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Salt-tolerant barley ideotypes for hot arid zones: Genotypic versus salinity effects on yield, grain quality and physiological traits

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ABSTRACT

Barley (*Hordeum vulgare* L.) is a key cereal crop in arid regions, where it is frequently grown under saline irrigation. This study investigated the effects of irrigation salinity and genotype on agronomic performance and grain quality in ten Syrian barley genotypes grown in sandy soils under three salinity levels (2.6, 10, and 15 dS m^{-1}) over two seasons at the International Center for Biosaline Agriculture (Dubai, UAE). Increasing salinity markedly reduced yield and biomass, and to a lesser extent grain weight, plant height, crop duration and leaf chlorophyll content. Salinity elevated sodium (Na) levels in grain and vegetative tissues, while also increasing grain carbon isotope composition ($\delta^{13}C$) and slightly decreasing leaf chlorophyll content. These results indicate that the main effect of salinity was osmotic, rather than ionic, causing water stress. Genotype had a significant effect on nearly all traits evaluated and was a stronger source of variation than salinity for grain mineral concentrations. Notably, grain Na concentration was more strongly influenced by genotype than by salinity, and was positively correlated with yield across genotypes, while higher-yielding genotypes also tended to exhibit lower grain $\delta^{13}C$, suggesting a more favorable water status. Lower-yielding genotypes tended to accumulate higher concentrations of N and minerals in the grain, indicating a potential trade-off between yield and nutritional composition. Overall, genotypic variation was the primary determinant of both yield and grain quality under saline irrigated conditions, highlighting the importance of genotype selection for productive and nutritionally adequate barley cultivation in arid environments.

1. Introduction

Salinity is one of the most critical abiotic stresses limiting crop growth and productivity worldwide, and it can also alter grain quality, affecting size, protein, and mineral concentration (Ashraf, 2014; De Santis et al., 2021; Turki et al., 2024). Nearly 1.4 billion hectares of land globally (10.7% of total global land area) are affected by salinity (FAO, 2024), with the issue being particularly severe in arid and semi-arid regions. In such areas, soil salinization is intensified by poor irrigation management and limited freshwater availability. Agricultural systems are increasingly reliant on lower-quality, saline water due to rising competition for freshwater resources among the domestic, industrial, and agricultural sectors (Araus, 2004). Additionally, climate change is expected to exacerbate water scarcity and soil salinity, reinforcing the need for salt-tolerant crops (Rukhsar et al., 2025). Barley (*Hordeum vulgare* L.) is the fourth most important cereal crop worldwide, following maize, wheat, and rice, with an annual production of approximately 150 million Mg (USDA-FAS, 2026). It is widely cultivated in the Mediterranean region, often in marginal environments characterized by drought, salinity, and nutrient limitations, particularly nitrogen deficiency (Araus et al., 2002; Oweis et al., 1998; Passioura, 2002). Barley is relatively more tolerant to salinity than other cereals (Isla et al., 1998; Munns et al., 2006), making it a promising target for improving agricultural sustainability in salt-affected regions. However, even barley suffers substantial yield losses under prolonged salinity stress (Zeeshan et al., 2020). Enhancing salt tolerance through the selection of more resilient barley genotypes and improved agronomic practices is therefore essential for securing productivity in these environments (Hammami et al., 2026).

Salinity stress in plants manifests in two sequential phases: an early

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osmotic phase and a subsequent ionic phase (Munns and Tester, 2008). The osmotic phase arises shortly after salt exposure, reducing water uptake, limiting cell expansion, and causing stomatal closure. These effects negatively impact photosynthetic efficiency (Boussora et al., 2024) and nitrogen metabolism (Yousfi et al., 2010b, 2012). As the stress continues, the ionic phase dominates, characterized by toxic accumulation of Na and Cl ions, which disturb ion homeostasis and accelerate tissue senescence (Zhang et al., 2019). Ionic imbalances can be quantified by shifts in ion ratios, such as increases in Na and Mg relative to K and Ca, along with reduced dry matter accumulation (El-Lethy et al., 2013; Yousfi et al., 2012; Rukhsar et al., 2025).

Physiological markers such as stable isotope composition have emerged as valuable tools to assess plant responses to salinity (Chamekh et al., 2016; Hussain et al., 2022b; Rukhsar et al., 2025). The carbon isotope composition ($\delta^{13}C$) reflects long-term changes in internal CO_2 concentrations of the photosynthetic organs, in most cases modulated by the stomatal conductance (Farquhar and Richards, 1984; Farquhar et al., 1989). Under saline conditions, stomatal closure during the osmotic phase increases $\delta^{13}C$ values (or decreases carbon isotope discrimination, $\Delta^{13}C$) in barley (Peñuelas et al., 1997; Isla et al., 1998; Yousfi et al., 2010a, Hussain et al., 2022a,b). Moreover, genotypic variability in $\delta^{13}C$ (or in $\Delta^{13}C$) under salinity has also been documented in barley (Jiang et al., 2006; Hussain et al., 2022a,b) and other cereals (Chamekh et al., 2016; Yousfi et al., 2010b, 2012; Rukhsar et al., 2025). Some studies report that salinity tolerant genotypes exhibit lower $\delta^{13}C$ (or higher $\Delta^{13}C$) values in mature grains (Chamekh et al., 2016).

Salt stress also affects nitrogen uptake and assimilation by altering root absorption and internal transport (Ashraf et al., 2018). In this sense, nitrogen isotope composition ($\delta^{15}N$) has been reported to provide insights into nitrogen metabolism under salinity (Yousfi et al., 2012). Typically, salinity results in increased $\delta^{15}N$ due to changes in nitrogen source discrimination, although responses can vary depending on environmental and genetic factors (Yousfi et al., 2010b; Rukhsar et al., 2025). Genotypic differences in $\delta^{15}N$ have been linked to the plant's ability to maintain nitrogen homeostasis under saline conditions (Yousfi et al., 2012).

Environmental variability in salinity (Chamekh et al., 2016; Rukhsar et al., 2025) and in general in water availability (Caldelas et al., 2023) also plays a significant role in determining grain quality in cereals, underscoring the need to consider both yield and quality traits in genotype evaluation for salinity tolerance. For example, salinity affects grain quality, including reductions in grain size and alterations in protein and mineral concentration (Ashraf, 2014; De Santis et al., 2021; Turki et al., 2024; Rukhsar et al., 2025). Typically, decreases in grain size in response to salinity often result in higher relative protein and mineral concentration per unit weight (Francois et al., 1986; Katerji et al., 2005; Rukhsar et al., 2025). Moreover, salinity modifies the uptake and distribution of essential macro- and micronutrients such as K, Ca, P, Mg, Mn, Fe, Cu, and Zn (Masoni et al., 2007; Rezzouk et al., 2020; Rukhsar et al., 2025). These changes reflect both reduced translocation due to osmotic stress and direct ionic effects of salinity. Furthermore, the composition of irrigation water and type of fertilizer used can influence grain mineral concentration. For instance, organic amendments like manure may exacerbate salt accumulation in sandy soils typical of arid regions (Yadav et al., 2015; El Sabagh et al., 2019) causing stress to the plants (Rezzouk et al., 2020). Despite the agronomic importance of micronutrients, studies evaluating the effects of salinity on grain mineral composition in barley are still limited (Ghafoor et al., 2015). Another factor to consider is the potential effect of salinity in decreasing grain size and therefore increasing mineral concentrations (Rukshar et al., 2025).

This study investigates the responses of a set of barley genotypes, with contrasting agronomic performance under Mediterranean semiarid conditions, to a wide range of irrigation salinity levels in the United Arab Emirates (UAE), one of the world's driest regions, characterized by sandy soils, extreme temperatures, and limited freshwater resources. We conducted a comprehensive, field-based analysis that combined agronomic performance, together with physiological indicators of response to salinity ($\delta^{13}C$, $\delta^{15}N$ of grain, leaf chlorophyll content and Na accumulation in different plant parts) and grain quality traits (grain weight, and total N and mineral concentrations in grain) to evaluate genotype performance and physiological adaptation to salinity stress. Importantly, this study addresses the underexplored relationship between salinity, grain mineral compositions, and physiological traits in barley, with implications for crop selection and breeding under saline and arid conditions. The minerals investigated included essential elements for plants and for human nutrition such as K, Ca, S, P, Mg, Mn, Mo Zn, Fe, and Cu (Prasad et al., 2016). By linking isotope-based physiological indicators with agronomic and nutritional outcomes, this work offers a novel framework for understanding genotype performance. Previous studies on barley and other cereals under saline conditions, including those conducted at ICBA, have largely focused on stable isotope composition and ionic parameters measured in leaves (Hussain et al., 2022a, b).

The present study departs from this approach in two important respects. On the one hand, $\delta^{13}C$ was measured in mature grains rather than in leaves, providing a time-integrated indicator of plant water status during the reproductive phase of the crop (Merah and Monneveux, 2015), which has proven useful for assessing irrigation salinity responses in field-grown cereals (Chamekh et al., 2016). By contrast, $\delta^{13}C$ analyzed in the dry matter of leaves (and other vegetative tissues) integrates water stress conditions earlier in the crop cycle. On the other hand, while the exclusion or compartmentalization of toxic ions such as Na and the maintenance of K homeostasis have been extensively characterized in roots and shoots (Munns and Tester, 2008) it has scarcely been examined in tissues of reproductive organs such as grains. In this context, Na accumulation in grains is of particular relevance, as it reflects not only the degree of ionic stress experienced by the plant but also the capacity of the shoot to grain transport system to regulate ion loading under saline conditions. While roots function as the primary barrier to Na uptake and shoots serve as the main storage compartment, the accumulation of Na in barley grains is considered particularly detrimental, as it directly affects final yield and compromises seed quality (Houston et al., 2020). Beyond Na and K, the essential mineral composition of the barley grain was determined, which is of direct relevance to crop quality and human nutrition, an aspect largely overlooked in previous physiological studies focused on salinity tolerance.

