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ARTICLE

RESEARCH ARTICLE

From seed to harvest: Salinity priming improves pea growth and yield under rainfed conditions

De la semilla a la cosecha: el acondicionamiento con tratamiento salino mejora el crecimiento y el rendimiento del guisante en condiciones de secano

Nevena Stevanović
BioSense Institute, University of Novi Sad, Dr Zorana Đinđića 1, 21101 Novi Sad, Serbia
Corresponding author: nevena.stevanovic@biosense.rs, https://orcid.org/0000-0002-1613-7509

Ružica Stričević
Faculty of Agriculture, University of Belgrade, Nemanjina 6, 11080 Belgrade, Serbia
https://orcid.org/0000-0003-0482-6718

Dragan Milošević
Meteorology and Air Quality Section & Hydrology and Environmental Hydraulics Section, Wageningen University & Research, P.O. Box 47, Wageningen 6700 AA, the Netherlands
https://orcid.org/0000-0001-5050-0052

Nikola Stanković
BioSense Institute, University of Novi Sad, Dr Zorana Đinđića 1, 21101 Novi Sad, Serbia
https://orcid.org/0000-0002-8601-8070

Maša Buđen
BioSense Institute, University of Novi Sad, Dr Zorana Đinđića 1, 21101 Novi Sad, Serbia
https://orcid.org/0000-0003-3825-5888

Nataša Ljubičić
BioSense Institute, University of Novi Sad, Dr Zorana Đinđića 1, 21101 Novi Sad, Serbia
https://orcid.org/0000-0001-5982-9401

Mirjana Vukosavljev
Institute of Field and Vegetable Crops, Laboratory for Biotechnology, Maksima Gorkog 30, 21101 Novi Sad, Serbia
Corresponding author: mirjana.vukosavljev@ifvcns.ns.ac.rs, https://orcid.org/0009-0002-9512-9992

Abstract: *Aim of study:* The aim of this research was to examine the effects of salinity-based seed priming on the growth, reproduction, and yield of pea (*Pisum sativum* L.) to determine its potential for enhancing drought resilience. *Area of study:* The field experiments were conducted over two vegetative seasons in Idvor, South Banat, Republic of Serbia. *Material and methods:* Pea seeds were subjected to pre-sowing salinity priming treatments using two concentrations of NaCl (40 mM and 80 mM), alongside a non-primed control group. The study assessed plant height, biomass, root growth, pod formation, and final yield. Data were analyzed using analysis of variance (ANOVA) to determine the influence of salinity levels and seasonal variations. *Main results:* Moderate salinity priming (40 mM NaCl) significantly enhanced plant height, biomass, and pod formation, suggesting that mild stress-induced adaptive mechanisms can improve performance. Conversely, high salinity (80 mM NaCl) inhibited germination and root development, leading to a complete loss of yield due to ion toxicity. ANOVA revealed that salinity concentration was the dominant factor influencing all examined traits, while seasonal variations had a significantly lesser impact. *Research highlights:* Optimizing salinity concentrations in seed priming is crucial for balancing stress adaptation; while 40 mM NaCl improves pea growth traits, concentrations as high as 80 mM are detrimental and lead to total reproductive failure.

Keywords: drought; growth parameters; NaCl treatment; peas; seed priming; yield.

Resumen: *Objetivo del estudio:* El objetivo de esta investigación fue examinar los efectos del acondicionamiento de semillas mediante tratamiento salino en el crecimiento, la reproducción y el rendimiento del guisante (*Pisum sativum* L.), con el fin de determinar su potencial para mejorar la resiliencia frente a la sequía. *Área de estudio*: Los experimentos de campo se llevaron a cabo durante dos temporadas vegetativas en Idvor, Banato Sur, República de Serbia. *Materiales y métodos:* Las semillas de guisante fueron sometidas a tratamientos de preparación con salinidad antes de la siembra, utilizando dos concentraciones de NaCl (40 mM y 80 mM), junto con un grupo control sin preparación. El estudio evaluó la altura de la planta, la biomasa, el crecimiento radicular, la formación de vainas y el rendimiento final. Los datos se analizaron mediante análisis de varianza (ANOVA) para determinar la influencia de los niveles de salinidad y las variaciones estacionales. *Resultados principales:* La preparación moderada de salinidad (40 mM NaCl) mejoró significativamente la altura de la planta, la biomasa y la formación de vainas, lo que sugiere que los mecanismos adaptativos inducidos por un estrés leve pueden mejorar el desempeño. Por el contrario, una alta salinidad (80 mM NaCl) inhibió la germinación y el desarrollo radicular, provocando una pérdida total del rendimiento debido a la toxicidad iónica. El análisis por ANOVA reveló que la concentración de salinidad fue el factor dominante que influyó en todos los rasgos examinados, mientras que las variaciones estacionales tuvieron un impacto significativamente menor. *Aspectos destacados de la investigación:* Optimizar las concentraciones de salinidad en la preparación de semillas es crucial para equilibrar la adaptación al estrés; mientras que 40 mM NaCl mejora los rasgos de crecimiento del guisante, concentraciones tan altas como 80 mM son perjudiciales y conducen a un fracaso reproductivo total.

Palabras clave: guisantes; parámetros de crecimiento; preparación de semillas; rendimiento; sequía; tratamiento con NaCl.

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Supplementary information ↓

1. INTRODUCTION

Pea (*Pisum sativum* L.) is a valuable high-protein crop widely cultivated across vast areas in temperate regions around the world (Gainullina *et al.*, 2025). Recent studies have emphasized the need to enhance pea resilience under abiotic stress, particularly salinity and drought, through seed priming techniques (Farooq *et al.*, 2006). As a leguminous crop, pea forms a symbiotic relationship with Rhizobium leguminosarum in its root nodules, allowing it to fix atmospheric nitrogen and thereby reducing its need for external nitrogen inputs (Kaziūnienė, J. *et al.*, 2025). Pea cultivations thrive in cool climates, preferring an average temperature range of 10–18°C during their growth period. Seed germination is inhibited when planting temperatures drop below 5°C, though peas can tolerate frost during the early stages of development (Tekin *et al.* 2024). Pea is one of the most important vegetable species in Serbia, particularly in Vojvodina, which accounts for most of the country's agricultural production (Strahinja *et al.*, 2019). Peas have long been an important component of the human diet due to their abundant starch, protein, and essential nutrients. Their health benefits are primarily attributed to the high levels of fiber, vitamins, minerals, phytochemicals, and macronutrients such as starch and protein (Gawłowska *et al.*, 2024). Moreover, peas are particularly valued during their early technological maturity stage for their high protein, sugar, and starch content, which makes them an excellent source of energy (Červenski *et al.*, 2024).

