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Impact of soil and climate on barley (*Hordeum vulgare* L.) salinity tolerance in diverse arid and saline conditions

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Although barley is the fourth most cultivated cereal and is crucial for food and feed, its yields suffer in saline and arid environments due to drought and salinity, despite its tolerance. This study examines how pedoclimatic factors shape salinity tolerance in barley across different arid environments. Forty barley genotypes from the Middle East-North Africa and Pakistan were tested over two growing seasons in both semi-arid and arid locations. Crops were irrigated with saline groundwater (13 dSm^{-1}) or non-saline water (2 dSm^{-1}). Grain yield reduction served as a stress tolerance index. High temperatures exceeding 30 °C and solar radiation during various barley growth stages acted as climate indicators, while soil Potassium (K^+)and Calcium (Ca^{2+}) contents were considered soil indicators. High temperatures (> 30 °C) and intense solar radiation during meiosis-anthesis negatively affect barley's salinity tolerance. Notably, solar radiation was the only climatic factor that significantly impacted even the tolerant genotypes, underscoring its critical role in determining stress sensitivity during this phase. Conversely, high soil levels of K^+ and Ca^{2+} positively influence salt tolerance. The research also revealed a significant correlation ($R^2 = 0.69$) between barley's salt tolerance and the salinity of the genotypes' geographic origin. The findings highlight the need to harness natural forces in crop selection and implement tailored, sustainable agronomic practices, including adequate potassium and calcium fertilization.

Keywords Barley, Salinity, Yield reduction, Environmental factors, Climate resilience, MENA region

The Food and Agriculture Organization[1] projects that the global population will reach 10 billion by 2050, leading to increased food demand. To meet these growing needs, main crop production must double, particularly in developing countries. Cereal crops are vital for ensuring food security and social stability worldwide, particularly in the Mediterranean, Middle East, and North Africa (MENA) regions. However, crop yields in these regions are subject to fluctuations due to various factors such as low soil fertility, water and soil salinity, and irregular rainfall[2]. These challenges are expected to worsen with climate change, creating a major challenge for agricultural research to develop high-yielding genotypes that can tolerate extreme weather and low soil fertility. Among cereal crops, barley (*Hordeum vulgare* ssp. vulgare) ranks as the fourth most widely ultivated globally, after wheat, maize, and rice[3]. Unlike other cereals, barley can produce high yields under marginal soil and limited water conditions[4,5]. It is a flexible crop suitable for both rainfed and irrigated systems, making it an ideal species for arid and semi-arid regions characterized by low rainfall and high precipitation irregularity[6]. However, inappropriate supplementary irrigation practices can lead to soil salt accumulation and yield reduction[7,8].

Hordeum spp. are widely cultivated in the southern Mediterranean region and irrigated with saline water[9,10]. Selecting suitable varieties is a vital step toward adapting to such cropping conditions. The selection of genotypes that have demonstrated superior performance and stability is a potential candidate as a valuable genetic resource for developing climate-resilient barley[5]. Therefore, understanding how salt stress affects plants and the mechanisms they employ to overcome it is essential for the success of these initiatives. Unfortunately, limited research has been conducted to investigate the multi-environmental factors influencing barley production. Hence, it is crucial to study the behavior of barley genotypes under saline stress in different environments to identify and select tolerant varieties.

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Researchers have shown that barley has a wide genetic variation[9,11–13]. This genetic diversity allows for the examination of different barley germplasms and their genotypic responses under various salinity levels[13].

Local barley is a valuable source of genetic variability that can be used in breeding programs in semiarid and arid environments to identify traits related to salinity tolerance. Researchers continuously identify and measure various traits associated with abiotic stress tolerance. Although many studies have aimed at developing plants with salinity tolerance, the latest research shows that saline stress affects many aspects of a plant's physiology[10], making it challenging to study it holistically. Therefore, it is advisable to analyze barley's response by dissecting specific varietal traits such as the retention capacity of potassium (K^+) and calcium (Ca^{2+}), which are believed to influence the plant's tolerance to salinity[14]. Genotypes that efficiently utilize K^+ not only demonstrate higher growth rates but also show resilience against stress, making them valuable for breeding programs aimed at improving salinity tolerance. Mitigating solar radiation stress is essential to maximize the benefits of K^+ and Ca^{2+} fertilization[15,16]. Techniques proposed to mitigate temperature stress, heat stress, and water stress[17]. Such approaches support optimal nutrient uptake, thereby improving crop yields and sustainability in agricultural practices[18].

Nevertheless, most studies on salt tolerance have been conducted in controlled environments for a limited period, and early assessments may not always reflect final performance under saline conditions[19].

Field trials in naturally saline environments can provide valuable data on the spatial and temporal variation in salt tolerance[8,20,21]. It is fundamental to identify morpho-physiological traits that discriminate salinity tolerance selection[22]. Given the complexity of tolerance mechanisms, it is essential to use multidisciplinary approaches.

Varietal phenotyping experiments provide a potentially rich source of information and are among the most efficient approaches for analyzing the interaction between genotypes and different bioclimatic factors[23]. Researchers, agronomists, and statisticians have proposed several tools to help interpret the interaction between varieties and environments, enabling the synthesis of this information by dissociating the effects of genotype, environment, and their interaction through statistical models[24].

In this context, this study provides cutting-edge findings on the impact of pedoclimatic factors on the salt tolerance of barley based on data collected from 40 genotypes grown in real-world conditions in five distinct biophysical environments. This study drives potential innovative agronomic practices that may significantly increase barley's yield and resilience grown under saline constraints.

Materials and methods

Plant material

Forty different barley genotypes (*Hordeum vulgare* L.) were evaluated for their tolerance to various levels of salinity across different water salinity concentrations and climatic conditions. This collection included four improved commercial Tunisian varieties: Rihane, Tej, Konouz, and Manel. Additionally, thirteen genotypes from international collections within the Near East and North Africa region (NENA), which includes Libya, Oman, Pakistan, Syria, and Saudi Arabia (genotype codes 5–17), were provided by the International Center of Biosaline Agriculture (ICBA). Furthermore, the study included twenty-three barley landrace accessions from the National Gene Bank of Tunisia (genotype codes 18–40), originating from various agroecological regions of Tunisia. All barley genotypes were obtained under formal agreements. Necessary permissions for collection and use were obtained in accordance with institutional and national regulations by the mentioned institution. Accession numbers and provenance details are documented in Hammami et al[9].

Field sites and climatic conditions

Two field experiments were carried out over two cropping seasons (2012–2013 and 2013–2014) in two locations: Kairouan (KAI) (Barrouta, in central Tunisia, 35°34′34.97″N;10°02′50.88″E) and Medenine (MED) (El Fjé, in southern Tunisia, 33°26′54″N; 10°56′31″E). These sites represent semi-arid and arid bioclimatic regions, respectively. The experimental area experiences an arid and semi-arid climate, characterized by hot, dry summers (May to October) and cool, dry winters (November to April). The maximum temperatures recorded at both sites during the two seasons were similar, reaching 33 °C. The minimum temperatures recorded were 5 °C in KAI and 10 °C in MED, respectively. During 2012/2013 and 2013/2014, the arid site of MED received annual rainfall of 32.5 mm in the first season and 86 mm in the second. In comparison, the semi-arid site of KAI received annual rainfall of 111 mm and 184 mm, respectively. Further details and visual representations can be found in Hammami et al.[9]. Soil texture at the MED site was sandy (sand 55.5–58.1%, silt 22.6–26.7%, clay 19.3–22,3%, depending on the depth), while the KAI site had clay-loam soil (sand 10.69–14.83%, silt 37–52.41%, clay 38.85–52.31%, depending on the depth) (Table 1). At the beginning of the experiment, soil samples were analyzed, and the results are reported in Table 1. The soil at KAI contains 4% organic matter, 0.02% available nitrogen, 9 mg/kg assimilable phosphorus, and 550 mg/kg available potassium. In contrast, the soil at the MED site contains 0.9% organic matter, 0.02% available nitrogen, 4.2 mg/kg assimilable phosphorus, and 60 mg/kg available potassium.