The specific research questions addressed were: (1) what is the effect of irrigation salinity on grain yield, agronomic traits, physiological indicators and grain quality, (2) what is the relative importance of salinity and genotypic effects and their interactions on the above characteristics, (3) is there any genotypic trade-off between grain yield and quality, and (4) what physiological characteristics may be used as phenotypic indicators to select genotypes better adapted to different irrigation salinity levels. It should be acknowledged that some of the findings reported here are correlative in nature, and further mechanistic studies will be required to substantiate these relationships, including the specific role of Na osmotic dynamics in barley grain under saline conditions.

2. Materials and methods

2.1. Field site description

Field trials were conducted over two consecutive winter growing seasons (2020–2021 and 2021–2022) at the experimental facilities of the International Center for Biosaline Agriculture (ICBA) in Dubai, UAE (25°05′49″ N, 55°23′25″ E). The soil at the ICBA site is predominantly sandy in texture (98% sand, 1% silt, 1% clay), highly porous (45% porosity), calcareous (containing 50–60% $CaCO_3$ equivalents), and moderately alkaline (pH 8.22), with extremely low organic matter content (<0.5%). The soil exhibited a high drainage capacity, with a

saturation percentage of 26, and an electrical conductivity of the saturated extract (ECe) measured at 1.2 dS m^{-1} . Prior to the experiment, soil samples were collected at four depth intervals (0–15, 15–30, 30–60, and 60–100 cm) and analyzed for key physicochemical and ionic properties. Organic matter (OM), total carbon (C), calcium carbonate ($CaCO_3$), and the ionic concentrations of calcium (Ca^{2+}), magnesium (Mg^{2+}), sodium (Na^+), potassium (K^+), chloride (Cl^-), bicarbonate (HCO_3^-), and carbonate (CO_3^{2-}) were determined in the saturated paste extract. The initial soil physicochemical and ionic composition across the sampled profile is presented in Table S1. Sodium concentration was highest in the upper soil layer. Potassium concentrations were consistently low across all sampled depths, CO_3^{2-} was not detected, and HCO_3^- was present only at negligible levels. These results confirm that the baseline soil chemistry did not introduce significant solute inputs that could confound the imposed salinity treatments.

2.2. Growth conditions and field evaluation

Ten genotypes of barley (*Hordeum vulgare* L.) with contrasting agronomic performance under Mediterranean semiarid conditions (Table 1) were cultivated under the specific arid climatic conditions of the UAE (Supplementary Table S2) across two consecutive growing seasons. It is noteworthy that the first growing season was characterized by higher maximum temperatures during the flowering period, compared to the second season (Supplementary Fig. S1). The genotypes evaluated in this study included “ACSAD 60,” “ACSAD 68,” “ACSAD 176,” “ACSAD 1230,” “ACSAD 1420,” “ACSAD 1630,” “ACSAD 1713,” “ACSAD 1746,” “ACSAD 1811,” and “Furat 4.” Most of these genotypes are recognized for their tolerance to the drought or salinity conditions prevalent in the southern and eastern Mediterranean basin (Table 1).

The experiment was conducted using a randomized complete block design, with three irrigation water salinity levels (2.6, 10 and 15 dS m^{-1}) as the main treatment factor, ten barley genotypes as the genotypic factor, and three complete blocks serving as replicates, resulting in 90 experimental plots per growing season and 180 plots across both seasons combined. Within each block, the assignment of genotypes to plots was performed independently and at random for each salinity level, ensuring an unbiased spatial distribution of genotypes across the field. Blocks were used to account for potential spatial heterogeneity within each trial. Each genotype by salinity combination was therefore replicated three times, providing sufficient degrees of freedom for the estimation of experimental error and the detection of treatment effects. Each experimental plot measured 2 m^2 and consisted of four rows, with 25 cm spacing between rows. Within each row, planting holes were spaced 20 cm apart, and five seeds were sown per hole, resulting in a final seeding density of 100 seeds m^{-2}. A drip irrigation system was employed, using emitters spaced at 20 cm intervals. This planting arrangement and density were adapted to optimize water use efficiency under drip irrigation, which is commonly practiced in arid regions such as the UAE. Throughout all three irrigation treatments, each crop cycle received a total water application of approximately 550 mm. Irrigation was carried out three times daily: morning, midday, and evening, providing a daily volume of 2.5 lm^{-2} from sowing until the beginning of stem elongation, which occurred about two months after planting. After this stage, the irrigation volume was increased to 5 lm^{-2} per day to meet the higher evapotranspiration demands driven by plant development and rising ambient temperatures later in the season.

Before planting, animal compost (Supplementary Table S1) was uniformly incorporated into all experimental plots at a rate of 50 Mg ha^{-1} to ensure consistent baseline conditions across treatments. The manure used in this study (Supplementary Table S1) had a composition that minimized potential confounding effects on salinity. It was relatively enriched in Mg (0.69 mmol g^{-1}) compared with Na (0.13 mmol g^{-1}), resulting in an approximate Mg:Na ratio of 5:1 and a total amount of Mg and Na of 839 kg and 149 kg per ha. The low Na content was critical to the experimental design, as it prevented manure-derived Na from interfering with the imposed salinity treatments and thereby preserved the integrity of the salinity gradient across plots.

Seeds were sown on December 6 in both the 2020–2021 and 2021–2022 cropping seasons. Agronomic practices were kept consistent across both seasons. Immediately after sowing, the soil surface was covered with mesh to protect the seeds from birds. The cover was removed approximately 10 days after sowing in the first season and about one week after sowing in the second, once seedling emergence was complete. For plant protection, an aphid-targeted pesticide was applied two weeks after sowing, and weeds were manually removed around mid-January in the first season and twice in the second season in late December and again in late January. To further protect developing spikes, bird netting was installed during grain filling on February 6, 2021, and February 15, 2022, for the first and second seasons, respectively. Irrigation salinity treatments were initiated approximately one month after sowing, once seedlings were fully established. Until that point, all plots were irrigated with control irrigation (2.6 dS m^{-1}) to ensure uniform germination and early growth, which are critical for crop resilience under subsequent saline conditions (Iqbal et al., 1998). Around one month after planting, salinity treatments were imposed as a one-time increase to reach the target concentration and were maintained until maturity. The irrigation salinity levels were: 2.6 dS m^{-1} (Control; no change in the salinity of the irrigation water), 10 dSm^{-1} (Salinity 1), and 15 dS m^{-1} (Salinity 2). Irrigation water was formulated by mixing reverse osmosis fresh-water with water taken from a well to reach the different electric conductivities. Water characteristics are detailed in supplemental Table S1.

During the first season, chlorophyll content in the flag leaf was assessed using a SPAD chlorophyll meter (Minolta, Japan) on February 15, 2021, while plant height measurements were taken on March 29, 2021. For wheat, it is widely recognized that SPAD values ranging from 20 to 50 show a strong correlation with chlorophyll content determined by standard spectrophotometric methods (Uddling et al., 2007).

Table 1
Provenance, origin and agronomic characteristics under the arid Mediterranean drought conditions of Syria and the southern and eastern Mediterranean basin of the ten barley varieties used in this study.

Genotype	Provenance/ Origin	Tolerant/ Susceptible to drought or salinity	Rows	Source
ACSAD 60	ACSAD - Syria	Tolerant to salinity	2	Ali Saleh (2015). Saleh and Almahasneh (2023)
ACSAD 68	ACSAD_ Syria	Tolerant to salinity	6	Ali Saleh (2015). Saleh and Almahasneh (2023)
ACSAD 176	ACSAD - Syria	Tolerant to salinity	6	Ali Saleh (2015). Saleh and Almahasneh (2023)
ACSAD 1230	ACSAD - Syria	Tolerant to salinity	6	Eleuch et al., (2005). Saleh and Almahasneh (2023)
ACSAD 1420	ACSAD - Syria	Tolerant to salinity	2	Ali Saleh. R. (2015). Saleh and Almahasneh (2023)
ACSAD 1630	ACSAD - Syria	Sensitive to drought	6	Saleh and Almahasneh (2023)
ACSAD 1713	ACSAD - Syria	Tolerant to drought	6	Saleh and Almahasneh (2023)
ACSAD 1746	ACSAD - Syria	Tolerant to drought	6	Faraj et al. (2023).
ACSAD 1811	GCSAR - Syria	Sensitive to drought	6	Sharqi et al. (2023a), b)
Furat 4	GCSAR - Syria	Tolerant to drought	6	Al-khalaf, (2021); Al-khalaf et al., (2022)).

ACSAD, Arab Center for the studies of Arid Zones and Drylands; GCSAR, General Commission for Scientific Agricultural Research

Moreover, portable meters of this type express pigment content on a per unit area basis, thereby capturing the potential influence of environmental conditions (such as salinity in the present study) on leaf anatomy (Shah et al., 2017; Zhang et al., 2022).

Harvest dates differed depending on the irrigation salinity treatments: plants subjected to the 15 dS m^{-1} level were harvested on April 17, whereas those grown under 10 and 2.6 dS m^{-1} irrigation salinity were harvested on May 1. After harvesting, total shoot biomass (SB), grain yield (GY), and thousand grain weight (TGW) were evaluated. In the second season, chlorophyll measurements were conducted on February 22, 2022, and plant height was recorded on March 25, 2022. Plants exposed to the 15 dS m^{-1} irrigation salinity were harvested on April 20, while harvesting for the 10 and 2.6 dS m^{-1} treatments occurred on May 3. As in the previous season, SB, GY, and TGW were measured following harvest. Additionally, days to maturity were recorded in both seasons, calculated as the number of days from sowing to physiological maturity. GY was assessed and a subset of grain used for further analysis of stable isotope composition and nitrogen and mineral concentrations. Additionally, shoot and root samples were collected from five randomly selected plants per plot at near maturity and used for Na and K analyses.

