.6	16.8	64	164.5

Table 2. Some physical and chemical properties of the field soil

Sand (%)	Silt (%)	Clay (%)	Potassium (ppm)	Phosphorus (ppm)	Nitrogen (%)	Organic Carbon (%)	pH	EC dS/m
20	61	17	369	14.2	0.08	0.68	7.8	1.22

Table 3. Analysis of variance (ANOVA) of the effect of the application of putrescine and salicylic acid treatments on evaluated traits of Camelina

Source of variance	DF	Mean square				
		Chl a	Chl b	Total Chl	Carotenoid	soluble sugar
replication	2	0.17	9.07	8.65	0.08	0.02
Putrescine (Put)	3	17.02*	5.23*	21.20**	2.68*	301.73*
Salicylic acid (SA)	3	5.72**	1.33*	11.71**	0.57**	95.43**
Put × SA	9	6.9**	1.59**	10.71*	2.35**	74.72**
Eerror	30	0.12	0.39	0.38	0.04	0.75
CV (%)	-	3.30	14.66	4.78	5.94	1.99

ns, * and **: non-significant and significant in the probability levels of 5%, and 1%, respectively

Continue of table 3.

Source of variance	DF	Mean square				
		Proline	Catalase	APX	Peroxidase	Grain yield
replication	2	21.65	0.0002	0.0001	5.63	32976.5
Putrescine (Put)	3	1014.52**	0.0137*	0.0090**	9.14*	13740.6**
Salicylic acid (SA)	3	156.08 ns	0.0030**	0.0008**	6.06**	1468.65**
Put × SA	9	2286.11**	0.0203**	0.0002*	3.64*	2740.14*
Eerror	30	150.71	0.0002	0.0003	4.23	1898.49
CV (%)	-	6.80	2.29	2.51	5.55	17.93

ns, * and **: non-significant and significant in the probability levels of 5%, and 1%, respectively

peroxidase activity (P<0.01) and also influenced chlorophyll a, chlorophyll b, carotenoids, soluble sugars, catalase, and peroxidase activity at the 5% level. Salicylic acid similarly exerted a significant effect on all traits except proline. The interaction between the two elicitors was significant for most measured variables except protein content (Table 3).

Photosynthetic pigments: The results demonstrated that foliar application of putrescine and salicylic acid significantly influenced photosynthetic pigment content in camelina grown under rainfed conditions (Table 4). The highest levels of chlorophyll a, chlorophyll b, total chlorophyll, and carotenoids were observed under the combined application of moderate concentrations of putrescine and salicylic acid, indicating a synergistic effect between these two regulators on pigment stability under limited soil moisture availability.

Under rainfed conditions characterized by limited and irregular soil moisture availability, partial restriction of carbon assimilation and increased oxidative pressure may impair chloroplast function rather than cause irreversible structural damage. The lower pigment contents observed in untreated plants therefore reflect suboptimal photosynthetic performance rather than severe drought injury.

Polyamines such as putrescine are known to interact with negatively charged thylakoid membranes, contributing to membrane stabilization and preservation of photosystem integrity under suboptimal environmental conditions (Wasaya *et al.*, 2023). Salicylic acid, on the other hand, modulates chloroplast redox signaling and regulates the expression of photosynthesis-related genes, thereby supporting pigment stability and photochemical efficiency (Miura and Tada, 2014). The observed increase in carotenoid content further indicates enhanced photoprotective capacity, as carotenoids play a critical role in dissipating excess excitation energy and limiting photooxidative damage (Ashraf and Harris, 2013). The significant positive correlations observed among chlorophyll a, chlorophyll b, and total chlorophyll further support the coordinated regulation of photosynthetic pigments under the applied treatments. Such correlations indicate that improvements in chlorophyll biosynthesis and

Table 4. Comparison of the mean interaction effects of putrescine and salicylic acid on photosynthetic pigments content in Camelina