Serbia traditionally offered favourable conditions for pea cultivation, including rising temperatures, changes in precipitation patterns, and more frequent extreme weather events. However, over the past decades, Serbia has experienced significant climatic changes, including rising temperatures, altered precipitation patterns, and an increased frequency and intensity of extreme weather events (Bezdan *et al.*, 2024; Vukovic-Vimic & Vujadinovic-Mandic, 2024). These changes have contributed to prolonged drought periods, posing a serious threat to agriculture, a key sector of the country's economy. Drought stress has become more prevalent, leading to reduced crop yields, soil degradation, and increased challenges in water resource management (Yu *et al.*, 2020; Mimić *et al.*, 2022). Given these climatic shifts, it is crucial to explore adaptive strategies that enhance plant resilience to water deficit conditions. Recent findings have demonstrated that seed priming—particularly with saline, osmotic, or nanoformulated agents—can significantly improve pea performance under drought and salinity stress (Farooq *et al.*, 2006; Tamindžić *et al.*, 2023; Tamindžić *et al.*, 2024).

Drought stress is a major environmental factor constraining plant growth and productivity globally (Fahad *et al.*, 2017; Seleiman *et al.*, 2021). Plants have evolved various physiological and biochemical mechanisms to cope with water deficit, including osmotic regulation, which is critical for maintaining cellular homeostasis (Blum, 2017; Ozturk *et al.*, 2020). These mechanisms are further enhanced through priming-induced metabolic reprogramming, as shown in recent studies on pea where nanopriming and microalgae-based treatments improved antioxidant activity, nutrient uptake, and early vigor (Tamindžić *et al.*, 2024; Abinandan *et al.*, 2025). One promising strategy to enhance plant drought tolerance is seed priming, a pre-sowing treatment that triggers physiological and biochemical changes, preparing seeds for adverse environmental conditions (Marthandan *et al.*, 2020).

Seed priming is a process in which seeds are pre-exposed to an eliciting factor, enhancing their tolerance to future stress conditions. This widely used agricultural practice involves subjecting seeds to mild abiotic stress, which prepares them for greater resilience against subsequent exposures (Tanou *et al.*, 2012; Ibrahim, 2016). By improving seed vigour, priming promotes better early plant development, uniform germination, and stable growth, even under stress. It enhances membrane repair, strengthens antioxidant defenses, and stimulates pre-germination metabolic activities, allowing for quicker and more synchronous emergence (Ibrahim, 2016). This approach can mitigate the negative effects of abiotic stress, improving plant growth, yield, and overall yield quality. Its benefits are particularly pronounced under rainfed or limited irrigation conditions, where plants better adapt to fluctuating soil moisture and respond more rapidly to stress (Harris *et al.*, 1999; Mustafa *et al.*, 2017).

Among different priming methods, seed priming with saline solutions has gained attention as a potential approach to enhance stress tolerance. The halopriming technique involves soaking seeds in a low-concentration salt solution, which induces mild stress and stimulates adaptive responses before germination (Choudhary *et al.*, 2021). In addition to conventional halopriming, recent work has explored alternative agents such as KNO_3, PEG, and calcium-silicate nanoparticles, which have demonstrated comparable or even superior effects on pea germination and drought tolerance (Tamindžić *et al.*, 2023; Tamindžić *et al.*, 2024). This method enhances seed germination, seedling vigour, and enzymatic activity, enhancing the plant's tolerance to osmotic stress during drought. According to Ding *et al.* (2020), saline priming contributes to better drought resilience and overall plant performance in water-limited environments by enhancing water uptake efficiency and ion homeostasis.

This study aims to determine the effect of seed priming with saline solutions on the development of pea plants, including their morphological traits, and on overall yield under rainfed conditions. Additionally, the research will investigate how seed priming influences growth parameters and overall plant health under stress conditions when sown in early spring (favourable for peas) and late spring (less favourable growing conditions). Understanding these effects is crucial for enhancing crop performance and resilience in regions with irregular rainfall, thereby supporting more sustainable agricultural practices under changing climatic conditions.

2. MATERIAL AND METHODS

2.1. Study area

The experiment was conducted in 2024 in Idvor, South Banat, Serbia (45.1883° N, 20.5134° E), across two sowing periods (Figure 1). The sowing occurred in two successive vegetation seasons. The first sowing took place on March 8th and was harvested on June 2nd, while the second sowing occurred on April 7th and was harvested on June 16th. The vegetative period for the first sowing was 86 days, and 73 days for the second.

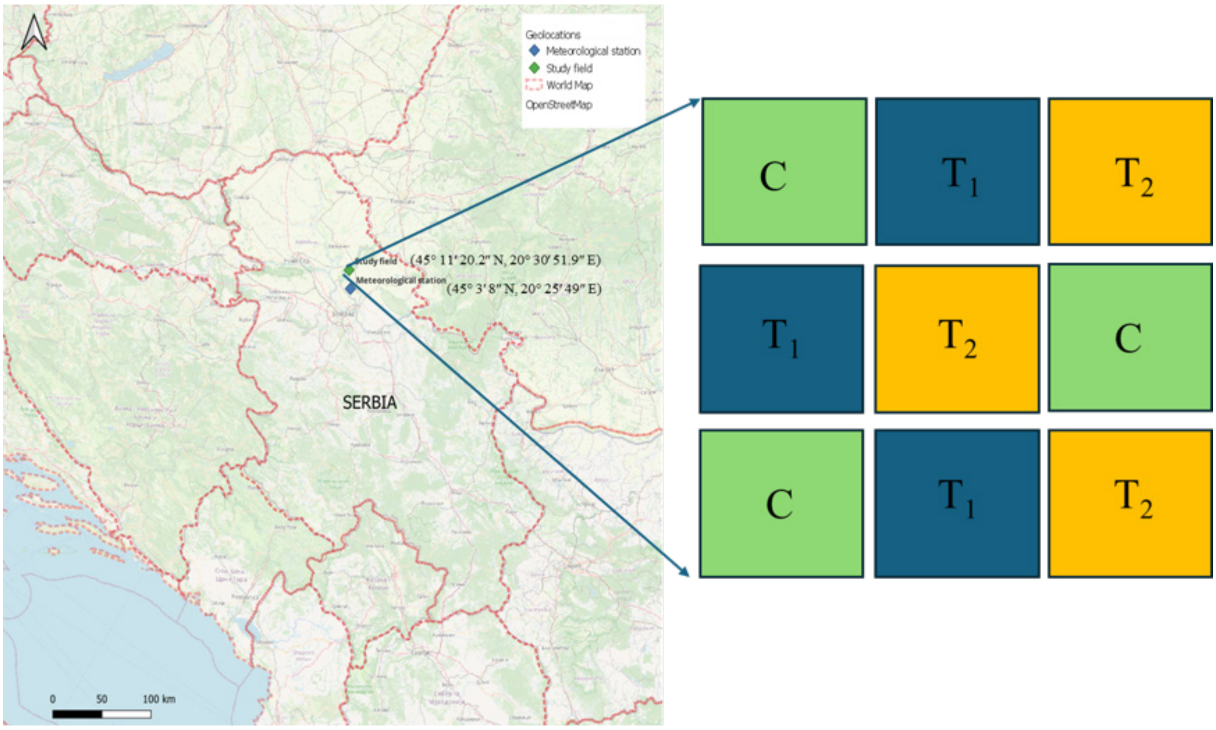


Figure 1. Location of the study field, meteorological station and schematic representation of the field trial layout indicating distribution of treatments. Coordinates are given in the WGS84 coordinate reference system.