2.3. Stable isotope composition and nitrogen concentration

Grain samples were first dried at 60°C until they reached a constant weight, then finely ground using a ball mill (MM 400, Retsch GmbH, Haan, Germany). Approximately 0.7–0.8 mg of the powdered samples were weighed into tin capsules for analysis of total nitrogen (N) concentration, as well as the stable carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) isotope ratios. The measurements were carried out using an elemental analyzer (Flash 1112 EA; Thermo-Finnigan, Bremen, Germany) coupled with an isotope ratio mass spectrometer (Delta V Advantage via Conflo IV interface IRMS, Thermo Fisher Scientific, Waltham, MA, USA) in continuous flow mode at the Scientific Facilities of the University of Barcelona. The $^{13}C/^{12}C$ ratio was expressed in δ notation (Coplen, 2008) as carbon isotope composition, $\delta^{13}C$ (‰), calculated by the equation: $\delta^{13}C$ (‰) = $[(R_{sample} / R_{standard}) - 1] \times 1000$, where sample refers to plant material and standard to Pee Dee Belemnite (PDB) calcium carbonate. International isotope secondary standards of known $^{13}C/^{12}C$ ratios (IAEA CH7, polyethylene foil; IAEA CH6, sucrose; USGS 40, L glutamic acid) were used with an analytical precision of 0.1‰. Similarly, the $^{15}N/^{14}N$ ratio was expressed in δ notation as nitrogen isotope composition, $\delta^{15}N$ (‰), using N_2 in air as the standard. For nitrogen, the international isotope secondary standards IAEA N1, $IAEAN_2$, $IAEANO_3$, and USGS40 were employed with a precision of 0.3‰.

2.4. Mineral analyses

Calcium (Ca), magnesium (Mg), manganese (Mn), phosphorus (P), iron (Fe), copper (Cu), molybdenum (Mo), zinc (Zn), sulfur (S), potassium (K), and sodium (Na) were analyzed in this study. Concentrations of Ca, Mg, Mn, P, Fe, Cu, Mo, Zn, and S were determined in grain, while K and Na were measured in grain, shoots, and roots. Barley grain flour (100 mg) was digested overnight with HNO_3 and H_2O_2 at 90°C in Teflon® beakers pre-cleaned by acid-washing and rinsing with MilliQ water, then diluted with MilliQ water prior to analysis. Macroelements (Ca, Fe, K, Mg, Na, P, S) were quantified by ICP-OES (Optima 8300, Perkin Elmer), while microelements (Cu, Mn, Mo, Zn) were measured by ICP-MS (Elan6000, Perkin Elmer). Quality control included procedural blanks and certified reference materials (BCR-60, BCR-62, BCR-279; JRC), with recovery rates of 90–94%. For vegetative tissues, shoots (excluding ears) and roots were washed, oven-dried, and ground. Samples (100 mg) were digested in HNO_3, and K and Na concentrations were determined using a PFP-7 flame photometer (Jenway, UK) at ICBA laboratory.

2.5. Statistical analysis

All agronomic, physiological, and analytical traits assessed in this study were subjected to factorial analysis of variance (ANOVA) to evaluate the effects of irrigation water salinity, genotype, season, and their interactions. Crop season (2020–2021 and 2021–2022), water irrigation salinity, and genotype were treated as fixed factors, while all measured agro-physiological variables were considered as dependent variables. The two seasons represent specific and consecutive agricultural cycles deliberately selected to evaluate the consistency of genotype responses across years. Moreover, except for some short-term differences in maximum temperature during the beginning of the reproductive period, environmental conditions were very similar across the two seasons, with rainfall being negligible (Table S2).

Mean comparisons were performed using Tukey's Honestly Significant Difference (HSD) test to identify significant differences among irrigation salinity and genotypes. To explore trait associations, a bivariate Pearson correlation analysis using all data was performed and visualized with a heat map. Additionally, phenotypic correlations among the ten genotypes were evaluated through bivariate Pearson correlation analysis. Principal component analysis (PCA) was conducted on GY, SB, plant height, days to maturity, thousand grain weight, leaf chlorophyll content, grain $\delta^{13}C$ and $\delta^{15}N$, grain N concentration, Na and K concentration in grain, shoots, and roots, as well as the concentrations of essential minerals in the grain. The PCA aimed to distinguish between control conditions (2.6 dS m^{-1}) and salinity treatments (10 and 15 dS m^{-1}). All measured variables were included in the PCA to provide an unbiased, holistic characterization of the performance of all the agronomic /physiological traits of the study in one case (or the grain quality traits in the other), as well as the genotypic responses to water irrigation salinity, and to avoid any a priori exclusion of potentially informative traits. Furthermore, path analysis (Li, 1975) was employed to develop a model linking days to maturity, grain $\delta^{13}C$, grain N concentration and grain Na concentration with GY and SB. The goodness of fit model was evaluated using the Comparative Fit Index (CFI) (Arbuckle, 1997). Path analysis was applied here as a correlational technique that partitions observed associations among variables into direct and indirect effects. Although path coefficients allow quantification of the relative contributions of individual traits to grain yield under salinity stress, they do not establish mechanistic causality. Accordingly, the inferred pathways should be interpreted as hypothesized associations consistent with the data structure, rather than as definitive causal relationships. All statistical analyses were conducted using IBM SPSS Statistics Version 25.0 (SPSS Inc., Chicago, IL, USA). Figures were generated in SigmaPlot 11.0 (Systat Software Inc., Point Richmond, CA, USA). The correlation heat map and PCA visualizations were produced using the Past (PAleontological STatistics) software developed through a collaboration between the University of Oslo, the University of Copenhagen, and the National University of Ireland.

3. Results

3.1. How irrigation salinity, genotype, and season drive grain yield and agronomic traits

Salinity stress had a significant impact ($p < 0.001$) on all measured agronomic traits across treatments and seasons (Table 2). Compared to control conditions (2 dS m^{-1}), increasing salinity levels slightly accelerated crop development, as evidenced by a reduction in days to maturity (DM). Plant height also declined by 8% and 15% under 10 and 15 dS m^{-1} irrigation salinity, respectively. A more substantial decline was observed in GY, which dropped by 31% and 38% under Salinity 1 (10 dS m^{-1}) and Salinity 2 (15 dS m^{-1}), respectively (Table 2). Similarly, SB also showed marked reductions of 30% and 41% under the same respective salinity levels (Table 2). By contrast, the TGW decreased only by 4% under 10 dS m^{-1} and by 9% under 15 dS m^{-1} .

Table 2
Effect of salinity, genotypes and season on the number of days to maturity, plant height, the biomass, the thousand grain weight (TGW) and the grain yield in barley genotypes. The values of each irrigation condition are the mean ± SE of 60 measurements (10 genotypes, three replicates per genotype and two seasons). Means followed by letters are significantly different ($p < 0.05$) according to Tukey's honestly significant difference (HSD) test. The associated sum of squares and probabilities (ns, not significant; *$p < 0.050$; **$p < 0.010$; ***$p < 0.001$) are shown for salinity, genotypes, season and their interactions.

	Days to maturity	Plant height (cm)	Biomass (Mg ha^{-1})	TGW (g)	Grain Yield (Mg ha^{-1})
Irrigation					
Control (2.6 dS m^{-1})	$134.10^{b} \pm 0.41$	$67.12^{c} \pm 1.39$	$16.18^{c} \pm 0.54$	$51.23^{c} \pm 0.56$	$2.43^{c} \pm 0.10$
Salinity 1 (10 dS m^{-1})	$133.98^{a} \pm 0.35$	$61.69^{b} \pm 0.96$	$11.26^{b} \pm 0.37$	$48.97^{b} \pm 0.52$	$1.68^{b} \pm 0.05$
Salinity 2 (15 dS m^{-1})	$132.35^{a} \pm 0.32$	$57.03^{a} \pm 0.57$	$9.51^{a} \pm 0.33$	$46.67^{a} \pm 0.51$	$1.50^{a} \pm 0.04$
Season					
2020–2021	134.47 ± 0.31	68.43 ± 0.82	12.28 ± 0.24	52.12 ± 0.37	1.71 ± 0.03
2021–2022	132.49 ± 0.26	55.46 ± 0.42	12.36 ± 0.59	45.79 ± 0.30	2.03 ± 0.09
Level of significance					
Salinity (S)	114.87***	3061.74***	1434.11***	623.68***	28.86***
Genotype (G)	256.91***	367.63***	376.54***	800.95***	11.06***
Season (Se)	176.02***	7576.38***	0.28^{ns}	1803.92***	4.64***
S x G	101.12^{ns}	492.81***	93.53^{ns}	100.29***	1.48^{ns}
S x Se	107.14***	901.97***	748.73***	1.66^{ns}	19.52***
G x Se	225.97***	692.70***	55.89^{ns}	55.48***	1.83^{ns}
S x G x Se	92.18^{ns}	802.02***	121.93^{ns}	126.62***	2.51^{ns}

Genotypic differences were highly significant ($p < 0.001$) for all agronomic traits studied (Table 2; Supplementary Table S3). Considering the mean values across the three irrigation salinities, ACSAD 60 exhibited the shortest and ACSAD 1630 the longest DM. Plant height also varied significantly, with ACSAD 1713 and ACSAD 60 being the tallest, and ACSAD 1811 the shortest. SB was the lowest in ACSAD 1420 and the highest in ACSAD 1746. TGW was highest in Furat 4 and ACSAD 1811, and lowest in ACSAD 1630. ACSAD 1746 recorded the highest GY, followed by ACSAD 1230 and Furat 4, while ACSAD 176 had the lowest GY).

Seasonal effects were significant ($p < 0.001$) for all traits except SB. In 2020–2021, plants were higher in TGW and slightly longer in DM compared to 2021–2022, although GY was lower in the 2020–2021 crop season (Table 2). For both GY and SB the main effect was associated with salinity, followed by genotype, whereas season had a minor effect (GY) or no effect (SB). Season was the main factor for plant height and TGW. Significant salinity by genotype (S × G) interactions were observed for plant height and TGW ($p < 0.001$), but not for DM, SB, or GY. Salinity by season (S × Se) interactions were significant for all traits except TGW, while genotype by season (G × Se) interactions were significant for DM, plant height, and TGW, but not for SB or GY. The three-way interaction (S × G × Se) was significant only for plant height and TGW (Table 2).

