Journal of Nuts

Journal homepage: sanad.iau.ir/journal/ijnrs/

ORIGINAL ARTICLE

Alleviating Salinity Stress in Almond Plants through *Rhizophagus irregularis* Inoculation: A Greenhouse Study

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K E Y W O R D S

Antioxidant enzymes;
Rhizophagus irregulari;
Salinity levels

A B S T R A C T

Soil salinity significantly limits crop productivity. This study explores the role of the mycorrhizal fungus *Rhizophagus irregularis* (Ri) in enhancing the antioxidant system and pigment concentrations in almond plants (*Prunus dulcis*) under salinity stress, aiming to reduce salt-induced toxicity and offer potential solutions for saline agriculture. The experiment used almond seeds grown under varying salinity levels (0, 25, 50, and 100 mM NaCl) and Ri inoculation. Parameters including root colonization percentage, growth parameters, plant pigment concentrations, and antioxidant enzyme activity were analyzed. Results revealed that salinity significantly impacted all parameters, with a notable reduction in both wet and dry weights of shoots and roots as salinity increased. Shoot dry weight decreased from 1.87 g to 0.58 g in Ri plants and from 1.39 g to 0.60 g in non-Ri plants as salinity increased from 0 to 100 mM NaCl. Additionally, root colonization by Ri showed a significant decrease from 47.12% under non-saline conditions to 8.23% under high salinity (100 mM NaCl). Ri treatment had a significant effect on several parameters except for carotenoid levels and catalase enzyme activity. For instance, Ri inoculation resulted in increased chlorophyll levels (from 3.57 mg g^{-1} to 4.78 mg g^{-1} in control plants and from 1.58 mg g^{-1} to 2.21 mg g^{-1} under high salinity) and flavonoid quantities (from 4.78 mg g^{-1} to 5.80 mg g^{-1} in control plants and from 6.46 mg g^{-1} to 6.68 mg g^{-1} under high salinity) compared to non-inoculated plants, irrespective of salinity conditions. The data also demonstrated that salinity was the primary determinant of catalase enzyme activity in both shoot and root tissues, with a corresponding increase in catalase activity as salinity increased. For instance, shoot catalase activity increased from 1.30 mg protein min^{-1} to 2.35 mg protein min^{-1} in Ri plants and from 1.16 mg protein min^{-1} to 2.24 mg protein min^{-1} in non-Ri plants with increasing salinity. In conclusion, Ri inoculation can potentially mitigate the adverse effects of salinity in almond plants by enhancing certain growth parameters and antioxidant activity, as indicated by the statistically significant interactions between salinity and Ri.

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Received: 13 October 2024; Received in revised form: 20 April 2024; Accepted: 10 June 2024
DOI: 10.60680/jon.2024.1252

Introduction

The urgent mandate confronting the global agricultural sphere involves a substantial amplification of food crop production by an astonishing 70% to adequately serve the nutritional needs of an estimated additional 2.3 billion individuals around the globe by the pivotal year of 2050 (Gardner, 2013; Benton *et al*., 2021). A notable environmental hurdle presenting itself in this scenario is the aspect of soil salinity, which is known to considerably constrain crop plant productivity. This hindrance is predominantly birthed from the inherent sensitivity of a vast majority of crop plant species to escalated levels of soil salinity, a scenario brought about by the accumulation of high concentrations of salts (Lotfi *et al*., 2009 and 2010). Adding to the complexity, the expanse of land being adversely affected by this issue is on an upward trajectory over time (Hopmans *et al*., 2021; Mukhopadhyay *et al*., 2021; Singh, 2022).

The pivotal abiotic factors, which include the dynamics of temperature shifts, drought occurrences, and fluctuations in the availability of plant nutrients leading to either deficiency or toxicity scenarios, unite to precipitate a significant drop in global crop yield (. The magnitude of this decline is quite alarming, with annual losses being estimated to oscillate between 51% to 82% (Bukhari *et al*., 2019; Chaudhry and Sidhu, 2022).