The study area can be characterized as a Cfa temperate climate according to the Köppen-Geiger climate classification system (Kottek *et al.* 2006). This climate type provides favorable conditions for pea cultivation, due to its temperate continental climate and distinct seasonal patterns. Peas thrive in cooler conditions, and the region's mild spring temperatures favor germination and flowering. The rainfall during spring, with 40.9 mm in April and 61.3 mm in May, ensures that the soil retains adequate moisture, meeting the water requirements of this crop (Table 1). Additionally, the absence of frost days from May onward allows for steady growth without the risk of cold damage. Humidity levels between 65.6% and 69.7% during this period, combined with moderate sunlight, provide a balance that supports healthy plant development. Together with long daylight hours in spring and early summer, these factors support smooth transition to pod formation and maturation. Climatological data were obtained from the Republic Hydrometeorological Service of Serbia for the official meteorological station Zrenjanin for the period 1991-2020. This is the closest official meteorological station to the study area, at about 25 km.

Table 1. Average monthly, annual and extreme values for the standard climatological period of 1991-2020 in Zrenjanin, Serbia. Source: Republic Hydrometeorological Service of Serbia

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	ANNUAL
Air temperature													
Average	0.7	2.4	7.0	12.6	17.5	21.2	22.9	22.7	17.5	12.2	7.0	1.8	12.1
max	3.8	6.7	12.5	18.5	23.4	26.9	29.0	29.5	24.0	18.1	11.2	4.7	17.4
min	-2.3	-1.3	2.2	6.8	11.5	15.1	16.4	16.3	12.1	7.5	3.6	-1.0	7.2
number of frost days	20.0	15.8	9.7	1.3	0.1	0	0	0	0	1.9	6.8	16.7	72.3
number of tropical days	0	0	0	0.1	1.9	8.2	13.5	14.2	3.3	0.1	0	0	41.3
Relative humidity (%)													
	84.5	78.7	69.7	65.6	66.1	67.6	65.3	64.4	70.3	75.4	80.5	86.1	72.9
Precipitation													
sum (mm)	36.6	33.7	35.1	40.9	61.3	84.3	59.4	50.9	54.9	49.7	43.6	46.7	597.1
number of days > =0.1 mm	12.2	10.7	10.3	10.6	12.4	11.8	9.4	7.5	10.1	9.2	10.3	12.3	126.8
number of days > = 10 mm	1.2	0.7	0.9	1.0	1.5	2.7	1.6	1.6	1.7	1.3	1.2	1.2	16.6
Number of days with													
Snow	6.1	5.6	2.7	0.3	0	0	0	0	0	0	1.7	4.7	21.1
Hail	0	0	0	0.2	0.2	0.4	0.1	0	0	0	0	0	0.9
Insolation (h)													
	70.9	104.0	164.1	206.5	248.7	276.3	307.5	292.9	209.4	165.0	98.1	61.2	2204.6

2.2. Experimental setup

The field experiment was conducted using the pea variety ‘Mali Provansalac’, a locally adapted genotype. Prior to sowing, seeds were primed in NaCl solutions and kept in darkness at 25°C for three days. Three treatments were applied: control (C, 0 mM NaCl), treatment 1 (T1, 40 mM NaCl), and treatment 2 (T2, 80 mM NaCl). After priming, seeds were air-dried at room temperature for 48 hours and stored in paper bags until sowing.

The experiment was arranged in a randomized complete block design (RCBD) with three treatments and three replications per treatment. Each plot measured 10 m² (2 m × 5 m), with 30 plants per plot spaced at 30 cm intervals. Replications were randomly distributed within blocks to minimize the influence of field heterogeneity. Buffer zones of 1 m were established between plots and blocks to prevent treatment interference. Sowing was performed under rainfed conditions, and no irrigation or fertilization was applied during the growing season.

To assess the influence of varying agroclimatic conditions on pea response to salinity priming, two sowing dates were implemented within the same growing year: early spring (March) and late spring (May). These sowings were treated as distinct agroclimatic phases due to differences in temperature, rainfall distribution, and crop development dynamics. Each sowing was analyzed separately to evaluate genotype × environment × treatment interactions.

The conditions were rainfed, with no additional irrigation applied. Meteorological data were obtained from a nearby weather station installed near the experimental field, including minimum and maximum temperatures, precipitation, relative humidity, wind speed and direction and solar radiation. For the research, daily reference evapotranspiration values (ETo) were determined using the standard FAO

Penman-Monteith method. The crop coefficient (Kc) values were obtained from relevant literature (Allen *et al.*, 1998), while crop evapotranspiration (ETc), was calculated as a product of the crop coefficient and reference evapotranspiration. The soil at the experimental site is classified as chernozem (Škorić *et al.*, 1985), which is suitable for pea cultivation.

At the end of the growing season, measurements were taken for germination rate, plant height, root length, number of pods, plant mass, number of seeds, pod mass and number of seeds per pod for both growing dates. Samples were collected from an area of 1 m2 within each treatment, across all three replications.

2.3. Measured traits

A range of morphological and yield-related parameters were recorded to assess the effects of salinity priming across genotypes and sowing dates. Germination rate (%) was determined by counting the number of emerged seedlings seven days after sowing, expressed as a percentage of total seeds sown per plot.

Plant height (cm) was measured from the soil surface to the apex of the main stem at the flowering stage using a standard measuring tape. Root length (cm) was assessed at harvest by carefully uprooting five randomly selected plants per plot and measuring the primary root from base to tip.

The number of pods per plant was counted manually at physiological maturity on ten randomly selected plants per plot. Pod mass (g) was measured by weighing all pods harvested from the same ten plants using a digital scale.

Plant fresh biomass (g) was recorded immediately after harvest, while grain number per pod was calculated by averaging the number of seeds per pod from ten pods randomly selected per plot. Final grain yield ($Mg \cdot ha^{-1}$) was determined by harvesting all plants within each plot, threshing the seeds, and converting the total seed weight to tons per hectare based on plot area.