Experimental design and agronomic practices

The experiment was conducted using a split-split plot design within a randomized complete block design (RCBD) framework. The main plot factor comprised two levels of irrigation water salinity, while the subplot factor included 40 genotypes. A total of 120 plots (40 genotypes × 3 replicates) were established, each consisting of ten planting rows, each 2 m in length and spaced 20 cm apart.

Manual sowing was carried out at a density of 200 viable seeds per square meter between November 15 and November 30 during both cropping seasons at the KAI and MED sites. Nitrogen fertilization was applied in three stages: 30 kg N/ha as ammonium nitrate at sowing, followed by 28 kg N/ha at mid-tillering, and 27 kg N/ha

	Composition en %																	
	Clay		Silt		Sand		OM		Nitrogen		P ass (mg/kg)		Na$^+$ (mg/kg)		Ca^{2+} (mg/kg)		K$^+$ (mg/kg)	
Depth (en cm)	KAI	MED	KAI	MED	KAI	MED	KAI	MED	KAI	MED	KAI	MED	KAI	MED	KAI	MED	KAI	MED
0–20	45.1	20.5	40.78	24.5	14.83	55.5	4.03	0.9	0.02	0.02	9.4	4.2	240	120	140	55	550	60
20–40	48.82	21.2	37.39	25.1	13.79	53.7	4.02	0.9	0.02	0.02	3.4	2.9	240	145	140	50	540	60
40–60	44.1	21.1	41.58	26.7	14.31	52.2	3.83	0.9	0.03	0.02	3.55	2.8	245	145	125	45	450	60
60–80	52.31	22.3	37	24.3	10.69	53.4	3.78	0.7	0.02	0.01	2.56	2.7	250	150	110	40	450	45
80–100	38.85	19.3	52.41	22.6	13.75	58.1	3.74	0.7	0.02	0.01	3.39	2.9	255	190	90	30	400	40

Table 1. Physico-chemical properties of soil at two experimental sites (KAI and MED) across different depths. Parameters include pH, organic matter (OM), assimilable phosphorus (P ass), sodium ions (Na$^+$), calcium ions (Ca^{2+}), potassium (K$^+$), and soil texture components. All concentrations are expressed in mg/kg (milligrams per kilogram), unless otherwise specified.

	KAI				MED			
	2012–2013		2013–2014		2012–2013		2013–2014	
Irrigation water	KAI-LS	KAI-HS	KAI-LS	KAI-HS	MED-LS	MED-HS	MED-LS	MED-HS
Na$^+$ (mg/kg)	150	550	150	560	180	650	170	628
K$^+$(mg/kg)	22	19	21	19	15	18	15	19
Ca^{2+} (mg/kg)	65	61	65	61	21	20	22	20
EC$_1$ (dS m^{-1})	1.2	12.8	1.23	13.0	1.59	13.5	1.59	13.2
EC$_2$ (dS m^{-1})	1.2	13.0	1.23	13.0	1.60	13.4	1.51	13.5
EC$_3$ (dS m^{-1})	1.2	13.0	1.24	13.1	1.58	13.6	1.51	13.1

Table 2. Chemical composition of irrigation water at KAI and MED experimental sites during two growing seasons, including electrical conductivity before sowing (EC1), at the terminal spikelet stage (EC2; Zadoks scale Z30–31), and after harvest (EC3), as well as concentrations of sodium (Na$^+$), calcium (Ca^{2+}), and potassium (K$^+$). All concentrations are expressed in mg/kg (milligrams per kilogram), unless otherwise specified.

at anthesis. No fungal diseases or insect infestations were observed at either site during the two cropping seasons, ensuring consistent crop health across all treatments.

Irrigation management

The assays were irrigated according to water demands and weather conditions during the growing seasons. Total water supplies were determined for each site based on climatic and soil data to meet the barley water requirement (440 mm). Each seedling row was equipped with a drip irrigation line featuring 4 L/h emitters, spaced 33 cm apart. Two sources of irrigation water were utilized at each site, each with different salinity concentrations: (a) low salinity treatment (LS) with concentrations of 1.2 dS m^{-1} and 1.6 dS m^{-1} at KAI and MED, respectively, and (b) high salinity treatment (HS) with concentrations of 13 dS m^{-1} and 13.3 dS m^{-1} at KAI and MED, respectively.

Irrigation water analysis

The electrical conductivity (EC) of the irrigation water and the concentrations of Na$^+$, K$^+$, and Ca^{2+} were analyzed (Table 2). No significant change was observed in the irrigation water EC at both sites throughout each cropping season. It ranges from 1.2 to 1.6 dS m^{-1} for low salinity (LS) water at KAI-LS and MED-LS, respectively. The high saline water (HS) used in the experimentation is approximately 13 dS m^{-1} at both sites.

Data collection

All barley genotypes were manually harvested approximately two weeks after reaching physiological maturity. Grain yield was determined using a plot shredder (Wintersteiger LD-180, Germany), and expressed in grams per square meter (g/m^2). Salinity tolerance of each genotype was assessed using the yield reduction ratio (YR), as described by Hammami et al[9].

The YR is calculated as 1 minus the yield stability index (YSI), where YSI is the ratio of the yield under saline stress (Ys) to the yield under non-stressed conditions (Yp).

$$\mathrm{YR} = 1 - \ \mathrm{YSI},$$

where $\mathrm{YSI} = \frac{Y_s}{Y_p}$

This metric provides a quantitative estimate of each genotype's sensitivity to salinity stress, with higher YR values indicating greater sensitivity, and lower values reflecting greater tolerance.

Creation of environmental covariable

Environmental covariables were defined for the key reproductive developmental stages of barley, as shown in Fig. 1. These stages were identified based on established phenological frameworks and previous studies[25–30]. The timing and progression of these stages are mainly influenced by genotype, environmental conditions, and crop management practices[28]. Each stage was characterized by specific environmental parameters recorded during its occurrence, allowing for a stage-specific analysis of genotype–environment interactions.

The reproductive stages used for covariable creation include:

- Stage 1: Single to the double ridge (Z20) to terminal spikelet (Z30-31).
- Stage 2: Terminal spikelet (Z30-31) to meiosis (Z40-49)
- Stage 3: Meiosis (Z40-49) to anthesis (Z60-69)
- Stage 4: Anthesis (Z60-69) to grain filling (Z70-Z79)

The schematic representation in Fig. 1 depicts the life cycle of barley, emphasizing the key developmental stages analyzed in this study. The growth stages were categorized using the Zadoks decimal growth scale[31], which offers a standardized framework for describing barley phenology. This classification was employed to generate environmental covariates at specific reproductive phases, which were subsequently utilized for analyzing genotype by environment interactions to identify the most significant factors influencing salinity tolerance.