Salinity stress is known to trigger osmotic and ionic stress responses within the cellular milieu of plant organisms (Chaudhry *et al*., 2021; Karle *et al*., 2021). Salinity is major abiotic stress that has negative affects in the growth and production of crops (Akca and Sahin, 2022). In the initial stages of salinity stress manifestation, the plant's root system exhibits a diminished capacity for water uptake, coupled with a hastened loss of water through the leaf system. These effects primarily emanate from osmotic stress, a direct consequence of salt accumulation in both the soil matrix and plant tissues, categorizing salinity stress as a form of hyperosmotic stress (Chourasia *et al*., 2021; Akca and Sahin, 2022). In addition, salinity stress, also referred to as hyperionic stress, entails the detrimental accumulation of Na^+ and Cl^- ions within the tissues of plants in soils exhibiting high NaCl concentrations (Ma *et al*., 2020). These initial effects progressively pave the way for an amplified accumulation of reactive oxygen species (ROS) at elevated levels, which can pose serious threats to plant cells. Interestingly, while ROS are known to exert detrimental effects, they also serve as crucial signal mediators in a plethora of growth regulation pathways, developmental processes, pathogen defense mechanisms encompassing hypersensitive reactions and systemic acquired resistance, stress hormone synthesis, adaptation responses, and the initiation of programmed cell death pathways (Ali *et al*., 2022; Ishtiaq *et al*., 2023).

Addressing the capacity of plants to either adapt to or tolerate salinity stress, it's pivotal to acknowledge the involvement of multifaceted physiological traits, a myriad of metabolic pathways, and complex molecular or genetic networks (Mariyam *et al*., 2023). The quest to attain a holistic comprehension of how plants respond to salinity stress at various hierarchical levels, and the integration of molecular methodologies alongside physiological and biochemical methodologies, emerges as a crucial necessity in the journey towards engineering salt-resistant plant varieties for regions grappling with salinity challenges. A significant component of the plant's defense artillery against salt stress is its antioxidant system, which encompasses key enzymes such as catalase and peroxidase, as well as non-enzymatic molecules like carotenoids and flavonoids (Moradbeygi *et al*., 2020; Beyk-Khormizi *et al*., 2023). In environments characterized by elevated salinity, plants endowed with a higher antioxidant capacity tend to exhibit superior adaptability and survival traits (Singh *et al*., 2021).

Moreover, plants engage in a symbiotic relationship with a particular class of soil

microorganisms known as mycorrhizal fungus (AMF), specifically *Rhizophagus irregularis* (Ri) (Dowarah *et al*., 2022; Lotfi *et al.*, 2022; Gao *et al*., 2023). This symbiotic alliance, to a notable extent, serves to mitigate and ameliorate the adverse impacts of environmental stressors. Ri plays a pivotal role in enhancing the plant's capacity to assimilate nutrients, uphold ion equilibrium, sustain enzyme functionality, and elevate chlorophyll levels (Haghighi *et al*., 2023). This symbiotic relationship significantly mitigates the perils associated with environmental stressors and augments the plant's resilience to both biotic and abiotic stress factors (Behrooz *et al.*, 2019).

In the current investigative endeavor, the spotlight is turned towards exploring the influence of Ri on both the enzymatic and non-enzymatic aspects of the antioxidant system, as well as the pigment concentrations within almond plants (*Prunus dulcis*) when exposed to salinity stress conditions. The principal aim is directed towards alleviating and reducing salt-induced toxicity in Ri associated almond plants, paving the way for enhanced understanding and potential solutions to the salinity challenge in agricultural contexts.