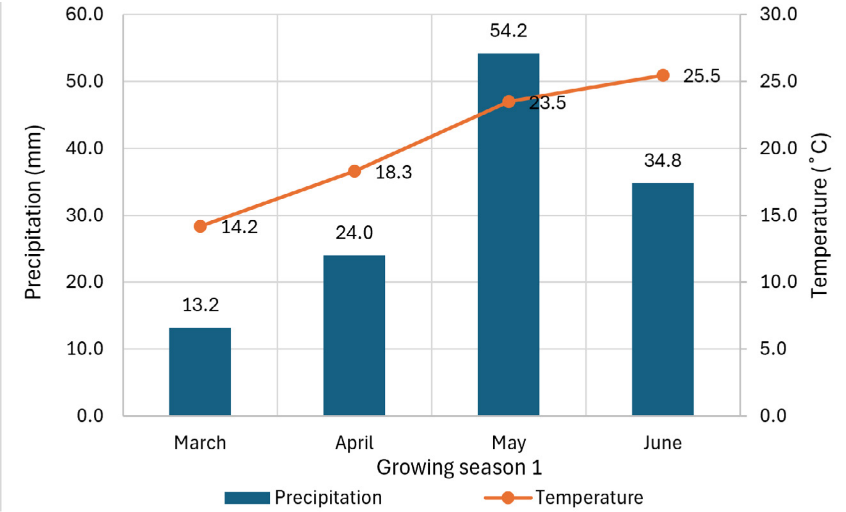
2.4. Statistical analysis

All statistical analyses were performed using Statistica 6.1 version (StatSoft Inc., Tulsa, OK, USA). A two-way analysis of variance (ANOVA) was conducted to evaluate the effects of salinity treatments, sowing date (March – growing season 1 [GS1]; May – growing season 2 [GS2]), and their interaction on yield-related traits. Prior to ANOVA, data were tested for normality and homogeneity of variances. Differences between treatment means were determined using Tukey's Honest Significant Difference (HSD) test at a significance level of $p < 0.05$.

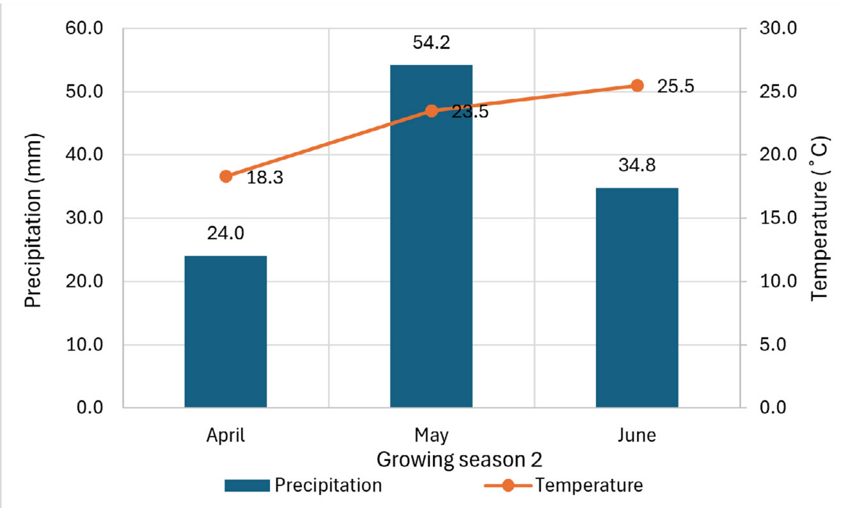
3. RESULTS

3.1. Meteorological conditions during the growing seasons

Data from the meteorological station indicate that during the growing season for the first sowing date, the total precipitation amounted to 91.4 mm, while for the second sowing date it was 113 mm. Although peas generally have high water requirements throughout the growing season, rainfall was unevenly distributed, with the majority occurring in May (54.2 mm) (Figure 2), coinciding with pod development and seed formation stages - periods of highest water demand. Due to the lack of irrigation, rainfall was insufficient to compensate for water loss through transpiration, resulting in a mild water deficit during the growing seasons (Table 2), as peas also relied on water stored in the soil during the cold period.



a)



b)

Figure 2. Average monthly air temperature and monthly precipitation totals during the first (a) and the second (b) growing season.

Table 2. A summary of reference evapotranspiration (ETo), crop evapotranspiration (ETc), and precipitation (ΣP) for both growing seasons (early spring and late spring, 2024) in Vojvodina region, Serbia

Season	ΣETo (mm)	ΣETc (mm)	ΣP (mm)
VG1	157.2	153.9	91.4
VG2	150.9	149.4	113

Average monthly air temperatures ranged from 14.2 °C in March to 25.5 °C in June (Figure 2), remaining within the optimal range for all stages of pea growth and development. The average monthly wind speed varied from 0.5 m/s in June to 1.1 m/s in May, while relative humidity fluctuated between 69% in June and 75% in May. Both wind speed and relative humidity remained within optimal values for the region.

Table 2 presents cumulative values of reference evapotranspiration (ETo), crop evapotranspiration (ETc), and precipitation during the growing seasons. During the first growing season (VG1), peas exhibited higher evapotranspiration values compared to the second growing season (VG2), despite having less precipitation available. It is important to note that during the early spring sowing, the pea crop in VG1 was able to utilize soil moisture accumulated over the winter period. Slightly lower evapotranspiration values (by only 4 mm) were observed in VG2, even though it received 12 mm more precipitation.

3.2. Pea growth parameters

Pea growth parameters were compared using descriptive statistics, and the results are presented in Table 3. In both seasons, the germination rate decreased with increasing salt concentration. For VG1, the control (C) had a germination rate of 70%, while T1 and T2 dropped significantly to 50% and 16.7%, respectively. A similar trend is observed in VG2. The plant height was highest under T1 treatment, while a slight reduction in plant height was observed in the control treatment. However, in T2, plant height was significantly reduced, particularly in VG2.