In each experimental environment, a comprehensive set of environmental covariables was generated to characterize the conditions experienced by barley genotypes during key reproductive developmental stages. The timing of these stages was recorded individually for each of the 40 genotypes, allowing for genotype-specific alignment of environmental data. Temperature and solar radiation covariables were calculated based on the actual phenological progress of each genotype. Specifically, the number of hot days (defined as days with maximum temperature ≥ 30 °C) and average daily solar radiation (J/m^2/day) were estimated for each developmental stage. This method allowed for a thorough analysis, helping to identify environmental factors that may influence barley salt tolerance.

The environmental covariables were categorized into four main groups:

- Temperature
  - $\mathrm{ND30}_{\mathrm{DR\text{-}TS}}$: Number of hot days from double ridge to terminal spikelet growth stage (tmax > = 30 °C)
  - $\mathrm{ND30}_{\mathrm{TS\text{-}M}}$: Number of hot days from the terminal spikelet tomeiosis growth stage (tmax > = 30 °C)
  - $\mathrm{ND30}_{\mathrm{M\text{-}An}}$: Number of hot days from meiosis toanthesis growth stage (tmax > = 30 °C)
  - $\mathrm{ND30}_{\mathrm{An\text{-}GF}}$: Number of hot days from anthesis to grain filling growth stage (tmax > = 30 °C)

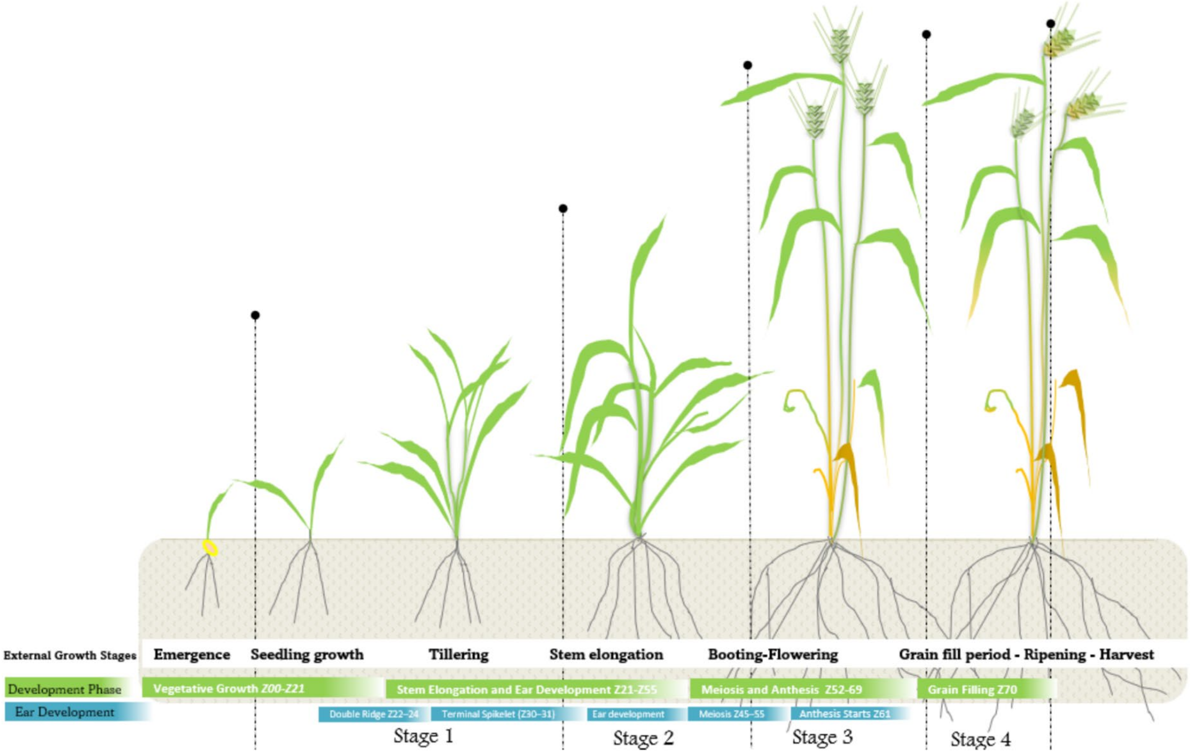


Fig. 1. The life cycle of a barley plant and the different barley development stages adopted in the study. Zadoks' decimal growth scale has been used to describe growth stages[31].

- Solar radiation
  - ADSR-TS: Average daily solar radiation from double ridge to terminal spikelet growth stage (Joule/m^2/day).
  - ADSR-M: Average daily solar radiation from the terminal spikelet to meiosis growth stage (Joule/m^2/day).
  - ADSR-M-An: Average daily solar radiation from meiosis to anthesis growth stage (Joule/m^2/day).
  - ADSR-An-GF: Average daily solar radiation from anthesis to grain filling growth stage (Joule/m^2/day).
- Soil
  - Soil-K^+: soil potassium (mg/kg) content.
  - Soil-Ca^{2+}: soil calcium (mg/kg) content.
- Irrigation Water
  - W K^+: Irrigation Water potassium (mg/kg) content.
  - W Ca^{2+}: Irrigation Water calcium (mg/kg) content.

Statistical analysis

Based on their tolerance to salinity, expressed by the yield reduction ratio (YR), the 40 genotypes were clustered using hierarchical ascendant analysis based on genotypic Euclidean distances and Ward's minimum variance[32]. The hclust function in R software was used. Additionally, the libraries "ggplot2" and "ggalt" were employed for ranking the genotypes in terms of yield reduction and for comparison between the semi-arid and arid sites.

The covariance-based statistical method, known as partial least squares analysis (PLS), was utilized as a multivariate statistical technique to assess the relationship between the dependent variable YR and multiple independent (explanatory) variables consisting of the environmental covariable.

Harmonized World Soil Database v 1.2 was used to generate the inputs for the soil salinity map.

(https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v12/en/). DIVA-GIS software (version 7.5) obtained from the DIVA-GIS website (http://www.diva-gis.org) was used to create water and soil maps.

Results

Genotypes ranking according to their tolerance to salinity upon the test environments

The adaptation of genotype 'i' to environment 'j' (regarding salinity tolerance) was evaluated using the genotype (Gi) and the genotype X environment (Gi X Ej) effects. Genotype adaptation to various environments was categorized through hierarchical ascending analysis based on Euclidean genotypic distances and Ward's minimum variance. The classification aimed to group the most similar genotypes concerning salinity tolerance based on the yield reduction ratio (YR). The number of groups was determined according to the portion of variability explained by the expression: $G_i + (G_i * E_i)$

The division into 2, 3, and 4 groups is explained, respectively, by 39%, 58%, and 68% of the varietal tolerance observed across the various environments of the test set (Fig. 2a, Table 3).