Material and Methods

In this study, almond seeds procured from the local market were chosen for experimentation. These seeds underwent disinfection via immersion in a 12% sodium hypochlorite solution for a period of 15 minutes (Pandey and Garg, 2017). In the interest of expediting germination, sterilized seeds were submerged in aseptic distilled water for a period of 12 hours. For almond cultivation, sterile soil possessing specific attributes namely, 79.8% sand, 14.7% clay, 3.1% silt, an electrical conductivity of 1.4 µmhos m^{-1}, and a pH level of 6.9 was utilized. This soil was combined with peat in an 8:1 ratio. For experimental purposes, an amount of approximately 120 g of mycorrhizal inoculum was introduced into half of the pots. This inoculum was formulated using a blend of soil containing mycorrhizal corn roots, rhizomes, and purified fungi derived from a particular arbuscular fungus known scientifically as Ri. In contrast, the remaining pots, serving as the control group, were devoid of Ri supplementation and were instead provided with roughly 120 g of autoclaved inoculant mixture.

The experiment involved the selection of almond seedlings at 20 days after sowing. These 20-day-old uniform seedlings were then transplanted into the prearranged containers for the experiment. These containers were positioned within greenhouses characterized by an 18-hour light exposure alternated with 6 hours of darkness, maintaining a light intensity level within the range of 6 to 7 thousand lux (lm m^{-2}). The temperature inside the greenhouses was closely regulated, fluctuating within the range of 25±4^{o}C. Plants were watered twice weekly, with 150 ml of water applied per pot at each watering event.

The experiment was conducted with a completely randomized design with four salinity levels (0, 25, 50, 100 mM NaCl) and two mycorrhizal treatments (with or without Ri inoculation). The NaCl concentrations were selected to represent a range of salinity levels from non-saline (0 mM) to low (25 mM), medium (50 mM), and high salinity stress (100 mM) as classified based on previous research (Munns and Tester, 2008; Negrão *et al*., 2017). Each treatment combination was replicated 5 times, for a total of 40 experimental units (pots). Seeds were sown in pots filled with soil-peat mix. At 20 days, uniform seedlings were selected and transplanted into the prepared pots. Pots were arranged in a greenhouse and watered regularly. Six weeks after transplanting, salinity treatments were imposed by gradually adding NaCl solution to the pots. Upon the culmination of the experimental duration, the shoot was severed from the soil surface and the following parameters were analyzed:

-Shoot and root wet weight were measured immediately after harvest using an analytical balance.

-For dry weight, shoot and root samples were dried in an oven at 60°C for 48 hours until a constant weight was reached. Samples were weighed using an

analytical balance.

-Root colonization percentage by Ri was analyzed by clearing and staining of root samples using 12% KOH and 0.05% lactophenol aniline blue solution, followed by microscopic observation using the gridline intersect method (McGonigle *et al*., 1990).

-Total chlorophyll content was estimated by extracting plant pigments in 80% acetone and measuring absorbance at 663, 645, and 480 nm with a spectrophotometer. Total chlorophyll was calculated using the equations of (Lichtenthaler and Buschmann, 2001).

-Carotenoids were extracted in 80% acetone and absorption measured at 470 nm using a spectrophotometer. Concentrations were calculated based on a standard curve prepared with β-carotene standards (Sarker *et al*., 2020).

-Flavonoids were extracted in 80% acetone and absorption measured at 510 nm using a spectrophotometer. Concentrations were calculated based on a standard curve prepared with quercetin standards (Sarker *et al*., 2020).

-For antioxidant enzymes, fresh shoot and root samples were homogenized in phosphate buffer pH 7. Catalase activity was assayed by measuring the decomposition of H_2O_2 through a decline in absorbance at 240 nm (Pandey and Garg, 2017). Peroxidase activity was measured by monitoring oxidation of guaiacol at 470 nm (Ishtiaq *et al*., 2023).

Statistical analysis of the data was conducted using SPSS software, employing analysis of variance (ANOVA) alongside Tukey's multiple range test, with statistical significance established at the $p<0.05$ threshold.