Treatment	Chl a (mg.g^{-1} FW)	Chl b (mg.g^{-1} FW)	Carotenoid (mg.g^{-1} FW)	Total Chl (mg.g^{-1} FW)
Non-Put × Non-SA	8.70 ^{i}	2.09 ^{e}	2.84 ^{fg}	10.79 ^{j}
Non-Put × SA 1 mM	8.73 ^{i}	2.34 ^{de}	3.87 ^{b}	11.07 ^{ij}
Non-Put × SA 2 mM	9.81 ^{g}	2.39 ^{de}	3.48 ^{c}	12.20 ^{fgh}
Non-Put × SA 3 mM	8.92 ^{hi}	2.42 ^{de}	3.12 ^{def}	11.34 ^{hij}
Put 1 mM × Non-SA	9.98 ^{fg}	2.12 ^{e}	3.50 ^{c}	12.10 ^{fg}
Put 1 mM × SA 1 mM	11.13 ^{d}	3.47 ^{a}	4.01 ^{b}	14.60 ^{c}
Put 1 mM × SA 2 mM	14.62 ^{a}	3.16 ^{ab}	4.66 ^{a}	17.78 ^{a}
Put 1 mM × SA 3 mM	9.80 ^{g}	2.5 ^{cde}	3.32 ^{cde}	12.30 ^{fg}
Put 2 mM × Non-SA	10.74 ^{de}	2.81 ^{bc}	3.34 ^{cde}	13.55 ^{d}
Put 2 mM × SA 1 mM	13.45 ^{b}	2.83 ^{bc}	4.47 ^{a}	16.28 ^{b}
Put 2 mM × SA 2 mM	12.38 ^{c}	3.48 ^{a}	3.45 ^{cd}	15.86 ^{b}
Put 2 mM × SA 3 mM	9.97 ^{fg}	2.67 ^{bcd}	3.00 ^{ef}	12.64 ^{ef}
Put 3 mM × Non-SA	9.78 ^{g}	2.35 ^{de}	3.02 ^{ef}	12.13 ^{fgh}
Put 3 mM × SA 1 mM	10.56 ^{ef}	2.69 ^{bcd}	3.49 ^{cd}	13.25 ^{de}
Put 3 mM × SA 2 mM	10.54 ^{ef}	2.11^{e}	3.03 ^{ef}	12.65 ^{ef}
Put 3 mM × SA 3 mM	9.41 ^{gh}	2.10 ^{e}	2.61 ^{g}	11.51 ^{ghi}

Means within each column followed by the same letter are not significantly different (LSD, 0.05 probability level).

stability occur in a concerted manner, reflecting the structural and functional integration of light-harvesting complexes. Additionally, the positive association between carotenoids and chlorophylls suggests that enhanced photoprotection contributed to maintaining pigment integrity under water-limited conditions rather than merely increasing pigment concentration. Similar coordinated responses among photosynthetic pigments under drought stress have been reported in other oilseed crops (Ashraf and Harris, 2013; Taiz *et al.*, 2015).

Overall, the interactive effects of putrescine and salicylic acid suggest a coordinated regulation of photosynthetic pigment homeostasis, enabling camelina plants to maintain photosynthetic functionality under conditions of limited soil moisture rather than eliminating stress effects entirely.

Osmotic adjustment and compatible solutes (soluble sugars and proline): The accumulation of soluble sugars and proline under elicitor treatments reflects improved osmotic adjustment and metabolic regulation in camelina subjected to water-limited conditions stress (Table 5). Soluble sugars act not only as osmolytes but also as signaling molecules involved in stress perception, carbon allocation, and maintenance of cellular turgor (Krasensky and Jonak, 2012). In the present study, elevated soluble sugar content under salicylic acid application suggests improved photosynthetic carbon fixation and delayed senescence. These results are consistent with the findings of Rezaiean *et al*. (2024), who reported that salicylic acid significantly increased soluble sugar levels in Camelina under drought conditions, supporting its role in enhancing osmotic adjustment and maintaining metabolic activity under stress.