3.2. Salt stress, genetic variation, and seasonal effects on isotopic signatures, N concentration, and chlorophyll content

Salinity stress significantly affected carbon ($\delta^{13}C$) and N isotopic ($\delta^{15}N$) composition, as well as the total N concentration of mature grain and leaf chlorophyll (LC) content (Table 3). $\delta^{13}C$ increased ($p < 0.001$, in absolute terms) 0.82‰ under Salinity 1 and 1.39‰ under Salinity 2 relative to control conditions. Similarly, $\delta^{15}N$ increased, in absolute terms, by 0.73‰ and 0.28‰, under Salinity 1 and 2, respectively ($p < 0.001$). N concentration also rose ($p < 0.001$), by 13% under Salinity 1 and 15% under Salinity 2. In contrast, LC declined ($p < 0.05$) under saline conditions, with reductions of 5% and 6% in Salinity 1 and Salinity 2, respectively (Table 3).

Significant genotypic variation ($p < 0.001$) was observed for $\delta^{13}C$, $\delta^{15}N$, and N concentration, whereas LC did not differ significantly among genotypes (Table 3; Supplementary Table S4). Considering the means across salinities and seasons, the most enriched $\delta^{13}C$ values were recorded in ACSAD 1811 and ACSAD 60, while ACSAD 1746 and Furat 4 exhibited the most depleted values. For $\delta^{15}N$, ACSAD 1811 and ACSAD 68 had the highest values, whereas ACSAD 1420 and ACSAD 60 had the lowest. N concentration was the lowest in ACSAD 60 and the highest in ACSAD 1630.

Table 3
The influence of salinity, genotype and season on the grain carbon isotope composition ($\delta^{13}C$), grain nitrogen isotope composition ($\delta^{15}N$), grain nitrogen concentration (N), and leaf chlorophyll content was assessed in barley genotypes. Data for each irrigation treatment during both crop seasons are presented as the mean ± standard error (SE) of 60 measurements (10 genotypes, three replicates per genotype and two seasons). Means with different letters are statistically significant ($p < 0.05$) according to Tukey's honestly significant difference (HSD) test. The corresponding sum of squares and significance levels (ns = not significant; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$) are provided for the effects of salinity, genotype, and their interactions.

	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	N (%)	Leaf chlorophyll (SPAD units)
Irrigation				
Control (2.6 dS m^{-1})	$-27.97^{a} \pm 0.11$	$5.83^{a} \pm 0.13$	$2.07^{a} \pm 0.02$	$39.93^{b} \pm 0.55$
Salinity 1 (10 dS m^{-1})	$-27.15^{b} \pm 0.06$	$6.59^{b} \pm 0.17$	$2.35^{b} \pm 0.03$	$38.07^{ab} \pm 0.76$
Salinity 2 (15 dS m^{-1})	$-26.58^{c} \pm 0.11$	$6.64^{b} \pm 0.17$	$2.38^{b} \pm 0.03$	$37.37^{a} \pm 0.76$
Season				
2020–2021	-27.32 ± 0.05	5.64 ± 0.08	2.17 ± 0.01	40.85 ± 0.19
2021–2022	-27.14 ± 0.13	7.06 ± 0.13	2.36 ± 0.03	36.06 ± 0.71
Level of significance				
Salinity (S)	58.72***	24.42***	3.36***	210.08*
Genotype (G)	19.09***	27.27***	2.27***	96.16^{ns}
Season (Se)	1.36***	90.78***	1.68***	1034.31***
S x G	6.09***	23.21***	0.95**	100.76^{ns}
S x Se	58.93***	31.71***	2.35***	141.33^{ns}
G x Se	6.20***	28.31***	1.10***	60.78^{ns}
S x G x Se	4.73 ***	16.87*	1.09**	124.73^{ns}

Seasonal effects were significant ($p < 0.001$) for the four traits, but particularly important for $\delta^{15}N$ and LC. The mean values across salinities and genotypes for $\delta^{13}C$ were (in absolute terms) more depleted and $\delta^{15}N$ higher in 2021–2022, whereas N concentration increased and LC decreased in 2021-2022 (Table 3). Salinity, followed by genotype were the main factors that affected $\delta^{13}C$ and N, whereas season was the factor that most affected $\delta^{15}N$ and LC. Significant S × G interactions were found for $\delta^{13}C$, $\delta^{15}N$, and N, but not for LC (Table 3). Similarly, S × Se, G × Se and S × G × Se interactions were significant for $\delta^{13}C$, $\delta^{15}N$, and N concentration, whereas LC showed no significant interactions (Table 3).

3.3. Mineral composition under saline irrigation: the combined influence of genotype and growing season

Salinity significantly altered the mineral composition of barley grain (Table 4). Compared to the control, salinity increased ($p < 0.001$) the concentrations of several minerals. In the case of Mn, Zn and S, increases were small (≤11%), while Mo responded strongly to salinity, increasing by 125% at Salinity 2. Ca only slightly (8%) increased under Salinity 2. In contrast, Mg, P and Fe were not affected by salinity, while Cu slightly (≤11%) decreased ($p < 0.05$) under salinity (Table 4). Among the three tissues analyzed, the grain exhibited much lower concentrations of K and particularly of Na compared with the roots and shoots (Table 5). Shoot K (K_{shoot}) increased by 14.7% and 23.4%, and grain K (K_{grain}) by 3.4% and 5.2%, under Salinity 1 and 2, respectively (Table 5). In contrast, the K concentration in roots (K_{root}) decreased by 33.3% and 39.8% under Salinity 1 and 2, respectively. Salinity had a significant ($p < 0.001$) effect on Na accumulation in roots, shoots, and grain (Table 5). Na concentration in roots (Na_{root}) increased by 52% under Salinity 1 and by 144% under Salinity 2. In shoots (Na_{shoot}), Na accumulation increased by 4% and 46%, while in the grain (Na_{grain}) it rose by 73% and 125% under Salinity 1 and 2, respectively. As a result, the K/Na ratio in the grain decreased significantly by 36% and 45% under Salinity 1 and 2, respectively. Similarly, the root K/Na ratio declined by 44.6% and 74.7% under the same salinity levels. In shoots, however, the K/Na ratio increased slightly by 12.7% under Salinity 1, but decreased by 14.5% under Salinity 2.

Except for grain Mo, and the K and Na concentrations in shoots and roots, along with their corresponding K/Na ratios, all other mineral traits exhibited significant ($p < 0.001$) genotypic variation (Tables 4, 5; Supplementary Tables S5, S6). For instance, considering the mean values across salinities and seasons, ACSAD 1420 and ACSAD 1230 exhibited the lowest and highest K in the grain, respectively, and corresponding extreme values for the tested elements were exhibited by ACSAD 60 and ACSAD 1811 for Ca, ACSAD 60 and ACSAD 1630 for Mg, ACSAD 60 and ACSAD 1630 for P, Furat 4 and ACSAD 1811 for Fe, ACSAD 60 and ACSAD 1811 for Mn, Furat 4 and ACSAD 1811 for Zn, ACSAD 1230 and ACSAD 1713 for Cu, ACSAD 1230 and ACSAD 68 for S, and ACSAD 1811 and ACSAD 1746 for Na_{grain}. The K/Na ratio in grain showed significant genotypic differences, with ACSAD 1811 having the highest ratios, and ACSAD 1746 the lowest.

Seasonal effects were also highly significant ($p < 0.001$) for all minerals except Mo and the K/Na ratio in the grain, with generally higher mineral concentrations recorded during the 2021–2022 season than in 2020–2021 (Tables 4, 5). Overall, genotypic and seasonal effects on mineral accumulation were markedly stronger than the effect of salinity (Tables 4, 5). Seasonal variation significantly affected the concentrations of K and Na in all tissues, as well as their corresponding K/Na ratios, with the exception of the K_{grain}/Na_{grain} ratio, which remained statistically unchanged. Compared to the 2020–2021 season, in 2021–2022, K concentrations decreased in roots and shoots, while the K in grain increased. Conversely, Na concentrations increased in roots and the Na in the grain increased sharply, while the Na in shoots decreased (Table 5). These shifts led to a significant decline in K/Na ratios in roots and shoots. Among all minerals, Zn was unique in that genotypic effects, followed by salinity, had a greater influence than the seasonal effect. Significant S × G interactions were detected for all minerals except Cu, Mo, K, and Na in both shoot and root tissues, as well as for their respective K/Na ratios (Tables 4, 5). The S × Se interaction was significant for all minerals except Mg, P, and Fe, while the G × Se interaction was significant for all minerals except Mo, K in shoots and roots, Na in shoots, and K/Na ratios in shoots and roots. Finally, the three-way interaction S × G × Se was significant for all minerals except Fe, Mo, K, and Na in shoot and root tissues, and for their corresponding K/Na ratios (Tables 4, 5).

Table 4
The effect of salinity, genotype and season on the concentration of essential minerals in the grain of barley genotypes was investigated. Data for each irrigation treatment across the crop seasons are presented as the mean ± standard error (SE) 60 measurements (10 genotypes, three replicates per genotype and two seasons). Means that are significantly different are indicated by distinct letters ($P < 0.05$), as determined by Tukey's honestly significant difference (HSD) test. Sum of squares and significance levels (ns = not significant; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$) are provided for the effects of salinity, genotype, and their interactions.