Table 3. Descriptive statistics of the effects of seed priming with NaCl solutions (C-0, T1-40, T2-80 mm) on pea traits across two growing seasons (early spring and late spring, 2024) in Vojvodina region, Serbia

Trait	Season	Treatment		
		C (mean ± SD)	T1(mean ± SD)	T2(mean ± SD)
Germination rate (%)	VG1	70.0 ± 10.0	50.0 ± 0.0	16.7 ± 5.8
	VG2	76.7 ± 5.8	53.3 ± 5.8	13.3 ± 5.8
Height (cm)	VG1	27.87 ±12.49	37.9 ± 9.4	20.07 ± 12.9
	VG2	27.4 ± 9.3	37.3 ± 7.7	18.2 ± 12.3
Root length (cm)	VG1	18.7 ± 53.4	11.5 ± 11.3	3.9 ± 1.3
	VG2	12.9 ± 4.3	12.0 ± 2.6	3.6 ± 1.3
Pod number	VG1	2.3 ± 2.5	3.6 ± 3.2	0.7 ± 1.0
	VG2	2.5 ± 1.9	3.9 ± 2.5	0.5 ± 1.0
Plant mass (g)	VG1	13.95 ± 11.1	19.1 ± 8.3	7.7 ± 8.8
	VG2	26.2 ± 7.9	26.1 ± 4.6	6.2 ± 8.6
Pod mass (g)	VG1	3.07 ± 4.4	2.1 ± 1.9	0.75 ± 1.4
	VG2	6.9 ± 3.5	1.2 ± 0.5	0,0 ± 0.0
Grain number per pod	VG1	1.25 ± 1.4	2.2 ± 1.4	0.0 ± 0.0
	VG2	2.4 ± 2.1	2.6 ± 1.2	0.0 ± 0.0
Yield ($Mg·ha^{-1}$)	VG1	3.3 ± 0.52	4 ± 0.68	0.0 ± 0.0
	VG2	5.6 ± 1.2	5.4 ± 0.92	0.0 ± 0.0

Root length was significantly affected by salinity levels. The highest values were recorded in the control treatment (C) for both seasons. While the T1 treatment resulted in a slight reduction, the T2 treatment caused a drastic decrease in root length, reaching only 3.9 cm in VG1 and 3.6 cm in VG2. These results indicate that high salt concentrations severely inhibit root system development regardless of the growing season.

The number of pods increased under the influence of moderate salinity priming compared to the control treatment, reaching the maximum numbers of 3.6 and 3.9 in VG1 and VG2, respectively. However, when more extreme salinity was present (T2 treatment), the number of pods was greatly decreased, with observations of 0.7 and even 0.5 pods in both VG1 and VG2. The number of pods in the control treatment remained stable, with approximately 2.5 pods observed in both VG1 and GV2. The highest plant mass was observed during VG2 on both C and T1 treatment (62.2 g), but significantly reduced under the T2 priming to 6.2 g. In VG1, plant mass ranked from highest to lowest as follows: T1 > C > T2.

The pod mass was also significantly reduced under the extensive priming in comparison with the control treatment, obtaining the maximal number of 3.6 and 3.9 in VG1 and VG2 under moderate priming. In VG1, pod mass decreased in T2 compared to the control, while in VG2, pods were not formed. These data highlight the serious negative impact of salt on pod production, particularly in the T2 treatment.

Plant dry biomass was highest under the moderate treatment (T1), with slight reductions observed in the C treatment. The greatest decline in biomass was observed in T2, with the control treatment in VG1 reducing biomass from 13.95 g to 7.7 g. A similar trend was noted in VG2, where biomass dropped from 26.2 g in the control treatment to 6.2 g in T2.

Grain number per pod was increased with mild salinization (T1 treatment), with complete absence of grain in both vegetative seasons under T2 (0.0 seeds per pod). These results indicate a significant decline in reproductive success under high salinity, while moderate salinization induced an increase in the number of pea grains.

The yield results demonstrated a significant variation between treatments and growing seasons. In VG1, the C treatment achieved a yield of 3.3 Mg·ha^{-1}, while mild salinity priming (T1) increased the yield. In VG2, the control yield was higher at 5.6 Mg·ha^{-1}; however, mild salinity priming (T1) resulted in a slight reduction, yielding 5.4 Mg·ha^{-1}. Notably, in both growing seasons, the high salinity treatment (T2) resulted in no yield, highlighting its detrimental effect on productivity. These findings underscore the complex interaction between salinity levels and crop yield under different environmental conditions.

4. ANALYSIS OF VARIANCE

The analysis of variance for pea traits indicated that the different treatments significantly affected certain plant characteristics. While the growing season and its interaction with treatment were not statistically significant ($p > 0.05$), salt-based seed priming had a highly significant effect on germination rate ($p = 0.00000004694$), indicating that salinity levels are the primary determinant of this trait (Table 4). Salt-based priming also had a highly significant effect on plant height ($p = 0.00006$), whereas the growing season and its interaction were not significant, suggesting that salinity is the main factor influencing this trait.

Table 4. Analysis of variance for the effects of growing season, salinity and their interaction on pea plant traits. Statistically significant differences are presented in bold in the table

Trait	Growing season (p-value)	Salinity (p-value)	Interaction (p-value)	Significant effect
Germination	0.539	**0.00000004694**	0.5158	Salinity
Plant height	0.8288	**0.00006**	0.9758	Salinity
Root length	0.6509	0.5372	0.8803	None
Plant biomass	**0.00164**	**0.000029**	0.7149	Growing season, Salinity
Pods number per plant	0.6288	**0.0057**	0.9628	Salinity
Pod weight	0.2361	**0.00177**	0.9128	Salinity
Grain number per pods	**0.02745**	**0.02727**	0.9384	Growing season, Salinity

For root length, neither the growing season, salinity, nor their interaction exhibited a statistically significant effect ($p > 0.05$), indicating that these treatments did not substantially impact this trait.

Regarding plant biomass, both the growing season and salinity showed significant effects ($p = 0.00164$ and $p = 0.000029$, respectively), while their interaction was not significant. Similarly, for pod weight, salinity had a significant influence ($p = 0.00177$), whereas the growing season and their interaction were not significant, with a similar pattern observed for the number of pods per plant.

For the number of grains per pod, both the growing season and salinity had significant effects (p = 0.02745 and p = 0.02727), while their interaction was not significant. These findings emphasize that salinity exerts a dominant influence on most evaluated traits, highlighting the importance of this treatment in enhancing pea crop characteristics.

4.1. Traits of pea plants across growing seasons

The analysis of variance in pea plant height revealed significant differences between the factors of growing season and salinity levels (Figure 3a). The first growing season showed greater overall variability compared to the second season, suggesting a more pronounced impact of seasonal conditions on plant growth. Treatments with moderate salinity (T1) showed the lowest variance in both seasons, suggesting a stabilizing effect on plant growth. In contrast, high salinity levels (T2) resulted in a substantial increase in variability, likely due to stress induced by salinity.