Proline accumulation exhibited a clear dose-dependent response to putrescine application. Moderate concentrations enhanced proline levels, whereas higher concentrations resulted in reduced accumulation. This pattern reflects the close metabolic interaction between polyamine and proline biosynthetic pathways, which share glutamate as a common precursor. Excessive polyamine availability may redirect nitrogen fluxes or exert feedback inhibition on Δ^1-pyrroline-5-carboxylate synthetase, thereby limiting further proline synthesis (Szabados and Savoure, 2010; Kavi Kishor and Sreenivasulu, 2013).

Importantly, the moderate accumulation of proline observed under combined putrescine and salicylic acid treatments appears to represent a regulated adaptive response rather than a symptom of severe stress. Under rainfed conditions characterized by reduced and irregular precipitation, moderate proline levels contribute to osmotic adjustment, redox buffering, and stabilization of proteins and membranes, while excessive accumulation may reflect metabolic imbalance and impaired growth. The observed negative or weak correlations between proline and photosynthetic traits (Table 7) further support the interpretation that higher proline levels primarily indicate stress intensity rather than improved physiological performance. Thus, the coordinated modulation of soluble sugars and proline under elicitor treatments reflects an optimized metabolic adjustment that supports stress acclimation without compromising photosynthetic efficiency.

Antioxidant enzyme activities: The significant enhancement of catalase, peroxidase, and ascorbate peroxidase activities under combined putrescine and salicylic acid application highlights the pivotal role of antioxidant defense in drought tolerance (Table 6). Water deficit leads to excessive production of reactive oxygen species, resulting in oxidative damage to lipids, proteins, and cellular membranes. The observed increase in antioxidant enzyme activities suggests an improved capacity to detoxify reactive oxygen species and maintain redox homeostasis.

Putrescine has been shown to stabilize membrane

Table 5. Comparison of the means interaction effect of putrescine and salicylic acid on soluble sugars and proline traits of Camelina

Treatment	Soluble sugar ($mg.gr^{-1}$ DW)	Proline ($\mu mol.g^{-1}$ FW)
Non-Put × Non-SA	38.56 hi	15.12 ef
Non-Put × SA 1 mM	40.09 g	21.93 b
Non-Put × SA 2 mM	58.07 a	21.25 b
Non-Put × SA 3 mM	44.56 de	16.88 def
Put 1 mM × Non-SA	38.94 h	18.84 ed
Put 1 mM × SA 1 mM	43.44 f	22.02 b
Put 1 mM × SA 2 mM	52.58 c	26.08 a
Put 1 mM × SA 3 mM	45.02 d	20.85 bc
Put 2 mM × Non-SA	40.03 g	22.01 b
Put 2 mM × SA 1 mM	43.41 f	22.32 b
Put 2 mM × SA 2 mM	44.53 de	22.31 b
Put 2 mM × SA 3 mM	54.42 b	17.81 de
Put 3 mM × Non-SA	34.85 j	21.95 b
Put 3 mM × SA 1 mM	43.82 ef	28.03 b
Put 3 mM × SA 2 mM	43.79 ef	14.05 f
Put 3 mM × SA 3 mM	36.94 i	16.11 def

Means within each column followed by the same letter are not significantly different (LSD, 0.05 probability level).

Table 6. Comparison of the average interaction effect of putrescine and salicylic acid on antioxidant enzymes activity in Camelina

Treatment	Ascorbate peroxidase	Peroxidase	Catalase
		(unitmg $protein^{-1}$)	
Non-Put × Non-SA	0.011 h	0.334 fg	0.522 g
Non-Put × SA 1 mM	0.016 fe	0.325 g	0.535 fg
Non-Put × SA 2 mM	0.019 e	0.376 c-f	0.646 b-e
Non-Put × SA 3 mM	0.032 abc	0.349 efg	0.701 abc
Put 1 mM × Non-SA	0.014 fg	0.353 d-g	0.593 c-f
Put 1 mM × SA 1 mM	0.017 ef	0.333 fg	0.638 b-f
Put 1 mM × SA 2 mM	0.029 cd	0.424 bc	0.739 a
Put 1 mM × SA 3 mM	0.031 abc	0.392 b-e	0.672 bcd
Put 2 mM × Non-SA	0.013 gh	0.345 fg	0.549 efg
Put 2 mM × SA 1 mM	0.020 e	0.373 c-g	0.573 d-g
Put 2 mM × SA 2 mM	0.027 d	0.400 bcd	0.781 a
Put 2 mM × SA 3 mM	0.030 a	0.485 a	0.609 c-g
Put 3 mM × Non-SA	0.014 gh	0.352 d-g	0.613 c-g
Put 3 mM × SA 1 mM	0.028 cd	0.373 c-g	0.621 c-g
Put 3 mM × SA 2 mM	0.030 bc	0.354 d-g	0.658 b-e
Put 3 mM × SA 3 mM	0.034 ab	0.447 b	0.575 d-g