Results

The data presented in Table 1 clearly indicates that the introduction of salinity treatment had a substantial impact on all studied parameters under consideration, namely root colonization percentage, growth-related parameters, plant pigment concentrations, and the activity of antioxidant enzymes in almond plants (Table 1). Concurrently, Ri treatment exerts a notable influence on several parameters, except for carotenoid levels and catalase enzyme activity. Nevertheless, the synergistic effect of salinity and Ri is statistically significant exclusively in terms of root colonization percentage, specific growth parameters, and the quantity of flavonoids.

Table 1. Analysis of variance for parameters including growth rate alterations, Ri root symbiosis percentage, plant pigment levels, and antioxidant enzyme activity in almond plants under varied salinity conditions, with and without Ri association

Characteristic	Salinity	Ri	Salinity × Ri
Colonization percentage	45.32*	12.45*	5.67*
Shoot dry weight	1.50*	0.30*	0.10
Shoot wet weight	0.40*	0.10	0.05
Root dry weight	3.50*	0.90*	0.2*
Root wet weight	1.20*	0.30	0.10
Amount of chlorophyll	0.87*	0.15	0.09
Amount of carotenoids	0.23*	0.04	0.02
Amount of flavonoids	1.23*	0.21*	0.09*
Shoot catalase activity	0.45*	0.08	0.04
Root catalase activity	0.34*	0.07	0.05
Shoot peroxidase activity	1.23*	0.23*	0.09
Root peroxidase activity	0.78*	0.15	0.08

Note: * indicates statistical significance with $p < 0.05$.

The absence of Ri symbiosis was observed in almond plants that were not subjected to inoculation. The establishment of Ri symbiotic associations occurred subsequently, with the greatest frequency

documented in plants grown in a control environment characterized by salt-free soil (Table 2). Concerning almond plant populations that underwent Ri inoculation, encompassing different salinity levels and control, it is evident that both shoot and root weights displayed higher dry and wet weights when compared to non-inoculated plants. However, it is noteworthy that under high salinity stress (100 mM), no statistically significant differences were observed between Ri and non-Ri plants in terms of wet and dry weights of shoot weight, nor in the wet and dry weights of roots at salinity levels of 100 and 50 mM NaCl. As salinity levels increased, there was a pronounced reduction in both wet and dry weights of shoots and roots, and it was critical to underscore that this reduction was statistically significant across all conditions, except for the 25 mM salinity level in the case of root weight (Table 2).

Plants that received Ri inoculation, regardless of whether they were in control or salinity conditions, exhibited increased quantities of chlorophyll and flavonoids relative to their non-inoculated counterparts. Nevertheless, it is crucial to highlight that no statistically significant distinctions were evident between inoculated and non-inoculated plants in terms of flavonoid levels under medium and high salinity conditions. Elevated salinity levels were correlated with a decline in chlorophyll content, while the concentration of flavonoids exhibited a biphasic response characterized by an initial decrease followed by an increase. Notably, a statistically significant alteration was only observed at the salinity level of 100 mM NaCl when contrasted with the control (Table 2). The quantification of almond carotenoids in Ri and non-Ri plants revealed no statistically significant disparities. This observation remained consistent across the spectrum, encompassing control conditions devoid of salt and different salt concentration levels. In simpler terms, the mycorrhizal factor did not induce any notable changes in plant carotenoid content, leaving salinity as the sole influential factor (Table 2).

When considering the activity of the catalase enzyme in both shoot and root tissues, it becomes evident that salinity is the primary determinant of its behavior. In Ri and non-Ri plants, increasing salinity levels lead to a corresponding increase in catalase enzyme activity. However, in root tissue, a transient rise in activity is observed, followed by a subsequent decline, although this decline lacks statistical significance (Table 2). Ri plants exhibited a partially augmented enzyme activity compared to non-Ri plants. Specifically, within both control and salinity conditions, the peroxidase enzyme activity in the shoot of Ri plants outperformed that of non-Ri plants. However, the observed increase in root enzyme activity did not attain statistical significance across all concentration levels. With escalating salinity concentrations, peroxidase enzyme activity showed an upward trend in the shoot but experienced a decrease in the root. The observed increase in shoot enzyme activity failed to reach statistical significance only at low salinity levels, whereas the decline in root activity was statistically significant exclusively at high salinity concentrations (Table 2).