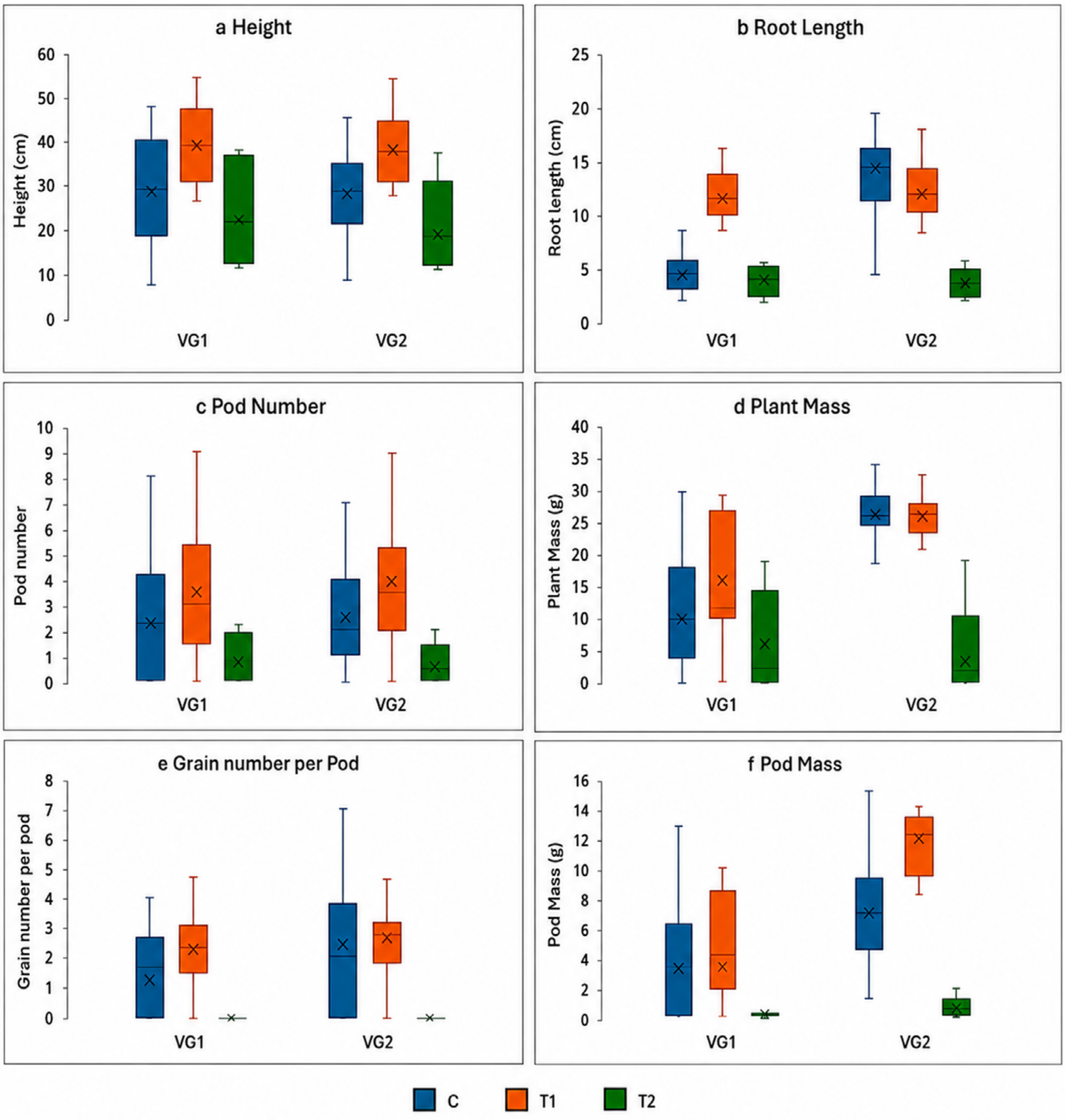


Figure 3. The average pea growth and yield traits for the control treatment (C), treatment 1 (T1) and treatment 2 (T2) during the two growing seasons.

Significant differences in variability of pea traits were observed between growing seasons and salinity treatments (Figure 3). For root system length (Figure 3b), the first growing season exhibited higher variability under control conditions (C) compared to the second season, highlighting a stronger seasonal influence under non-stressed conditions. Moderate salinity (T1) reduced variability in the first season and slightly increased it in the second, indicating a stabilizing effect on root growth. High salinity (T2) resulted in the lowest variability in both seasons, reflecting uniform but stress-limited root development. For the number of pods per plant (Figure 3c), variability was greater in the first season under control conditions, whereas T1 increased variability in both seasons, suggesting a less consistent response of pod production. T2 showed the lowest variability, indicating uniform but limited pod formation under severe salinity. Plant biomass (Figure 3d) followed a similar pattern: the first season displayed higher variability under control treatment, T1 stabilized biomass accumulation in both seasons, and T2 produced consistently low biomass. Variability in grain number per pod (Figure 3e) was higher in the first season under control conditions, while T1 reduced variability in both seasons, leading to more consistent grain production. No grains were produced under T2, resulting in zero variability. Finally, pod mass (Figure 3f) showed higher variability in the first season under control treatment; T1 increased variability across both seasons, whereas T2 produced minimal pod mass with very low variability, particularly in the first season. These results emphasize that seasonal conditions and salinity treatments significantly influence variability in pea growth and yield traits.

5. DISCUSSION

In both seasons under study, the use of a salt solution for seed priming considerably decreased the rates of seed germination. This outcome demonstrates how high osmotic potential impairs the seed's capacity to germinate successfully. Analysis of variance (ANOVA) was used to statistically confirm the data, showing a consistent trend across both seasons. The comparison between our findings and previous studies suggests that the applied salt concentration during seed priming was excessively high, leading to toxic effects on the seed embryo. Similar results have been reported in earlier research (Wang *et al.*, 2022), where elevated salt concentrations during priming were shown to create osmotic stress and ion toxicity, which disrupted metabolic processes essential for seed germination. These findings emphasize the need to carefully optimize salt concentrations in priming solutions to avoid such inhibitory effects while still achieving potential benefits like stress adaptation. Further studies are recommended to determine the threshold concentrations that balance stress alleviation with germination enhancement. Furthermore, recent studies (Dahal *et al.*, 1990, Schwember & Bradford, 2010, Monajjem *et al.*, 2023) have demonstrated that seed priming in crops such as tomato, rice, and lettuce is genotype-dependent. This suggests that the effectiveness of priming treatments may vary significantly among different genetic backgrounds, influencing seed germination, seedling vigor, and overall plant performance. Given these findings, it is essential to consider genotype-specific responses when optimizing priming protocols to maximize their benefits. Understanding these responses can help develop more effective agricultural practices to enhance crop resilience and productivity.

Hamad (2023) found that salt stress significantly reduces germination, radicle and plumule length, and seedling weight in some legume species. El-Sanatawy *et al.* (2021) in their research found that NaCl priming of seeds before sowing can increase salt tolerance – it stimulates germination by regulating metabolic activities. Although higher NaCl levels reduce seed viability and seedling growth, NaCl priming mitigates the negative effects of salinity on seedling emergence and growth.