Means within each column followed by the same letter are not significantly different (LSD, 0.05 probability level).

structures and modulate the expression of antioxidant-related genes, thereby indirectly enhancing enzymatic antioxidant capacity (Wasaya *et al*., 2023). Salicylic acid functions as a key signaling molecule that regulates redox-sensitive pathways and activates antioxidant defense responses (Miura and Tada, 2014). In agreement with these mechanisms, previous studies have reported enhanced activities of catalase, peroxidase, and ascorbate peroxidase in camelina and other oilseed crops following foliar application of salicylic acid or polyamines under drought stress (Rezaiean *et al*., 2024; Naderi *et al*., 2023).

The improved redox balance likely played a central role in preserving cellular integrity and metabolic activity under drought conditions, thereby supporting sustained growth and productivity. Among the antioxidant enzymes evaluated, ascorbate peroxidase (APX) exhibited the most pronounced response to combined putrescine and salicylic acid application, followed by catalase and peroxidase. This pattern reflects the central role of APX in fine-tuning hydrogen peroxide detoxification within chloroplasts and cytosol, particularly under moderate oxidative stress. The stronger responsiveness of APX compared with CAT suggests a greater reliance on the ascorbate–glutathione cycle under water-limited conditions, where precise redox regulation is required rather than bulk detoxification. Similar hierarchical activation of antioxidant enzymes under mild to moderate stress has been reported in other oilseed crops (Miura and Tada, 2014; Naderi *et al*., 2023).

Overall, the coordinated upregulation of antioxidant

Table 7. Correlation coefficients among evaluated traits in camelina

	Chla	Chlb	Total Chl	Carotenoid	soluble sugar	Proline	Catalase	APX	Peroxidase
Chla									
Chlb	0.141								
Total Chl	0.849**	0.643**							
Carotenoid	0.596**	-0.201	0.354*						
soluble sugar	-0.099	-0.092	-0.126	0.087					
Proline	-0.636**	0.175	-0.586*	-0.448**	0.154				
Catalase	-0.558**	-0.106	-0.488**	-0.345*	0.152	0.448**			
APX	-0.123	-0.413**	-0.315*	0.066	0.419**	0.408**	0.323*		
Peroxidase	0.389*	-0.187*	-0.398**	-0.192	0.202	0.430**	0.541**	0.488**	
Grainyield	0.145	0.222	0.230	0.048	-0.278*	0.019	-0.287	-0.302	-0.061

***, **: Significant at the 0.05 and 0.01 probability levels, respectively**

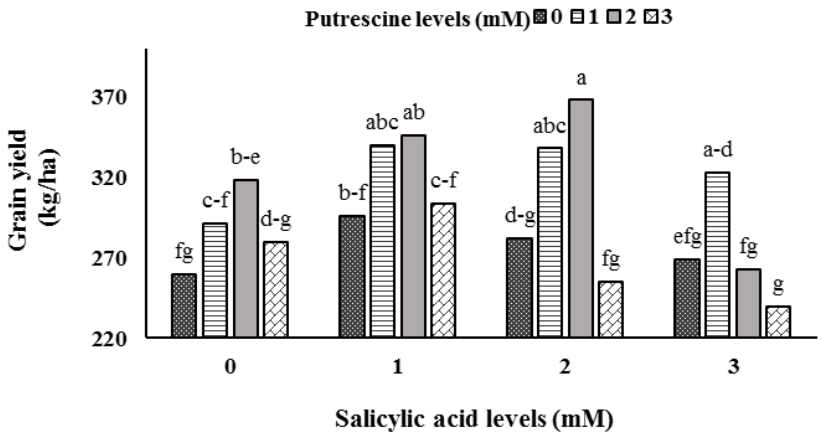

Figure 1. Effect of different concentrations of salicylic acid and putrescine levels on grain yield of camelina. The values represent the mean ± SE, and different letters in the columns indicate the significance of the means based on the LSD test (P<0.05).