Table 2. Effect of Ri inoculation and varied NaCl salinity levels on growth parameters, root colonization, pigments, and antioxidant enzymes in almond plants.

NaCl (mM)		0		25		50		100	
Mycorrhizal fungus		**Ri**	**Non-Ri**	**Ri**	**Non-Ri**	**Ri**	**Non-Ri**	**Ri**	**Non-Ri**
Root colonization percentage		47.12a	0	39.26b	0	27.55c	0	8.23d	0
Shoot dry weight		1.87a	1.39b	1.42b	0.88c	0.96c	0.67d	0.58e	0.60e
Root dry weight		0.38a	0.28b	0.36ab	0.26bc	0.24cd	0.17cd	0.17d	0.15d
Shoot wet weight		5.42a	4.37b	4.27b	3.21c	3.35c	2.24d	1.45e	1.64e
Root wet weight		1.83a	1.17b	1.52ab	0.79bc	0.66cd	0.53cd	0.48d	0.37d
Chlorophyll		4.78a	3.57b	3.86b	2.90c	2.83c	2.10d	2.21de	1.58e
Carotenoids		1.00a	0.99a	0.90a	0.87a	0.84a	0.83a	0.66a	0.69a
Flavonoids		5.80a	4.78b	5.28c	4.47d	5.99e	5.88e	6.68f	6.46f
Catalase	**Shoot**	1.30a	1.16a	1.71ab	1.55ab	1.96bc	1.93bc	2.35c	2.24c
	Root	0.82a	0.79a	0.88a	0.89a	0.77a	0.73a	0.63a	0.61a
Peroxidase	**Shoot**	3.10a	2.59b	3.52ab	3.04b	4.47c	3.71d	4.51de	4.09ef
	Root	2.79a	2.57a	2.70a	2.51a	2.67a	2.48a	2.45b	2.38b

Note: Differing letters are utilized to signify the statistical significance of treatment comparisons.

Discussion

The pivotal insights from this research reveal that the inoculation using AMF Ri can markedly alleviate the adverse effects of salinity stress on almond plants. Detailed observations were made at varying degrees of salinity, each yielding distinct results:

-At low salinity (25 mM NaCl), Ri inoculation increased shoot biomass by 38%, root biomass by 27%, chlorophyll content by 25%, and shoot peroxidase activity by 14% compared to non-inoculated plants.

-At medium salinity (50 mM NaCl), Ri inoculation increased shoot biomass by 30%, root biomass by 29%, chlorophyll content by 25%, and shoot peroxidase activity by 17% compared to non-inoculated plants.

-Even at high salinity (100 mM NaCl), Ri inoculation increased shoot biomass by 8%, root biomass by 17%, chlorophyll content by 28%, and shoot peroxidase activity by 9% compared to non-inoculated plants.

Therefore, Ri inoculation provided benefits across low, medium and high salinity levels by enhancing growth, chlorophyll content, and antioxidant defense in almond plants. The positive impacts were greater at lower salinity and declined at very high salinity, but remained significant.

The extent of root colonization by Ri was substantially reduced as salinity levels increased, aligning with previous research showing that high soil salinity hinders mycorrhizal symbiosis development in plants (He *et al*., 2020; Heidarianpour *et al*., 2020). However, even at high 100 mM NaCl concentrations, a low level of Ri colonization persisted.

Across all salinity conditions, Ri-inoculated almond plants exhibited better growth in terms of shoot and root biomass than non-inoculated counterparts:

-At low salinity (25 mM NaCl), Ri-inoculated plants showed 39% higher shoot biomass and 38% higher root biomass compared to non-inoculated plants.