Compared to previous studies on pea seed priming under salinity stress (Okcu *et al.*, 2005; Tamindžić *et al.*, 2023; Abinandan *et al.*, 2025; Goufa *et al.*, 2025), our protocol yielded higher shoot biomass and improved acclimatization rates. Earlier approaches typically employed shorter priming durations (6–12 h) and lower NaCl concentrations (25–50 mM), whereas our extended 72 h exposure to 40-80 mM NaCl resulted in enhanced germination. These improvements likely stem from the optimized priming duration and recovery phase, underscoring the importance of fine-tuning stress parameters in relation to genotype-specific resilience.

The results reveal a complex effect of salinity priming on plant height, with the greatest values recorded under the T1 treatment (40 mM NaCl), suggesting that moderate salinity may promote growth in conditions with limited water availability, potentially through mild stress-induced activation of growth-related pathways. This phenomenon has been reported in other studies, where low to moderate salinity levels enhance water-use efficiency and activate osmotic adjustment mechanisms, resulting in slight growth stimulation (Martínez *et al.*, 2003; Hmidi *et al.*, 2018). However, the control group showed a slight reduction in plant height compared to T1, which might suggest that mild salinity priming acts as a trigger for improved physiological performance compared to non-stressed conditions. This effect, known as "hormesis," occurs when low levels of stress enhance plant growth through the upregulation of stress-response pathways (Malkowski *et al.*, 2020). In contrast, the significant reduction in plant height under T2 (80 mM NaCl), particularly in VS2, highlights the deleterious effects of high salinity concentration priming. The reduced plant height in VS1 (20.07 cm) under T2 further supports the detrimental impact of excessive salinity priming stress. The contrasting effects of 40 mM and 80 mM NaCl treatments can be explained by their physiological impact on the seed and seedling. Moderate salinity (40 mM) likely triggered osmotic adjustment, stabilizing cellular membranes and promoting water uptake, while also activating antioxidant defense systems such as superoxide dismutase and catalase (Hussain *et al.*, 2019). These responses contribute to improved early vigor and stress resilience. In contrast, the 80 mM concentration may have exceeded the threshold for beneficial stress, leading to ion toxicity, disrupted metabolic activity, and impaired germination and growth (Wang *et al.*, 2022).

The alignment of our field-based results with controlled-condition studies emphasizes how moderate priming concentrations can enhance early vigor, while excessive levels impair germination. High salinity levels disrupt water and nutrient uptake, induce osmotic stress, and cause ion toxicity, primarily due to $Na+$ and $Cl-$ accumulation. This results in impaired cell elongation and division, stunting overall plant growth (Ma *et al.*, 2020). The seasonal variation, with VS2 showing more pronounced reductions in plant height, may be attributed to environmental factors such as differences in temperature, humidity, and light intensity between the growing seasons, which could influence the plant's tolerance to drought stress. The relevance of genotype-specific responses and environmental context, supported by recent literature (Nowicki *et al.*, 2025), further explains the variability in priming outcomes and highlights the need for tailored approaches. These findings emphasize the importance of optimizing salinity levels during seed priming to balance the benefits of stress-induced growth stimulation against the risks of excessive ion toxicity. Understanding these physiological thresholds is essential for tailoring priming protocols to specific agroecological conditions, enabling farmers to enhance crop resilience without compromising germination or early growth. Such dose-dependent responses are consistent with the concept of stress memory, where priming induces protective mechanisms only within an optimal range.

Building on this, the proposed dual-phase priming regime—initial salinity stimulation followed by a recovery period under controlled conditions—offers a biologically grounded strategy to enhance stress resilience (Kambona *et al.*, 2023; Kumar & Singh, 2024) and improve seedling establishment under variable field conditions, particularly in rainfed systems affected by salinity and drought. This approach aligns with the concept of induced stress memory (Lagiotis *et al.*, 2023; Pissolato *et al.*, 2024), increasingly recognized in contemporary legume research, where early exposure to moderate stress primes the plant for improved performance under subsequent challenges. By integrating this regime into our protocol, we observed genotype-specific NaCl tolerance thresholds, suggesting that such priming not only improves physiological outcomes but also holds promise for selecting salt-tolerant cultivars adapted to climate variability.

The observed reduction in root length under salt priming treatments highlights the sensitivity of root growth to salinity stress. While the control group showed substantial root length in both VS1 (18.4 cm) and VS2 (12.9 cm), the slight reduction in T1 indicates that moderate salinity priming affects root elongation without completely inhibiting growth. In contrast, the drastic reduction in T2 (3.9 cm in VS1 and 3.6 cm in VS2) highlights the severe impact of high salt concentrations on root development. These results are consistent with previous studies on salinity stress, where high NaCl levels impair water uptake, create osmotic stress, and cause ion toxicity, leading to reduced cell expansion and division in roots (Mahmood *et al.*, 2024). The more pronounced reduction in VS2 suggests that seasonal environmental factors may influence the severity of stress. This trend underscores the importance of optimizing salinity levels in seed priming to minimize root damage and support plant establishment under stress conditions.

The increase in pod number under moderate salinity priming (T1) suggests that mild salt stress can enhance reproductive performance by activating adaptive stress-response mechanisms (Munns & Tester, 2008). However, the sharp decrease in pod number under extreme salinity (T2) indicates that high salt concentrations severely hinder reproductive processes, likely due to osmotic stress and ion toxicity, which disrupt pod formation and flowering (Xiao & Zhao, 2023). These results emphasize the importance of balancing salinity levels during seed priming to avoid levels that inhibit reproduction.

Pod formation initially increased under mild salinity priming (T1). However, pod mass was significantly reduced under extreme salinity (T2), clearly indicating the detrimental impact of high salt concentrations on reproductive success. In the second growing season (GS2), pod mass dropped to zero, indicating that although pods formed, they failed to develop into mature seeds. This demonstrates that excessive salinity disrupts critical processes for seed formation, including nutrient uptake, water absorption, and metabolic functions, ultimately leading to pod and seed failure (Kordrostami & Rabiei, 2019). These findings highlight the importance of identifying threshold salinity levels beyond which reproductive performance is severely compromised.

Plant mass was highest under moderate salinity treatment (T1), slightly lower in the control group, and showed the greatest decline under T2 in both growing seasons. This reduction reflects the negative effects of high salinity on plant growth, likely caused by osmotic stress and ion toxicity, which impair nutrient uptake and cellular processes (Ahmed *et al.*, 2024).