Mineral concentration (mg kg^{-1})	Ca	Mg	P	Fe	Mn	Zn	Cu	S	Mo
Irrigation									
Control (2.6 dS m^{-1})	794.15^{a} ± 20.94	1372.05^{a} ± 38.13	5073.62^{a} ± 62.97	41.76^{a} ± 1.50	19.95^{a} ± 0.29	61.89^{a} ± 1.21	5.78^{b} ± 0.17	1235.81^{a} ± 11.94	1.26^{a} ± 0.05
Salinity 1 (10 dS m^{-1})	795.82^{a} ± 23.95	1389.15^{a} ± 38.37	5077.47^{a} ± 66.88	42.30^{a} ± 1.34	21.06^{ab} ± 0.40	67.30^{c} ± 1.05	5.38^{ab} ± 0.11	1339.63^{b} ± 20.55	2.40^{b} ± 0.29
Salinity 2 (15 dS m^{-1})	860.89^{b} ± 28.07	1387.74^{a} ± 40.89	5027.08^{a} ± 63.14	45.00^{a} ± 1.74	22.12^{c} ± 0.52	65.77^{b} ± 1.13	5.16^{a} ± 0.23	1367.97^{c} ± 25.84	2.84^{b} ± 0.27
Season									
2020–2021	677.69 ± 10.91	1100.03 ± 10.00	4707.63 ± 34.47	37.18 ± 0.95	19.17 ± 0.24	64.20 ± 0.83	4.86 ± 0.15	1196.40 ± 8.31	1.99 ± 0.20
2021–2022	956.22 ± 16.20	1665.93 ± 11.61	5411.15 ± 39.17	48.87 ± 1.22	22.92 ± 0.33	65.78 ± 1.05	6.02 ± 0.11	1432.54 ± 15.33	2.35 ± 0.20
Level of significance									
Salinity (S)	173784.80***	10817.16^{ns}	94415.47^{ns}	361.14^{ns}	142.17***	934.12***	11.59**	580965.35***	79.80***
Genotype (G)	1812354.72***	1090140.02***	14282803.52***	6036.95***	808.97***	8133.80***	80.77***	608848.20***	25.33^{ns}
Season (Se)	3491023.88***	14410632.16***	22272286.84***	6147.88***	632.48***	112.16***	59.83***	2509337.21***	5.82^{ns}
S x G	335167.89***	103686.39*	1127439.68 *	2202.86*	44.53***	961.36***	23.25^{ns}	165689.87***	65.15^{ns}
S x Se	190357.80***	18168.79^{ns}	21847.57^{ns}	147.04^{ns}	155.53***	960.70***	31.44***	569266.13***	87.52***
G x Se	86326.41***	146475.62***	1177770.22***	1340.43*	34.63***	1348.07***	17.19*	103259.42***	29.47^{ns}
S x G x Se	248522.45***	138243.97**	1160770.28 *	1716.81^{ns}	46.06***	983.72***	29.83*	134558.37***	47.97^{ns}

Ca, calcium; Mg, magnesium; P, phosphorus; Fe, iron; Mn, manganese; Zn, zinc; Cu, copper; S, sulfur; Mo, molybdenum

Table 5
The effect of salinity, genotype and season on the concentration of potassium and sodium minerals in barley roots, shoots and grain was assessed. For each irrigation treatment across the crop seasons, values are presented as the mean ± standard error (SE) 60 measurements (10 genotypes, three replicates per genotype and two seasons). Means with different letters are significantly different ($p < 0.05$), as determined by Tukey's honestly significant difference (HSD) test. The sum of squares and significance levels (ns = not significant; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$) are provided for the effects of salinity, genotype, and their interactions.

Mineral concentration (mg kg^{-1})	K_{root}	K_{shoot}	K_{grain}	Na_{root}	Na_{shoot}	Na_{grain}	K_{root}/Na_{root}	K_{shoot}/Na_{shoot}	K_{grain}/Na_{grain}
Irrigation									
Control (2.6 dS m^{-1})	$32300.00^{c} \pm 2767.06$	$36566.67^{a} \pm 1473.18$	$6091.07^{a} \pm 137.00$	$18916.67^{a} \pm 467.77$	$22766.67^{a} \pm 574.09$	$451.01^{a} \pm 35.34$	$1.66^{c} \pm 0.08$	$1.65^{b} \pm 0.13$	$16.82^{b} \pm 0.90$
Salinity 1 (10 dS m^{-1})	$21550.00^{b} \pm 965.33$	$41933.33^{b} \pm 766.851$	$6297.28^{b} \pm 161.32$	$28700.00^{b} \pm 1195.16$	$23600.00^{a} \pm 604.69$	$779.33^{b} \pm 68.57$	$0.92^{b} \pm 0.07$	$1.86^{c} \pm 0.07$	$10.77^{a} \pm 0.64$
Salinity 2 (15 dS m^{-1})	$19433.33^{a} \pm 630.38$	$45116.67^{c} \pm 1045.59$	$6407.61^{c} \pm 178.70$	$46216.67^{c} \pm 624.85$	$33183.33^{b} \pm 1208.13$	$1014.34^{c} \pm 91.48$	$0.42^{a} \pm 0.01$	$1.41^{a} \pm 0.03$	$9.24^{a} \pm 0.66$
Season									
2020–2021	34466.67 ± 1501.57	48122.22 ± 543.45	5138.22 ± 37.76	29288.89 ± 1388.75	29066.67 ± 1053.12	525.46 ± 37.56	1.48 ± 0.10	1.84 ± 0.06	12.27 ± 0.58
2021–2022	14388.89 ± 406.16	34288.89 ± 782.01	7392.42 ± 65.76	33266.67 ± 1322.503	23966.67 ± 446.22	944.00 ± 72.50	0.51 ± 0.03	1.45 ± 0.03	12.28 ± 0.80
Level of significance									
Salinity (S)	5711877777.77^{***}	2240744444.44^{***}	3097932.46^{***}	22956744444.44^{***}	4020833333.33^{***}	9607131.43^{***}	45.69^{***}	5.96^{***}	1926.46^{***}
Genotype (G)	190450000.00^{ns}	13589444.44^{ns}	22580694.44^{***}	2352222222^{ns}	2085611111.111^{ns}	21284545.91^{***}	0.60^{ns}	0.69^{ns}	2071.46^{***}
Season (Se)	1814027222.22^{***}	8611250000.00^{***}	2286638921.9^{***}	7120222222.22^{***}	1170450000^{***}	6898596.60^{***}	42.58^{***}	6.84^{***}	0.01^{ns}
S x G	168566666.66^{ns}	393588888.89^{ns}	3369166.24^{***}	247144444.44^{ns}	44572222222.222^{ns}	3444737.37^{***}	0.57^{ns}	2.53^{ns}	253.56^{***}
S x Se	11271411111.11^{***}	13094333333.33^{***}	3779612.71^{***}	3733344444.44^{***}	2886100000^{***}	9687057.19^{***}	22.76^{***}	12.92^{***}	2116.36^{***}
G x Se	94227777.77^{ns}	117583333.33^{ns}	1926989.07^{***}	349755555.55^{**}	228827777.77^{ns}	1500020.05^{***}	1.84^{ns}	1.25^{ns}	805.08^{***}
S x G x Se	238588888.88^{ns}	384233333.33^{ns}	3656161.08^{***}	138544444.44^{ns}	249122222.22^{ns}	3453043.58^{***}	2.41^{ns}	2.91^{ns}	280.93^{***}

K_{root}, potassium in roots; K_{shoot}, potassium in shoots; K_{grain}, potassium in grain; Na_{root}, sodium in roots; Na_{shoot}, sodium in shoots; Na_{grain}, sodium in grain; Ratio of potassium to sodium in roots K_{root}/Na_{root}, shoots, K_{shoot}/Na_{shoot} and grain K_{grain}/Na_{grain}

3.4. Relationships among agronomic, physiological, and mineral traits

The heatmap plot correlation indicates that across all irrigation salinities and seasons (Fig. 1), GY exhibited strong positive correlations with SB and DM. Both GY and SB were strongly negatively correlated with $\delta^{1}{}^{3}C$, while TGW and LC showed no correlation with GY, a marginal positive correlation with SB, and a weak negative correlation with $\delta^{1}{}^{3}C$ (Fig. 1). Similarly, GY, SB, TGW, and LC were negatively correlated with $\delta^{1}{}^{5}N$ and grain N concentration. Both N and $\delta^{1}{}^{5}N$ exhibited strong positive correlations with the concentrations of most minerals analyzed, including K_{grain}, Ca, Mg, Mn, P, Fe, Zn, and S (Fig. 1). In contrast, Na_{grain} exhibited weak negative correlations with GY, SB, and TGW, while Na_{root} showed stronger negative correlations with these same traits. Notably, Na_{shoot} was only weakly negatively correlated with GY and SB. LC showed weak negative correlations with Na concentrations in both grain and root tissues. Furthermore, both Na_{grain} and Na_{root} were positively correlated with $\delta^{1}{}^{3}C$, $\delta^{1}{}^{5}N$, and N concentration (Fig. 1).

A principal component analysis (PCA) was conducted using agronomic and physiological traits, as well as the concentration of essential minerals in grain, and both the K and Na concentrations in roots, shoots and grain, across three salinity treatments (Fig. 2). The first two principal components explained 65% of the total variation, with PC1 accounting for 44% and PC2 for 21%. The PCA revealed a clear separation between the control and salinity-stressed treatments. Control samples (blue dots) were positioned on the negative side of PC1 and were associated with superior agronomic (higher GY, SB, TGW, PH, DM and LC) and physiological performance (lower $\delta^{13}C$ and $\delta^{15}N$ in the grain and lower accumulation of Na in roots, shoots, and grain), together with lower concentrations of N and minerals (K, Ca, Mg, P, Zn, Mn, Cu, Fe, S, Mo, and Zn) in the grain. In contrast, plants subjected to 10 and 15 dS m^{-1} (green and red dots) were overlapped and clustered closely together on the positive side of PC1, indicating a similar agronomic, physiological and seed quality response to salinity. Given the similar trends observed under 10 and 15 dS m^{-1} , genotypic correlations related to salinity were assessed using data pooled from both salinity treatments.