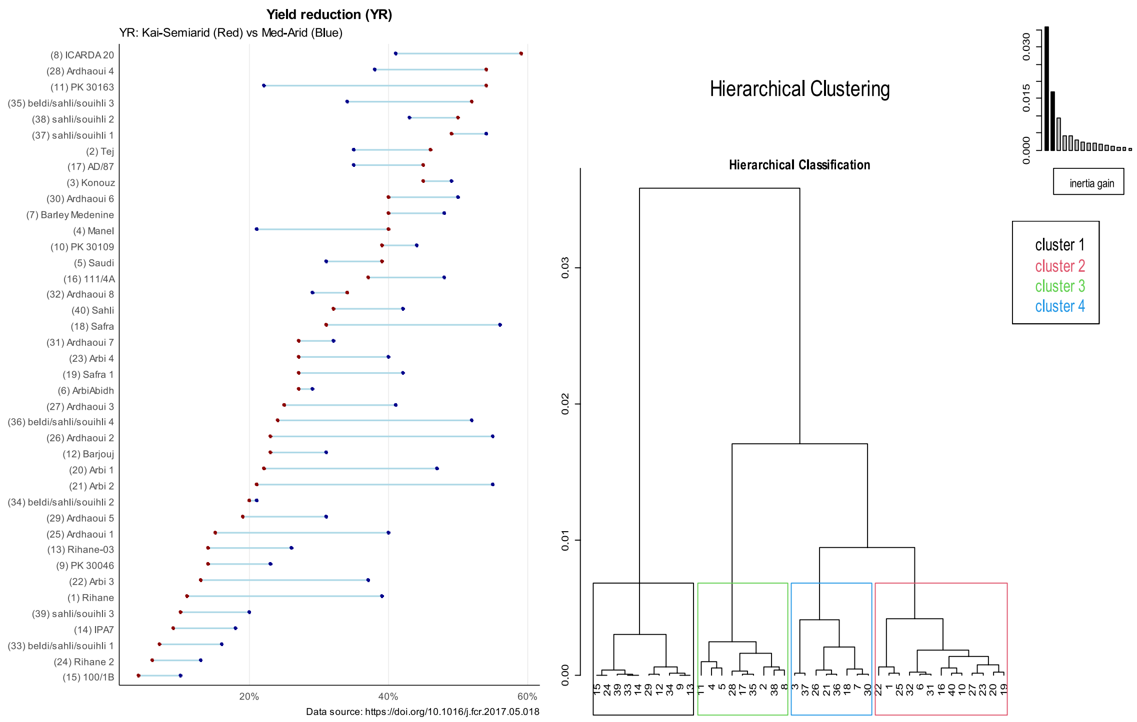
Clustering revealed four distinct tolerance groups, highlighting clear differences in salinity response. Group 1 (G1) corresponds to the varieties with high salinity tolerance, resulting in YR ranging from 7 to 20%. Groups 2 (G2) and 3 (G3) include the most sensitive genotypes. Genotypes in G2 exhibited yield reductions ranging from 35 to 50% at the Kai site, while G3 genotypes showed yield reductions ranging from 38 to 52% at the MED site (Fig. 2b, Table 3). The fourth group (G4) consists of genotypes that are moderately sensitive across all environments and notably tolerant at the KAI site during the second cropping season (2013–2014), with yield reductions ranging from 25 to 42%.

However, the typology of interactions indicates that the tested genotypes, except for G1, had site-specific adaptations. The genotypes from group 1 displayed a general adaptation to all studied environments (Table 3, Fig. 1a). These genotypes included those introduced: Batini landrace, 100/1B (15) from Oman; IPA7 (14) from Iraq; Barjouj (12) from Libya; PK30046 (9) from Pakistan; and Rihane-03 (13) from ICARDA, and local Tunisian genotypes: Arbi (24); Souihli (39); Beldi (33); Ardhaoui (29); beldi/sahli/souihli (34).

Impacts of high temperature and average daily solar radiation on salinity tolerance during the reproductive stages

Figures 3 and 4 illustrate the effects of temperature and average daily solar radiation, recorded across various developmental stages (double ridge, terminal spikelet, meiosis, anthesis, grain filling), on salinity tolerance, as indicated by the YR. Values below zero denote the capacity of the climatic factor to mitigate the adverse impact of salinity on yield reduction, while values above zero signify the exacerbation of the salinity effect by the climatic factor. The influence of temperature was assessed based on the number of days with temperatures exceeding 30 °C, while solar radiation was evaluated using its daily average (Figs. 3, 4). The impact of these climatic indicators (temperature and average daily radiation) on yield reduction under saline stress exhibits significant variation across genotypes.

The findings suggest that certain genotypes from G2, G3, and G4 exhibited an increased harmful impact of salinity on yield due to elevated temperatures, as indicated by the positive value in Fig. 3. In contrast, the 10 tolerant and stable genotypes in G1, marked by a red asterisk in Fig. 3, showed that high temperatures did not exacerbate the effects of salinity, represented by the negative values of standardized coefficients (Fig. 3). Importantly, for these genotypes, high temperature does not introduce an additional stress factor to salinity



(a)

(b)

Fig. 2. (**a**) Yield reduction ratio (YR) of 40 barley genotypes under saline irrigation across two contrasting environments: semi-arid (Kairouan, KAI) and arid (Medenine, MED). (**b**) Genotypic clustering based on salinity tolerance using hierarchical ascendant analysis with Euclidean distances and Ward's minimum variance method. Genotypes are grouped into four categories (G1–G4) reflecting different levels of salinity tolerance. G1 includes genotypes with broad adaptability and minimal yield reduction (7–20%), while G2–G4 represent site-specific sensitivity and moderate tolerance. This classification helps identify resilient genotypes for saline conditions.

Description	Group	YR range (%)	Number of genotypes
Tolerant	G1	7–20	10
Moderately sensitive	G4	25–42	13
Sensitive			
KAI	G2	35–50	9
MED	G3	38–52	8

Table 3. Classification of barley genotypes based on grain yield reduction ratio (YR).

tolerance during specific growth stages. The remaining genotypes, which are either sensitive or moderately sensitive, displayed varied responses to temperature depending on the growth stage. Overall, the results indicate that barley is highly sensitive to elevated temperatures, especially during the reproductive stages. The improved varieties Tej (2), Konouz (3), and Manel (4) were found to be the most susceptible to climatic constraints, particularly during anthesis, when temperatures exceed 30 °C.