enzymes contributed to improved redox balance, preservation of cellular integrity, and maintenance of metabolic activity under limited water availability. These responses support the conclusion that the combined application of putrescine and salicylic acid enhanced stress tolerance primarily through regulated antioxidant adjustment rather than through nonspecific stress-induced enzyme activation.

Grain yield: Grain yield represents the cumulative outcome of multiple physiological processes. In the present study, the enhanced yield observed under combined putrescine and salicylic acid application (Figure 1) reflects the integration of improved photosynthetic efficiency, effective osmotic regulation, and reinforced antioxidant defense.

Drought stress typically shortens the grain-filling period and limits assimilate translocation to developing seeds. However, the maintenance of higher chlorophyll content, improved carbon assimilation, and stabilized cellular metabolism under elicitor treatments likely contributed to sustained sink activity and improved assimilate partitioning. Polyamines have been reported to stabilize membrane integrity and influence hormonal balance, thereby supporting reproductive development and grain filling under stress conditions (Martin-Tanguy, 2001).

Consistent with previous reports on camelina and other oilseed crops, the present findings indicate that yield improvement under drought conditions arises from coordinated physiological regulation rather than from isolated enhancement of a single trait (Eskandarzadeh *et al*., 2025). These findings are in agreement with previous studies on camelina, where improved physiological traits under stress directly contributed to yield stability. For instance, Rezaiean *et al*. (2024) demonstrated that foliar application of putrescine along with nano-iron significantly increased grain yield in Camelina through enhanced photosynthetic pigments and antioxidant enzyme activity. Similarly, Naderi *et al*. (2023) reported that salicylic acid application improved grain yield under moderate drought stress by enhancing photosynthetic rate and antioxidant capacity. Furthermore, Alberghini *et al*. (2025) highlighted that drought-tolerant camelina lines maintained higher seed yield by preserving silique photosynthesis and assimilate partitioning under water deficit.

By mitigating oxidative damage and maintaining carbon assimilation under drought, elicitor-treated plants were able to sustain sink strength and grain-filling duration. These findings indicate that yield improvement was not a direct effect of growth stimulation alone, but rather the consequence of coordinated physiological regulation under stress conditions.

Conclusion

Collectively, the results of this study demonstrate that foliar application of salicylic acid and putrescine positively modulated several physiological traits of camelina under rainfed conditions, as evidenced by improved photosynthetic pigment content, enhanced antioxidant enzyme activities, and partial maintenance of metabolic balance. These responses indicate that both elicitors contributed to improving physiological resilience under limited soil moisture availability. However, the magnitude of these positive effects was strongly influenced by the prevailing climatic conditions, particularly the markedly low rainfall during the growing season.

Under such conditions, plants experienced prolonged water limitation, which intensified stress responses such as proline accumulation and activation of antioxidant systems. While these responses reflect effective protective mechanisms induced by salicylic acid and putrescine, they also indicate that stress intensity remained sufficiently high to constrain full physiological recovery and yield expression. Therefore, the observed improvements should be interpreted as stress-mitigating rather than stress-eliminating effects. Similar patterns have been reported in other studies under severe or prolonged drought, where elicitor applications improved physiological stability but could not fully offset the limitations imposed by water scarcity (Bukhari *et al*., 2022; Szabados and Savoure, 2010).

Consequently, although foliar application of salicylic acid and putrescine enhanced tolerance-related traits in camelina, the strong dependence of plant responses on seasonal rainfall highlights the necessity of multi-year and multi-environment evaluations to better assess the consistency and agronomic relevance of these treatments under rainfed conditions.

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