3.5. Physiological mechanisms associated with genotypic variability in GY

A phenotypic relationship between GY, Na accumulation in grain, and $\delta^{1}{}^{3}C$ was evaluated across the ten barley genotypes under control conditions (Fig. 3 A) and both salinity stresses combined (Fig. 3B). For this purpose, genotypic values were calculated as the mean across replicates and seasons for each genotype cultivated either under control conditions or combining Salinity 1 and Salinity 2. Na accumulation in the roots and shoots was not used for genotypic comparisons because no genotypic differences were detected for these two traits, and in fact, genotypic relationships with GY were not significant (Supplementary Fig. S2). Under control conditions, GY was strongly and positively correlated with Na concentration ($r = 0.77$, $p < 0.01$) and negatively correlated with $\delta^{1}{}^{3}C$ ($r = -0.72$, $p < 0.05$). Moreover, under salinity stress, the positive correlation between GY and grain Na remained significant ($r = 0.67$, $p < 0.05$), whereas the negative relationship with $\delta^{1}{}^{3}C$ weakened and became non-significant ($r = -0.37$, $p > 0.05$). In both panels, a cluster of high-yielding genotypes, ACSAD 1746, ACSAD 1230, and Furat 4, was consistently highlighted (blue ellipse). Under control conditions, these genotypes exhibited the highest GY and Na accumulation, and the lowest $\delta^{1}{}^{3}C$ values in the grain (Fig. 3 A). Likewise, under salinity, these same three genotypes again showed the highest GY and also exhibited the highest Na accumulation in the grain (Fig. 3B).

Additionally, the phenotypic relationship across genotypes between $\delta^{1}{}^{3}C$ and Na content was assessed under both control and salinity conditions separately (Fig. 4). A strong negative correlation was observed in both growing conditions: $r = -0.85$ ($p < 0.01$) under control and $r = -0.80$ ($p < 0.01$) under salinity. Under control, genotypes such as ACSAD 1746, Furat 4, and ACSAD 1230, which clustered on the left side of the

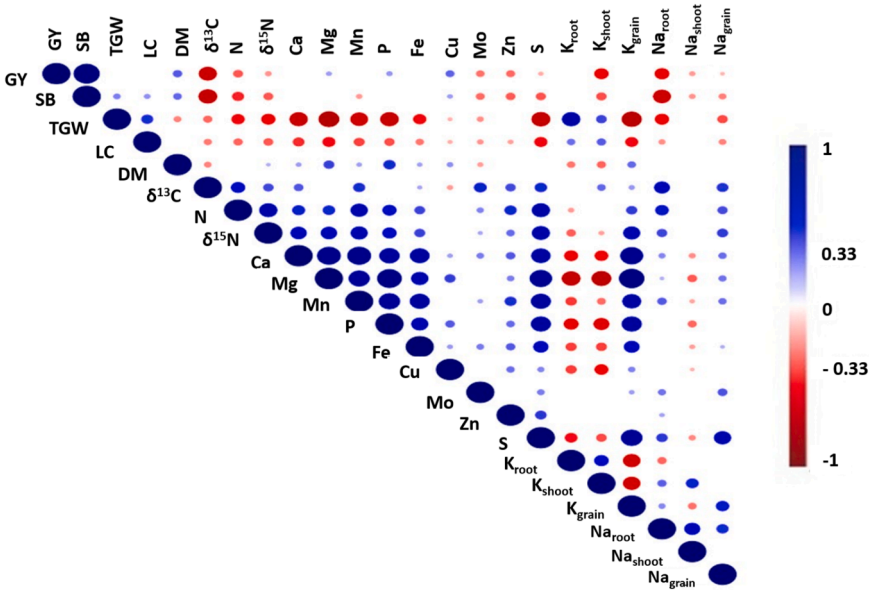

Fig. 1. Correlation matrix for barley genotypes between various traits and across the three different growing conditions. The data were analyzed using the individual values under each salinity condition. Only correlations with a $p < 0.05$ are shown. White blocks represent non-significant correlations, while the size of the circles and the intensity of the color indicate the strength of the correlation. Larger circles with more intense colors reflect higher correlation coefficients, while smaller circles with lighter colors represent lower correlations. Blue circles indicate positive correlations, while red circles represent negative correlations. Traits included in the correlation matrix: GY, grain yield; SB, shoot biomass; TGW, thousand grain weight; LC, leaf chlorophyll content; DM, days to maturity; $\delta^{13}C$, grain carbon isotope composition; $\delta^{15}N$, grain nitrogen isotope composition; N, grain nitrogen concentration; K_{root}, K_{shoot}, and K_{grain}, potassium concentration in root, shoot, and grain, respectively; Na_{root}, Na_{shoot}, and Na_{grain}, sodium concentration in root, shoot, and grain, respectively; and grain mineral concentrations of Ca, calcium; Mg, magnesium; Mn, manganese; P, phosphorus; Fe, iron; Cu, copper; Mo, molybdenum; Zn, zinc; and S, sulfur.

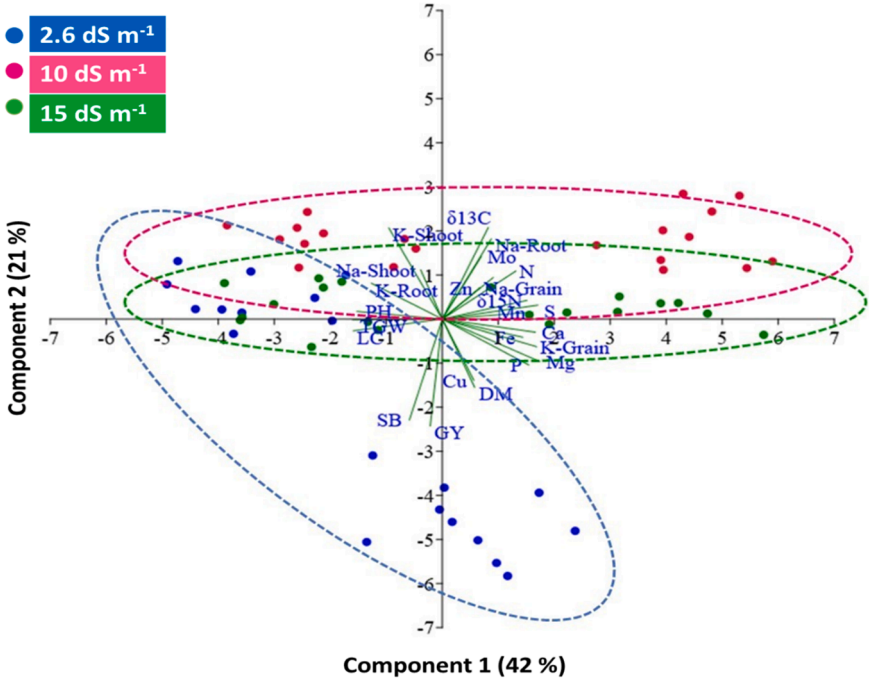

Fig. 2. Principal component analysis (PCA) across the three different growing conditions assayed in this study using GY, grain yield; SB, shoot biomass; TGW, thousand grain weight; LC, leaf chlorophyll content; DM, days to maturity; $\delta^{13}C$, grain carbon isotope composition; $\delta^{15}N$, grain nitrogen isotope composition; N, grain nitrogen concentration; K_{root}, K_{shoot}, and K_{grain}, potassium concentration in root, shoot, and grain, respectively; Na_{root}, Na_{shoot}, and Na_{grain}, sodium concentration in root, shoot, and grain, respectively; and grain mineral concentrations of Ca, calcium; Mg, magnesium; Mn, manganese; P, phosphorus; Fe, iron; Cu, copper; Mo, molybdenum; Zn, zinc; and S, sulfur. The blue circle represent data from the control condition (2.6 dSm^{-1}), the crimson correspond to the 10 dS/m^{-1} salinity treatment, and the green circle indicate the 15 dS/m^{-1} salinity treatment.

plot, exhibited lower δ^{1} ^{3}C values and higher Na levels. Under salinity, these same genotypes shifted to the right cluster, reflecting increased Na accumulation and lower δ^{1} ^{3}C values, particularly for ACSAD 1746 and Furat 4 (Fig. 4).

The phenotypic relationship between DM and key agronomic traits such as SB, GY, and TGW was also analyzed across the set of 10

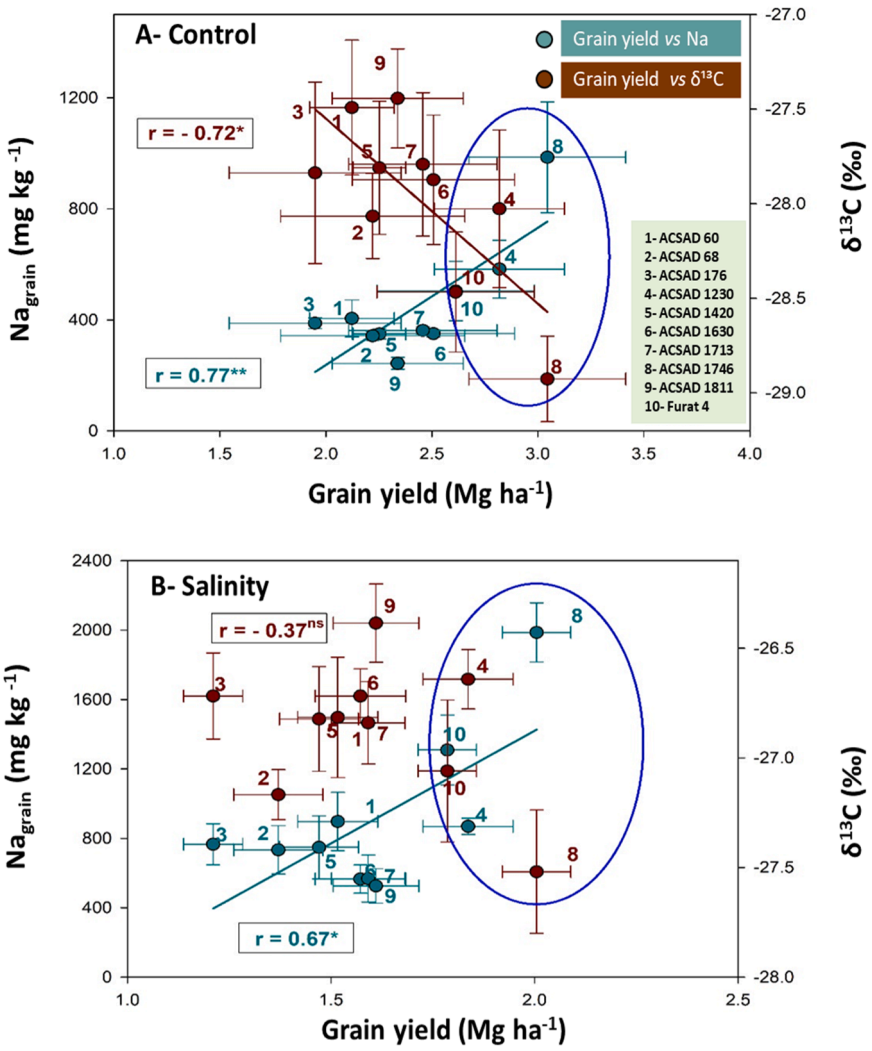

Fig. 3. The relationship of the grain yield with the sodium content (Na) (left y-axis) and the carbon isotope composition ($\delta^{13}C$) (right y-axis) across the ten genotypes and under control conditions (A) and salinity (B). For each genotype, the values under the control conditions represent the mean ± SE of 6 observations (based on three replicates per genotype across two growing seasons). Under salinity conditions, the values represent the mean ± SE of 12 observations per genotype (two salinity levels across two seasons, with three replicates each).