This investigation evaluated the impact of solar radiation on salinity tolerance using PLS analysis alongside stage-specific climate data. The results show that genotypes classified as highly tolerant (G1) experienced minimal effects from solar radiation during most developmental stages. However, a notable exception occurred during the meiosis–anthesis stage, where solar radiation had a strong negative impact. This stage-specific sensitivity is depicted in Fig. 4, which displays positive standardized coefficients for solar radiation during meiosis–anthesis, indicating an increase in salinity-induced yield reductions. Notably, this was the only growth stage where G1 genotypes showed vulnerability, suggesting that the combined stress of high solar radiation and salinity during meiosis might disrupt vital reproductive processes like pollen viability and fertilization. In contrast, genotypes in groups G2, G3, and G4 demonstrated broader and more variable sensitivity to solar radiation across several developmental stages, reflecting lower overall resilience. The evidence from PLS analysis and climate data supports the conclusion that solar radiation negatively influences salinity tolerance in G1 genotypes exclusively during the meiosis–anthesis stage, whereas other genotypes exhibit a wider range of sensitivity. This

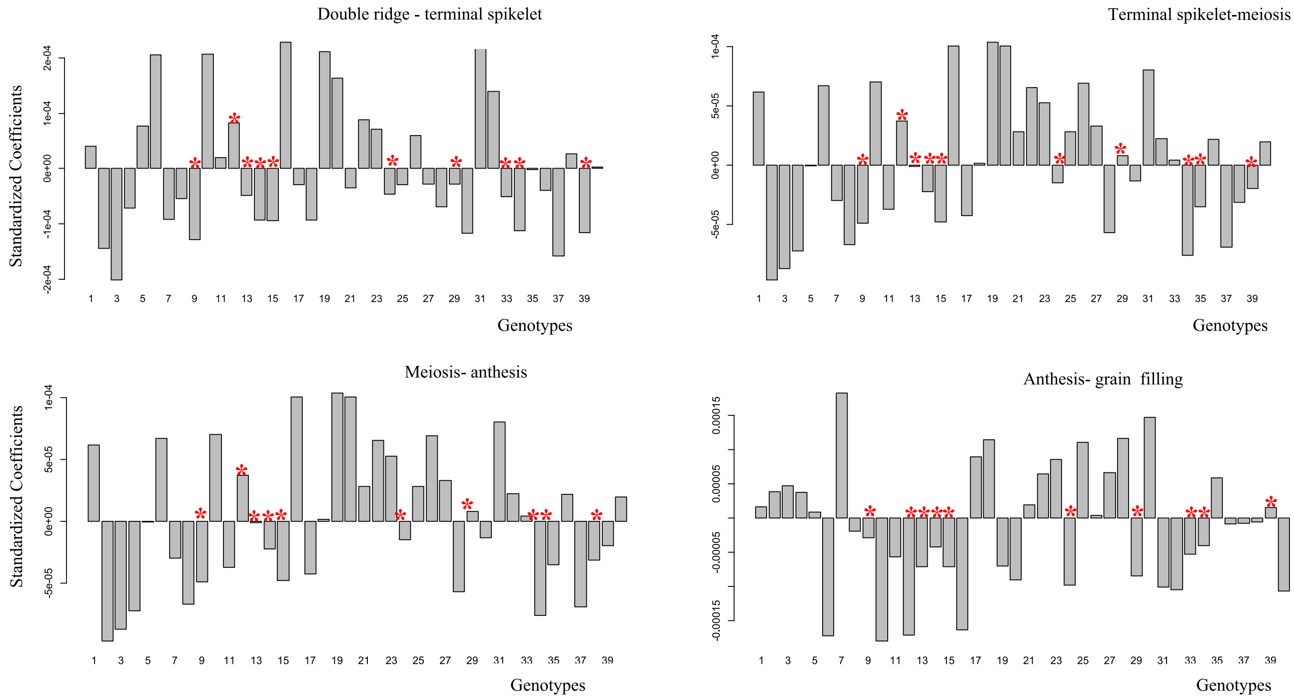


Fig. 3. Effect of high temperature (days with Tmax ≥ 30 °C) on salinity tolerance of barley genotypes across four reproductive stages, double ridge to terminal spikelet, terminal spikelet to meiosis, meiosis to anthesis, and anthesis to grain filling. Values represent standardized coefficients from Partial Least Squares (PLS) analysis linking temperature stress with yield reduction ratio (YR). Positive values indicate that temperature during a specific stage exacerbates salinity-induced yield loss; negative values suggest no adverse effect of salinity impact.. Genotypes classified as highly tolerant (G1) are marked with a red asterisk (*).

also highlights that solar radiation, more than temperature, was the only climatic factor significantly affecting tolerant genotypes, emphasizing its critical role during this reproductive phase. These insights underscore the importance of considering both genotype and phenological timing when assessing environmental stress impacts and suggest that meiosis–anthesis is a key period for managing radiation stress, even in otherwise resilient barley lines.

Impacts of potassium and calcium contents in soil and water on salinity tolerance

The covariance-based statistical method, partial least squares analysis (PLS), was used to assess the relationship between the dependent variable (YR) and potassium (K^+) as well as calcium (Ca^{2+}) as environmental covariates (explanatory variables). Figure 5 shows the effects of soil and water K^+ and Ca^{2+} concentrations across various sites on the salinity tolerance of different genotypes. Values below zero indicate the potential for mitigating the negative impacts of salinity on yield reduction. A red asterisk signifies the genotypes exhibiting salinity tolerance.

As shown in Fig. 5, seven of the ten G1 genotypes identified for their tolerance to salinity exhibited a strong ability to utilize potassium and calcium from both soil and water regarding their salinity resilience. Notable genotypes include Batini landrace 100/1B (15) from Oman, beldi/sahli/souihli (34), IPA7 (14) from Iraq, PK30046 (9) from Pakistan, along with souihli (39), Arbi (24), beldi (33), and Barjouj (12) from Libya, as well as Ardhaoui (29). The findings of this study suggest that the concentrations of K^+ and Ca^{2+} in both soil and water are essential factors that enhance the ability of specific barley genotypes to tolerate salinity. Importantly, the influence of potassium and calcium on salinity tolerance extends beyond the top-performing genotypes in group G1. This effect is also evident in commercially improved genotypes and those in the breeding pipeline, including Rihane (1), Tej (2), Konouz (3), Manel (4), ICARDA 20 (8), 111/4A (16), and Rihane-03 (12) from ICARDA.

The presence of potassium and calcium in irrigation sources or within the soil appears to strengthen the salinity tolerance of these genotypes significantly.

Relationship between salinity tolerance and geographic origins of the genotypes

To explore a potential link between genotype, salinity tolerance, and the soil salinity at the geographic origin, the distribution of 23 local Tunisian genotype origins among the 40 genotypes studied was mapped based on water and soil salinity (Fig. 6). On the map, water salinity is represented by blue areas, which correspond to Sabkha (Natural Salt Lake). Soil salinity is indicated by two soil types: Solonetz, a sodium-rich soil (with over 15% exchangeable sodium) that has clay accumulation on the surface, and solonchak, a highly saline soil. Solonchak soils are typically found in arid regions with higher evaporation rates than precipitation and in poorly drained soils (as classified by the FAO).