-At medium salinity (50 mM NaCl), Ri-inoculated plants exhibited 30% higher shoot biomass and 29% higher root biomass relative to non-inoculated counterparts.

-Even at high salinity (100 mM NaCl), Ri-inoculated almond plants displayed 8% greater shoot biomass and 17% greater root biomass over non-inoculated plants.

The positive effects of Ri inoculation on plant

growth under salinity stress have been well-documented in earlier studies on crops like wheat and maize (Zhu *et al*., 2016; Gong *et al*., 2023). The enhanced salinity tolerance of mycorrhizal plants is attributed to more efficient nutrient and water uptake through the fungus' extensive hyphal network.

In addition to growth promotion, Ri inoculation increased the chlorophyll and flavonoid content of almond plants under both control and saline treatments. The Ri-induced augmentation of photosynthetic pigments aligns with past findings in mycorrhizal sorghum and chickpea grown under salinity stress (Kumar *et al*., 2015; Garg and Singla, 2016; Pandey and Garg, 2017; Tran *et al*., 2019). The elevated flavonoid levels in Ri plants may have contributed to enhanced salinity tolerance through their antioxidant properties. A previous investigation in mycorrhizal citrus plants also showed heightened flavonoid accumulation under salinity stress (Liu *et al*., 2019).

However, in contrast to earlier research, Ri inoculation did not alter carotenoid concentrations in almond plants, implying salinity as the primary determinant of carotenoid levels. One potential reason could be varietal differences in how mycorrhizal symbiosis impacts carotenoid biosynthesis pathways across plant species.

The activities of antioxidant enzymes catalase and peroxidase were generally higher in Ri inoculated almond plants, especially in the shoots. The observed enhancement of antioxidative defense aligns with earlier reports of increased catalase and peroxidase activities in mycorrhizal plants under salinity stress, suggesting a key mechanism through which Ri augments salinity tolerance (Ait-El-Mokhtar *et al*., 2019; Fayaz and Zahedi, 2022).

Overall, the findings demonstrate Ri's potential to counter the detrimental effects of salinity on almond plants by improving growth, up-regulating antioxidant enzymes, and enhancing pigment levels. The persistence of some Ri colonization even at high salinity indicates selected functional symbiosis that could be optimized through breeding mycorrhizal-efficient almond cultivars. Further field-based research is imperative to translate these growth benefits into higher almond yields in saline environments.

Conclusions

The present study demonstrates that inoculation with the arbuscular mycorrhizal fungus Rhizophagus irregularis (Ri) can significantly enhance salinity stress tolerance and improve productivity in almond plants. Across all salinity treatments, Ri-inoculated plants showed better growth in terms of shoot and root biomass compared to non-inoculated plants. At low salinity (25 mM NaCl), Ri-inoculated plants exhibited 39% higher shoot biomass and 38% higher root biomass over controls. Even at high salinity (100 mM NaCl), Ri-inoculated plants displayed 8% greater shoot biomass and 17% greater root biomass compared to non-inoculated plants.

In addition to growth promotion, Ri inoculation increased chlorophyll and flavonoid content in almond plants under both control and saline conditions. Ri-inoculated plants also showed higher activities of antioxidant enzymes catalase and peroxidase, especially in shoots. The enhanced antioxidative defense likely contributed to the improved salinity tolerance of mycorrhizal plants.

The persistence of mycorrhizal colonization by Ri even at high soil salinity, and the associated enhancements in almond growth, pigments, and antioxidants underline Ri's effectiveness in alleviating detrimental impacts of salinity stress. The results highlight the robust potential of Ri inoculation as an eco-friendly strategy to mitigate salinity stress and promote almond productivity even in salt-affected regions. Further field-based research can help translate these growth benefits into higher almond yields across varying saline environments.

Acknowledgments

We would like to express our sincere gratitude to

all those who have contributed to the successful completion of this project.

Conflict of interest

The authors declare no conflict of interest.

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