genotypes under control and both salinity conditions together (Fig. 5). A significant positive correlation was found between DM and SB under control ($r = 0.67$, $p = 0.03$), and a similar trend under salinity ($r = 0.61$, $p = 0.05$). The ACSAD 1230, ACSAD 1746, and Furat 4 genotypes exhibited longer crop durations and higher SB under control, while ACSAD 176, ACSAD 60 and ACSAD 1420 matured earlier and showed lower SB under salinity (Fig. 5 A). Moreover, the relationship between DM and GY was positive but not statistically significant under both control ($r = 0.46$, $p = 0.17$) and salinity ($r = 0.41$, $p = 0.23$). Notably, high-yielding genotypes such as ACSAD 1746, ACSAD 1630, and ACSAD 1713 tended to mature later, while ACSAD 60 was an early-maturing and low-yielding genotype across treatments. Interestingly, DM showed a negative trend with TGW under both control ($r = -0.52$, $p = 0.11$) and salinity ($r = -0.47$, $p = 0.16$). Furat 4 had the highest TGW under control and salinity despite late maturity, followed by ACSAD 60 (early-maturing genotype).

Further, we pursued a genotypic structural equation modeling approach (path analysis) to evaluate the direct and indirect effects of agronomic, physiological and biochemical traits on GY under control (Fig. 6 A) and both salinities together (Fig. 6B). The analysis was designed to identify key traits influencing genotypic GY, either directly or indirectly, through intermediary variables. Genotypic means across salinity treatments and seasons for the 10 genotypes were used in the model. Standardized path coefficients (β) are presented to indicate the strength and direction of relationships between variables, along with their corresponding significance levels. Under control conditions (Fig. 6 A), GY was directly and positively influenced by SB, with a strong standardized path coefficient ($\beta = 0.70$). SB itself was negatively affected by grain $\delta^{13}C$ ($\beta = -0.66$), while Na_{grain} had a strong negative direct effect on grain $\delta^{13}C$ ($\beta = -0.86$). However, Na_{grain} did not significantly influence GY directly. DM showed a moderate positive effect on SB ($\beta = 0.48$), thereby affecting GY indirectly via SB. N concentration had no significant effect on DM under control conditions. The model demonstrated a good fit to the data (CFI = 0.89). Under salinity conditions (Fig. 6B), the relationships among traits shifted markedly. As observed under control conditions, GY remained strongly and directly dependent on SB ($\beta = 0.85$). However, $\delta^{13}C$ no longer had a significant direct effect on SB. Even so, Na_{grain} retained a strong negative direct effect on $\delta^{13}C$ ($\beta = -0.80$). Notably, the pathway involving N, DM, and SB became more pronounced under salinity: N exerted a strong positive effect on DM ($\beta = 0.74$), which in turn positively influenced SB ($\beta = 0.61$), while Na_{grain} (like under control conditions) had a significant and positive direct effect on GY. The model fit remained acceptable (CFI = 0.82).

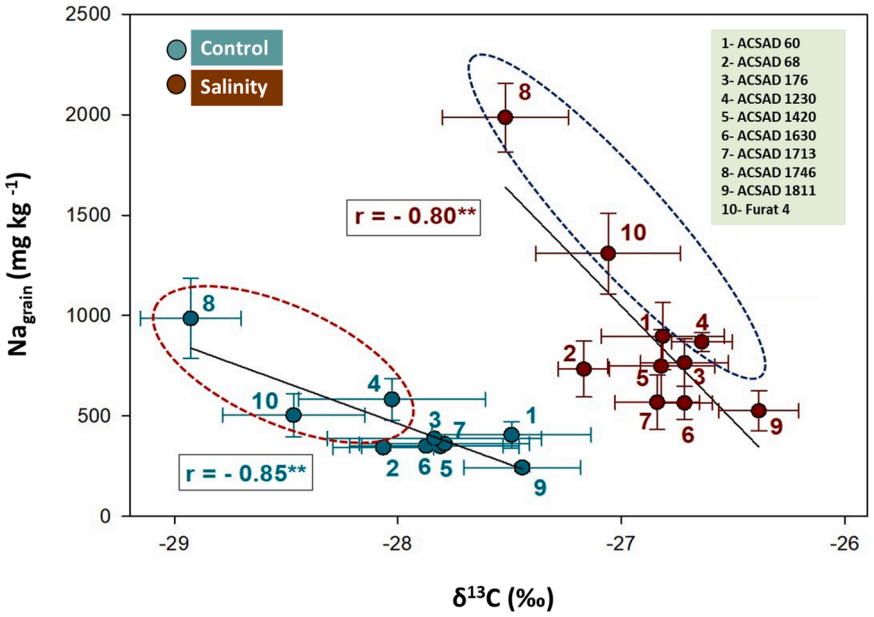

Fig. 4. The relationship of the sodium content (Na) and the carbon isotope composition ($\delta^{13}C$) across the ten genotypes and under control and salinity condition. For each genotype, the values under the control conditions represent the mean ± SE of 6 observations (based on three replicates per genotype across two growing seasons). Under salinity conditions, the values represent the mean ± SE of 12 observations per genotype (two salinity levels across two seasons, with three replicates each).

4. Discussion

4.1. Agronomic performance of barley under arid saline irrigation

Irrigation with saline water significantly affects barley plant height, SB, TGW and GY with most pronounced reductions observed in GY and SB. These trends align with previous studies in barley under arid (Hussain et al., 2022a,b) and semiarid (Hammami et al., 2020) conditions in response to increases in irrigation salinity comparable to our study. Reductions in growth and productivity were far lower than those reported for durum wheat under similar experimental conditions (Rukhsar et al., 2025), in line with the relatively salinity tolerant behavior of barley compared with other more susceptible cereals such as durum wheat (Munns and Tester, 2008). The modest reduction in crop duration represents an adaptive mechanism rather than a growth limitation. Reduced crop duration is a common adaptive strategy in cereals exposed to abiotic stress, enabling completion of the life cycle before stress intensifies (Amin et al., 2010).

The seasonal effect was significant for all agronomic traits except SB (Table 2). The higher TGW, despite lower GY, in the first crop season could be attributed to high temperature events during the flowering stage in the 2020–2021 season (Supplementary Fig. S1), which likely reduced the number of fertile grains per spike (Saini and Aspinall, 1982; Bagues et al., 2018), while increasing TGW due to the greater availability of assimilates for a smaller number of developing grains (Slafer et al., 2014).

GY did not correlate with TGW, which contrasts with the study of Mansur et al. (2021) who concluded that TGW was the agronomic component best correlated with GY in barley across salinity conditions. Differences may be correlated with the far higher sowing density of this study compared with our study. The observed positive association between GY and SB is consistent with previous studies (El-Hendawy et al., 2011) and highlights the importance of vigorous vegetative growth in mitigating the adverse effects of salinity. Notably, structural equation modeling (path analysis) further confirmed that SB is the dominant and most direct contributor to GY under both control and saline conditions (Fig. 6), reinforcing its role as a central integrator of physiological vigor and source capacity.

4.2. Tracking the effect of irrigation salinity on yield through δ^1 ^{3}C, Na concentration and chlorophyll content

The enrichment of δ^1 ^{3}C in barley grain under saline conditions agrees with earlier studies in barley grain under field conditions (Peñuelas et al., 1997; Isla et al., 1998; 2005), as well as in flag leaves (Yousfi et al., 2010a), and whole seedlings (Jiang et al., 2006) under greenhouse conditions. This enrichment in δ^1 ^{3}C is likely attributed to reduced stomatal conductance, reflecting water stress induced by saline conditions (Shaheen and Hood-Nowotny, 2005; Yousfi et al., 2010a,b). However, Hussain et al. (2022a),b), under arid experimental conditions quite comparable to those in our study (three different irrigation salinity levels in the UAE), did not observe an effect of salinity on the δ^1 ^{3}C of barley. Notably, these authors analyzed δ^1 ^{3}C in leaves, rather than in mature grain or other late-developing organs. The selection of the appropriate dry matter sample for δ^1 ^{3}C analysis under field conditions is critical, as salinity is a progressive stress, and early-developed leaves may not fully reflect the isotopic response to salinity over time.

The strong negative correlation between grain δ^1 ^{3}C and grain yield across salinity treatments (Fig. 1) supports a direct mechanistic link between stomatal behavior affected by water status and productivity. Similar negative relationships between grain δ^1 ^{3}C, (or positive relationships when expressed as carbon isotope discrimination $\Delta^{13}C$), and GY have been reported in barley under varying salinity conditions in the semiarid conditions of inner Spain (Peñuelas et al., 1997; Isla et al., 1998). These findings support that higher yields under less saline conditions are associated with greater stomatal conductance and higher photosynthetic rates. In fact, a negative correlation between grain/seed δ^1 ^{3}C and GY under similar salinity conditions in the UAE has also been reported for other C_3 crops, such as durum wheat (Rukhsar et al., 2025) and quinoa (Yousfi et al., 2025).