By inducing adaptation mechanisms that improve seed development, moderate salt stress may boost reproductive success, as seen by the increase in grain number per pod under mild salinization (T1). According to Acharya *et al.* (2024), mild salinity has been demonstrated to promote growth and stress tolerance, which may result in better pod and seed development. Nonetheless, the total lack of grains in both growing seasons under excessive salinity (T2) emphasizes how harmful high salt concentrations are to reproduction. Osmotic stress and ion toxicity brought on by high salinity can interfere with pollination, fertilization, and grain development, ultimately resulting in reproductive failure.

The yield outcomes demonstrate the nuanced effects of salt priming and salinity stress on pea production. In VS1, mild salinity priming (T1) led to a notable increase in yield compared to the control, rising from 3.3 $Mg \cdot ha^{-1}$ to 4 $Mg \cdot ha^{-1}$. This aligns with findings by Harris *et al.* (1999), which emphasize that seed priming under mild stress can enhance metabolic readiness and nutrient uptake, contributing to improved yields. However, in VS2, T1 resulted in a slight reduction in yield from 5.6 $Mg \cdot ha^{-1}$ (control) to 5.4 $Mg \cdot ha^{-1}$. This suggests that the positive effects of priming may vary depending on environmental conditions and crop baseline resilience, as noted by Farooq *et al.* (2009).

The absence of yield under the high salinity treatment (T2) in both growing seasons is consistent with studies indicating that excessive salt levels can cause osmotic stress and ion toxicity, ultimately inhibiting reproductive success and biomass accumulation (Parida & Das, 2005; Munns & Tester, 2008). These results underscore the importance of optimizing salinity levels in priming protocols to balance stress-induced benefits and mitigate harmful effects.

The analysis of variance (ANOVA) revealed that salinity levels had a significant impact on several key pea plant traits, particularly germination rate, plant height, and biomass. Salinity-based seed priming was the dominant factor influencing these traits, while the growing season had a lesser effect. Moderate salinity (T1) tended to stabilize plant growth and biomass, with reduced variability observed in both seasons. In contrast, high salinity (T2) resulted in significant stress, limiting plant growth and pod production, with zero grain production under T2. These results underscore the critical role of salinity in determining plant growth and reproductive success, with moderate salinity offering potential benefits for plant vigor while excessive salinity severely hampers growth and reproductive processes. The interaction between season and salinity further demonstrated that environmental conditions play a role, but salinity levels were the more influential factor in determining the outcome of the plant traits evaluated.

The results of this study align with previous research on the effects of salinity priming on plant growth and reproduction. Salinity, especially at moderate levels (T1), often leads to enhanced stress tolerance and improved plant performance, as seen in several studies where moderate salt stress led to increased biomass and plant height (Munns & Tester, 2008). Similarly, other studies have shown that mild salinity can stimulate some aspects of reproductive development, such as pod formation and grain number (Ashraf *et al.*, 2008). However, excessive salinity (T2) priming had a profoundly negative impact on seed production, a finding consistent with the literature, which demonstrates that high salt concentrations result in osmotic stress, nutrient imbalances, and ion toxicity, severely limiting reproductive success and biomass accumulation (Wang *et al.*, 2024). In our study, no grains were produced under T2 treatment, a result in line with findings from other research, which reports complete reproductive failure under high salinity conditions (Hossain *et al.*, 2017). Thus, the present study reinforces the critical role of managing salinity levels for optimizing plant growth and reproductive outcomes. These findings underscore the importance of optimizing salinity levels in priming protocols to balance stress-induced benefits and mitigate harmful effects.

Given the increasing frequency of drought events worldwide, the use of salinity-based seed priming may offer a scalable strategy for enhancing legume resilience in diverse rainfed systems. Although the experiment was conducted in a specific agroclimatic region, the relevance of the findings extends beyond local conditions, particularly in the context of climate change and global water scarcity.

Although this study focused on morphological and agronomic traits, the observed genotype-specific responses to salinity priming suggest underlying physiological and biochemical mechanisms that warrant further investigation. Future studies should include measurements of osmoprotectants (e.g., proline, glycine betaine), antioxidant enzyme activities (e.g., superoxide dismutase, catalase, peroxidase), and ion homeostasis (Na^+/K^+ ratios) to clarify the stress adaptation strategies induced by low-dose NaCl priming. Additionally, proteomic profiling may help identify key regulatory proteins and signaling pathways involved in priming-induced tolerance. Such integrative approaches would provide a mechanistic basis for optimizing priming protocols in pea cultivation under rainfed conditions.

6. CONCLUSION

This study highlights the significant impact of salinity levels during seed priming on osmotic regulation, which plays a key role in maintaining cellular homeostasis under drought conditions. It also examines how different salinity treatments during seed priming affect the growth and reproductive success of pea plants (*Pisum sativum* L.) over two growing seasons. The analysis revealed that moderate salinity (40 mM NaCl) enhanced certain traits, such as plant height and pod number, while high salinity (80 mM NaCl) severely impaired germination rates, plant biomass, and overall yield. These findings highlight the complex interplay between salinity and plant physiology, where moderate stress may stimulate certain growth processes, while excessive salinity proves detrimental.

The uneven distribution of precipitation during the growing season, particularly concentrated in May, coincided with critical developmental stages for the pea plants, underscoring the importance of adequate water supply during these phases. Statistical analysis confirmed that salinity was a primary determinant of germination rate, plant height, and other morphological traits, while the interaction between growing season and salinity showed no significant effects. This suggests that while environmental conditions play a role, salinity levels exert a dominant influence on crop characteristics, emphasizing the need for careful management of salt concentrations in agricultural practices.

Overall, the results of this research provide valuable insights into the challenges faced by pea crops under drought conditions, offering guidance for future studies aimed at improving drought tolerance in legumes. These findings are particularly relevant for agricultural systems subjected to drought stress, advocating for the development of management strategies that mitigate the negative effects of drought on plant growth and productivity.

Future studies should incorporate analyses of osmoprotectants, antioxidant enzyme activities, and proteomic profiles to better understand the stress adaptation pathways activated by salinity conditioning. Such insights will contribute to the development of optimized priming protocols tailored to genotype and environmental context.

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Supplementary material

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Data availability

Data will be available on request.

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Authorship contribution statement

Nevena Stevanović: Conceptualization, Data curation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing.

Ružica Stričević: Conceptualization, Supervision, Validation, Writing – review & editing.

Dragan Milošević: Conceptualization, Methodology, Supervision, Validation, Writing – review & editing.

Nikola Stanković: Writing – review & editing.

Maša Buđen: Writing – review & editing.

Nataša Ljubičić: Writing – review & editing.

Mirjana Vukosavljev: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Competing interests

The authors have declared that no competing interests exist.

Statement on the use of Artificial Intelligence

The authors employed Microsoft Copilot version 2026 in order to translate the title, abstract and keywords from English to Spanish while preparing this work. Following their use, the authors assumed full responsibility for the publication's content and reviewed and edited it as necessary.

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