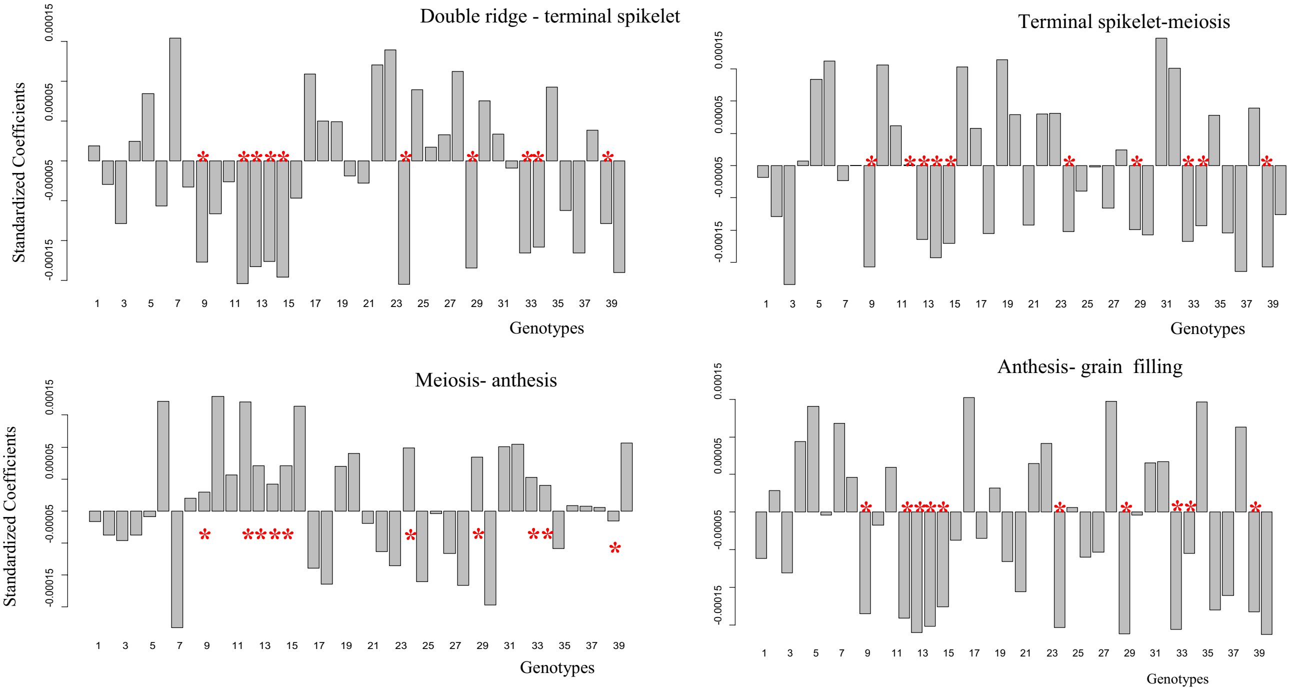


Fig. 4. Effect of solar radiation (average daily radiation in Joules/m^2/day) on the salinity tolerance of barley genotypes across four reproductive stages,double ridge to terminal spikelet, terminal spikelet to meiosis, meiosis to anthesis, and anthesis to grain filling. Values show standardized coefficients from Partial Least Squares (PLS) analysis linking radiation stress with yield reduction ratio (YR). Positive values indicate that temperature during a specific stage exacerbates salinity-induced yield loss; negative values suggest no adverse effect of salinity impact. Genotypes classified as highly tolerant (G1) are marked with a red asterisk (*).

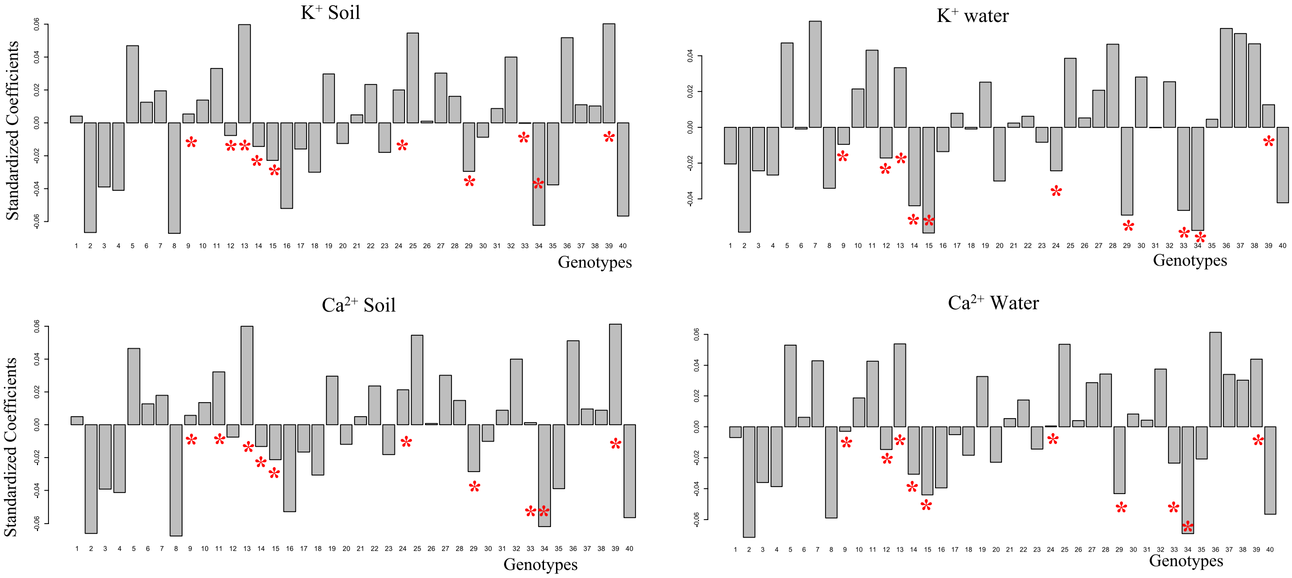
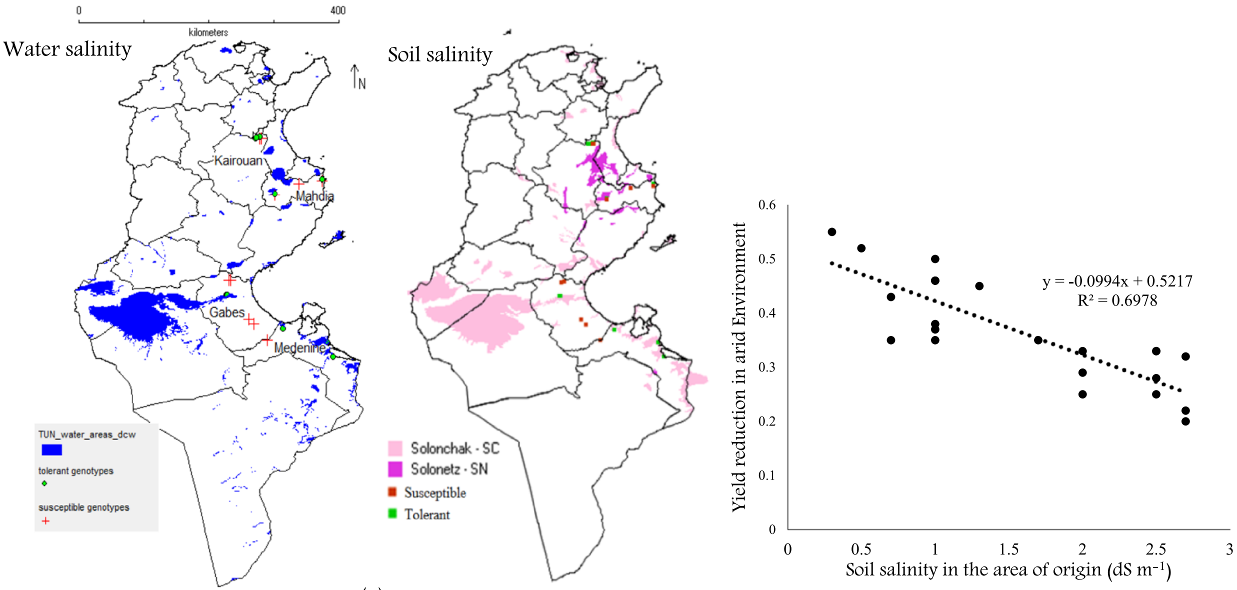


Fig. 5. Influence of potassium (K^+) and calcium (Ca^{2+}) levels in soil and irrigation water on barley genotypes' salinity tolerance. Nutrient concentrations are expressed in parts per million (ppm). Values represent standardized coefficients from Partial Least Squares (PLS) analysis linking nutrient availability to yield reduction ratio (YR) under saline conditions. Positive values indicate that temperature during a specific stage exacerbates salinity-induced yield loss; negative values suggest no adverse effect of salinity impact. Genotypes classified as highly tolerant (G1) are marked with a red asterisk (*).



(a)

(b)

Fig. 6. (**a**) Geographic distribution of 23 Tunisian barley genotypes mapped against soil and surface water salinity indicators in their regions of origin. Blue areas represent saline surface water (Sabkha), while soil salinity is indicated by Solonetz and Solonchak types. Map generated using DIVA-GIS software (version 7.5; http://www.diva-gis.org) with salinity distribution data from the Harmonized World Soil Database v1.2 (FAO; https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v12/en/) (**b**) Correlation between genotype yield reduction ratio (YR) under arid conditions and soil salinity at the original site. The analysis shows a strong relationship ($R^2 = 0.69$), indicating that genotypes from naturally saline regions tend to have higher salinity tolerance. This supports the importance of local adaptation in breeding strategies for stress tolerance.

Among the 40 genotypes analyzed, 23 local Tunisian barley genotypes, previously classified as either tolerant or sensitive, were examined to investigate the relationship between salinity tolerance and the soil salinity levels of their native regions. The analysis showed a strong link between salinity tolerance and the presence of saline soils in the origin area from which these genotypes were collected, as depicted in Fig. 6b, with an R^2 of 0.69, indicating a significant statistical association. Additionally, Fig. 6a demonstrates that proximity to natural saline surface water (Sabkha) at their original sites also influences the observed tolerance levels.

Tolerant genotypes were primarily collected from regions known for high soil salinity, especially in southern Tunisia (Gabes and Medenine) and central Tunisia (Kairouan and Mahdia) (Fig. 6a). These areas are naturally affected by salinity due to factors such as poor drainage, high evaporation rates, and saline irrigation practices. The findings indicate that genotypes from these saline-prone environments have likely experienced natural selection, resulting in improved physiological and genetic mechanisms for salt stress tolerance. This supports the idea that local adaptation is crucial in determining salinity tolerance. It also highlights the importance of including geographic and environmental data in breeding strategies to develop stress-tolerant barley cultivars for arid and semi-arid regions.

Discussion

Genetic diversity and salinity tolerance in Tunisian barley

The identification of solar radiation as a major limiting factor during meiosis–anthesis highlights a physiological bottleneck that breeders must address through targeted selection and agronomic interventions. This finding, combined with the strong influence of soil K^+ and Ca^{2+} availability, provides actionable insights for improving barley tolerance in saline environments.

Grouping patterns underscore barley's genetic diversity and its potential for breeding programs targeting saline environments[33]. Group 1 (G1) includes genotypes with high salinity tolerance. Hammami et al.[9] have already confirmed the stability of these genotypes by analyzing Wricke' s ecovalence related to their average salinity tolerance. Therefore, G1 genotypes are especially important for selecting salinity-tolerant varieties. This group features Tunisian landraces, one improved cultivar, and accessions from the Middle East. These genotypes include the Batini landrace and 100/1B (15) from Oman, beldi/sahli/souihli (34); IPA7 (14) from Iraq; PK30046 (9) from Pakistan, and Rihane-03 (12) from ICARDA, as well as souihli (39), Arbi (24), beldi (33), Barjouj (12) from Libya, and Ardhaoui (29). Sbei et al.[34] reported phenotyping 120 Tunisian barley accessions under irrigation with water containing 6 g/L of salt and found that some landraces showed high tolerance. Similarly, Kadri et al.[35] studied the morpho-physiological and agronomic traits related to salinity tolerance in 30 barley accessions from an oasis ecosystem in southern Tunisia. Their results highlighted the salinity tolerance of several local Tunisian genotypes, such as Ardhaoui, as well as introduced genotypes from the NENA region, including Pakistan. This emphasizes the adaptability of these genotypes in tough environments[9,19,36]. Additionally, Snoussi et al.[36] found that 83% of the genetic variation among the landraces occurs between populations, indicating a rich genetic pool important for conservation efforts. This level of diversity surpasses that of barley germplasm from many other parts of the world. Furthermore, Jaradat et al.[37] examined salt stress tolerance in a collection of 2,2308 Omani barley 'Batini' accessions, revealing significant variation in yield loss ranging from 10 to 70% under different salinity levels. Al-Dakheel et al.[38] further validated this variation by studying the same collection under varying salinity conditions. These findings highlight the importance of identifying and using salt-tolerant genotypes to enhance barley resilience in saline environments. Moreover[36], assessed the genetic diversity of 60 Tunisian barley landraces, and their research suggests that these landraces are not only suited to local conditions but also serve as a source of beneficial traits to improve salinity tolerance.

To mitigate climate-related impacts on crop yield and enhance salinity tolerance, selecting resilient genotypes, like G1, is vital. This study shows that both local and introduced genotypes have significant potential to adapt to saline conditions.

Temperature and average daily solar radiation impact differently on the salinity tolerance of the tested genotypes

The effect of temperature on YR caused by salt stress varies among barley genotypes, especially during reproductive stages. Our study confirmed that 10 tolerant genotypes (G1) maintained stable performance under rising temperatures, consistent with Hammami et al.[9]. In contrast, sensitive and moderately sensitive genotypes showed variable responses, with some exhibiting improved performance at higher temperatures during certain stages, reflecting both adaptability and instability[8–10,34,37]. Reproductive stages such as meiosis and anthesis are critical periods for barley's response to environmental stress. High temperatures during these phases can impair pollen development, reduce anther length, and cause sterility, leading to significant yield loss[39]. Prolonged heat exposure further reduces pollen viability and ear size[40], while elevated temperatures during grain filling shorten this phase and decrease yield[41]. Temperatures above 30 °C significantly affect barley growth and productivity. For example, raising ambient temperature from 20 to 28 °C delays inflorescence development and lowers floret and grain numbers per spike[42]. Every 1 °C increase above the optimal can decrease yield by 5–6%, mainly due to disruptions in reproductive development that impact grain number, size, and weight. Genotypic responses to heat vary, with some lines performing better under heat stress while others excel in cooler conditions, highlighting the importance of developing thermally resilient cultivars[43].

Our findings also show that even moderate heat stress can disrupt meiosis, especially in Tunisian improved varieties like Tej, Konouz, and Manel. These genotypes are sensitive to rapid temperature rises and simultaneous salinity stress during anthesis, aligning with previous observations[44]. Such genotypes provide valuable insights into how meiosis functions under stress, a topic that remains underexplored despite barley's agricultural significance[45]. Although the focus was on cold stress, Liu et al.[46] highlighted the importance of antioxidant enzyme activity and gene expression in stress tolerance. These results are similar to our findings on the physiological resilience of certain barley genotypes under combined salinity and heat stress, emphasizing the role of molecular and physiological markers in breeding efforts.

Group 1 genotypes generally showed tolerance to average daily solar radiation during developmental stages, with a notable exception during the meiosis-anthesis phase, where radiation had a disproportionately negative effect on salinity tolerance. This finding, also supported by Demotes-Mainard et al.[47], emphasizes meiosis as a key physiological bottleneck in barley's reproductive cycle. Solar radiation, more than temperature, seems to disrupt these processes by causing oxidative stress and impairing carbohydrate metabolism.

Physiological stress during meiosis, particularly from high radiation, can hinder the sugar supply to anther cells, which is essential for pollen development. This disruption compromises pollen viability and leads to male sterility, while female fertility remains largely unaffected[48]. The result is a significant reduction in grain number per ear, ultimately lowering overall yield. Studies have shown that excessive solar radiation during meiosis increases the risk of pollen abortion and reduces starch accumulation in pollen grains, which are vital for fertilization success[49,50]. Since meiosis plays a key role in ear fertility, controlling exposure to solar radiation at this stage is essential. Agronomic practices such as changing sowing dates, using reflective foliar sprays (e.g., kaolin), or altering canopy architecture can help reduce radiation stress. When timed correctly, these methods can help maintain reproductive health and stabilize yields in saline and high-radiation environments.

Soil nutrients could impact barley behavior toward salinity

The findings show that several top-performing genotypes within group G1 have different abilities to utilize soil calcium (Ca^{2+}) under saline conditions. While some genotypes struggle to take advantage of Ca^{2+}, others effectively use it to reduce salt stress. Notably, the Kairouan site had high levels of K^+ and Ca^{2+}, whereas Medenine showed lower amounts of both nutrients[9]. Potassium (K^+) and calcium (Ca^{2+}) are essential for salinity tolerance[51–53]. Adequate levels of these nutrients boost barley's resilience, especially during sensitive growth stages[15,16]. Calcium functions as a secondary messenger in stress signaling, helps maintain ion balance, and supports cell wall integrity[16]. Potassium controls osmotic pressure, activates enzymes, and aids in selective ion transport, helping to counteract sodium (Na^+) toxicity[50]. Together, they support ion balance and cellular stability under saline conditions[54]. Importantly, genotypes that are naturally salt-tolerant can benefit from better soil K^+ and Ca^{2+} availability. Under saline stress, plants sustain cytosolic K^+ by mobilizing vacuolar stores and sequestering Na^+ into vacuoles, preserving metabolic functions like protein synthesis. This energy-efficient mechanism contrasts with costly osmotic regulation through compatible solutes[19]. Physiological traits such as photosynthetic efficiency and membrane stability also impact genotype performance[21,55]. Farouk et al.[56,57]

demonstrated that foliar potassium application increased wheat yield under stress, highlighting the synergistic role of nutrient availability. Our results confirm that genotypes with higher K^+ and Ca^{2+} uptake perform better at both KAI and MED sites. Even commercial genotypes exhibited improved tolerance when nutrient levels were adequate. Potassium is vital for maintaining Na^+/K^+ balance, enzyme activity, and photosynthesis[58,59], and it strengthens antioxidant defenses against oxidative damage[60]. In addition, soil texture and organic matter also affect salinity response. The clay-loam soil at Kairouan, with organic matter content reaching up to 4%, likely enhanced water retention and nutrient supply, mitigating salinity stress. Conversely, the sandy soil at Medenine, with only 0.9% organic matter, may have limited nutrient uptake. These physical differences probably contributed to variations in genotype performance and warrant further investigation. Other research supports the importance of nutrient availability for crop performance under drought and salinity. AbdElaal et al.[61,62] found that deficit irrigation combined with sufficient nitrogen improved quinoa yield and water productivity, supporting our integrated approach. Recent transcriptomic studies in soybean have shown that salt-alkali stress tolerance involves regulation of ion transporters and antioxidant pathways, especially root-based Na^+ sequestration and K^+ retention[46,63]. These findings reinforce our observations regarding the roles of K^+ and Ca^{2+} in barley salinity tolerance.

Integrating these mechanisms into agronomic practices can improve crop management in saline environments and promote food security in arid regions.

Relationship between salinity tolerance and geographic origins of the genotypes

This study investigated the relationship between salinity tolerance and the geographic origin of 23 Tunisian barley genotypes, previously classified as either tolerant or sensitive[9,19].

These genotypes originate from central and southern Tunisia, where landraces are still cultivated by farmers[32]. A strong correlation was found between salinity tolerance and native soil salinity ($R^2 = 0.69$), as well as proximity to natural saline surface water (Fig. 6a). Genotypes from highly saline areas (2–3 dS m^{-1}) exhibited less yield reduction, while those from less saline regions (0.5–2 dS m^{-1}) were more sensitive. This supports the idea that long-term exposure to saline conditions promotes the development of adaptive mechanisms[52,64]. The observed correlation suggests that salinity tolerance traits are genetically ingrained and shaped by environmental selection. Barley's natural genetic variability, enhanced through mutation and recombination, allows adaptation to various stressors[65]. Landraces are especially well-suited to their native soil and climate conditions[4,66], having evolved under persistent abiotic stresses such as salinity[32,67]. Understanding genotype-environment interactions is essential for breeding programs aimed at improving salinity tolerance. However, efforts focused on arid and saline regions are still limited, and many commercial cultivars remain sensitive to salinity[68–71]. In our study, three of the four Tunisian commercial cultivars tested were susceptible to salt stress, highlighting the need for more targeted selection strategies. These findings provide actionable strategies for breeding programs and agronomic management in saline-prone regions. Adjusting sowing dates, applying reflective foliar sprays, and optimizing K^+ and Ca^{2+} fertilization can mitigate combined salinity and radiation stress during critical reproductive stages. As noted by Schmidt et al.[4], leveraging the inherent resilience of locally adapted genotypes can significantly increase barley productivity in saline and arid environments.

Conclusion

The results highlight the importance of ongoing research into the effects of high temperatures during the barley reproductive stages, particularly during gamete establishment. Moreover, high radiation can worsen susceptibility to salinity during these critical phases. Selecting more stable and tolerant genotypes, referred to as "climate-resilient barley genotypes," for salinity-prone and extreme climatic conditions is an effective strategy for sustaining high barley yields. Our study proposes that combining geographic and agroecological data with predictive climate modeling and crop simulation, along with trait-based ensemble modeling, can facilitate the search for stress tolerance genes and aid in developing environmental ideotypes through targeted breeding. Also, local landraces from naturally saline regions demonstrated strong adaptive traits, making them valuable for breeding programs aimed at developing stress-tolerant barley cultivars. Lastly, the presence of potassium and calcium in irrigation appears to significantly enhance the salinity tolerance of these genotypes. These findings emphasize the importance of managing soil nutrient levels to improve salinity tolerance in barley, ultimately ensuring better crop health and yield in saline environments.

Data availability

All data supporting the findings of this study are available within the article and its supplementary materials. Additional raw data can be requested from the corresponding author.

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Author contributions

Z.H. Data curation, Investigation, Methodology, Writing the main manuscript text. Y.T.: Methodology and Supervision. S.J.: Writing parts of the main manuscript text. S.A.: Methodology and Data curation. All authors reviewed the manuscript.

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Declarations

Competing interests

The authors declare that all necessary land-use permissions were obtained before the commencement of the experiment.

Additional information

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