The minor reduction in leaf chlorophyll content, despite significant yield losses, is in line with previous results in durum wheat under similar experimental conditions (Rukhsar et al. (2025). In a controlled pot experiment, Yousfi et al. (2010a) reported no changes in LC in barley in response to salinity. The relatively minor decrease in LC observed in our study may be attributed to anatomical adaptations such as increased leaf thickness or enhanced mesophyll cell packing in response to

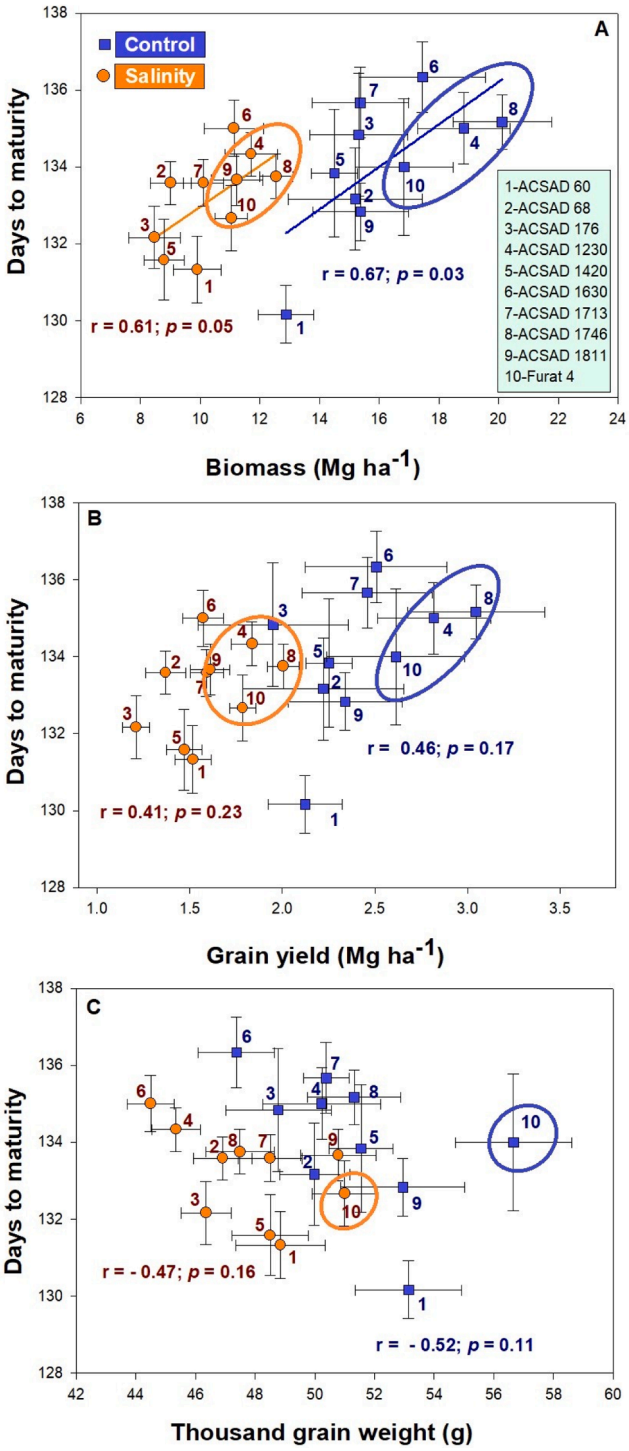

Fig. 5. The relationship of the days to maturity (DM) and the shoot biomass (A), grain yield (GY) (B) and the thousand grain weight (TGW) (C) across the ten genotypes and under control and salinity conditions. For each genotype, the values under the control conditions represent the mean ± SE of 6 observations (based on three replicates per genotype across two growing seasons). Under salinity conditions, the values represent the mean ± SE of 12 observations per genotype (two salinity levels across two seasons, with three replicates each).

salinity-induced impaired growth, leading to constant chlorophyll build-up despite the ionic effect of salinity (Munns et al., 2010). In fact, the weak or absent correlations of LC with GY, $\delta^{1}\,^{3}C$, $\delta^{1}\,^{5}N$, and N concentration suggest that chlorophyll content is a poor proxy for the functional limitations imposed by salinity.

4.3. Genotypic yield performance explained through $\delta^{1}\,^{3}C$, Na concentration and crop duration

The strong negative phenotypic correlation between $\delta^{1}\,^{3}C$ and GY across the 10 genotypes under control conditions (Fig. 3) indicates that genotypic variation in water status substantially influences carbon acquisition strategy. Higher-yielding genotypes maintain superior water

status that permits greater stomatal conductance and photosynthetic rates, thereby avoiding the ^{13}C enrichment characteristics of stomata-limited photosynthesis. This mechanism has been consistently documented across multiple crop species and water-limited environments for barley and durum wheat grown under Mediterranean rainfed conditions (Voltas et al., 1999; Araus et al., 2003) and durum wheat under high salinity in Tunisia and the UAE (Chamekh et al., 2016; Rukhsar et al., 2025). Isla et al. (1998) working in barley only reported positive phenotypic correlations between Δ^1 ^3C, and GY (i.e. a negative correlation between $\delta^{13}C$, and GY) across a set of barley genotypes under non-saline conditions, while under high salinity conditions the relationship was not significant, even when the positive trend remained. The negative correlations between δ^1 ^3C and GY under the control conditions of our study support the hypothesis that higher-yielding genotypes have the ability to mitigate water stress, therefore maintaining higher stomatal conductance, and consequently higher photosynthetic rates. Nevertheless, the control conditions in our study, with the EC of the irrigation water being 2.6 dS m^{-1}, may already be considered as a moderate salinity level. In practical terms, the so called "control conditions" in our study are the most favorable irrigation conditions deployed for field crops in the UAE. It is worth mentioning that control conditions were also exposed to an additional source of salinity given the huge manure application, which has been reported in quinoa to cause some salinity effect through Mg in the same experimental site (Rezzouk et al., 2020). On the other hand, the weakening in our study of the negative relationship between δ^1 ^3C and GY under salinity compared with control conditions is in line with the relationships reported in barley (Voltas et al., 1999) and durum wheat (Araus et al., 2003) as drought stress conditions increase. These results suggest that the study of the physiological mechanisms underlying genotypic differences in GY becomes more complex as stress increases.

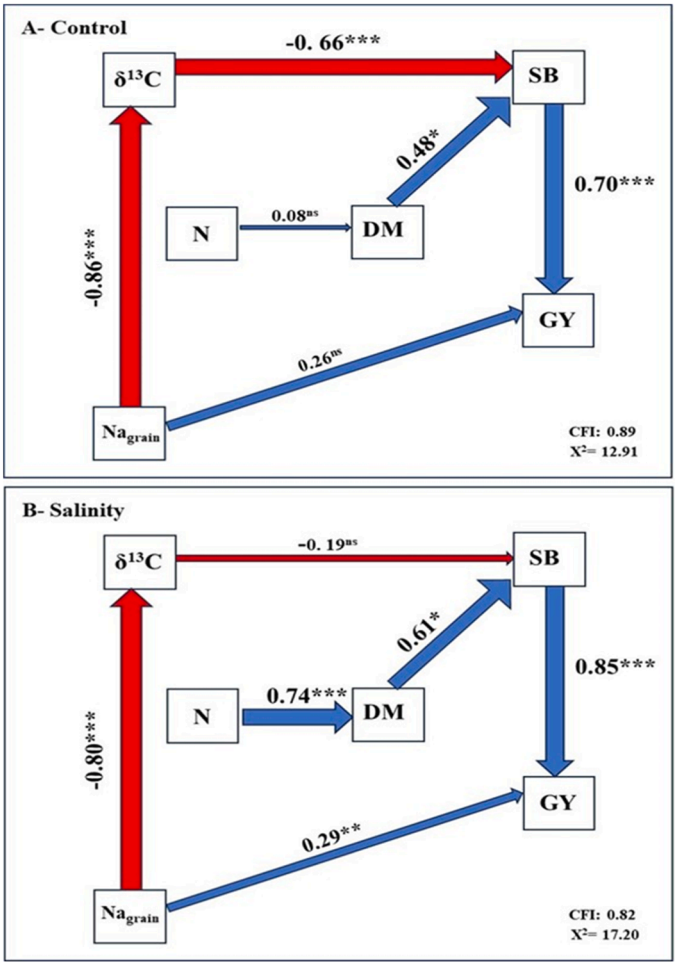

Fig. 6. Path analyses conducted on the ten barley genotypes grown under three different salinity irrigation levels across the two consecutive years. The conceptual model quantifies the relative contributions of both direct and indirect effects of various physiological stress indicators ($\delta^{13}C$, Na concentration in grain), a grain quality trait (grain N), and agronomic traits (shoot biomass and days to maturity) on grain yield under the control conditions (A) and salinity (B). Blue lines represent positive relationships, while red lines indicate negative relationships. The width of the arrows is proportional to the path coefficient values. Overall fit statistics for each path model, including chi-squared and the comparative fit index (CFI), are presented at the bottom right of each panel. A CFI value greater than or close to 0.90 is considered indicative of a good fit, particularly for small sample sizes. Statistical significance levels are indicated as ns, not significant; *p < 0.05; **p < 0.01 and ***p < 0.001.

Mechanisms underlying the negative genotypic relationship between GY and δ^1 ^3C may be attributed to osmotic adjustment, a trait potentially associated with GY, plant growth, and various physiological characteristics (Blum, 2017; Mahmood et al., 2020). It has been reported under field conditions that osmotic adjustment in the flag leaf was positively correlated across barley genotypes with turgor, stomatal conductance and yield under drought stress (González et al., 1999, 2008). The ability to preserve cell turgor through the accumulation of available inorganic ions such as Na for osmotic adjustment, together with the capacity of plant organs to sustain their function despite high internal Na levels, are recognized as two primary strategies plants use to cope with salinity stress (Munns and Tester, 2008). In fact, in our study, relationships across genotypes between Na concentration in different plant parts and GY were positive and increased in strength when compared roots, shoots and grain (Supplementary Fig. S2) but only reached significance for Na in the grain. These results suggest that alongside the sugar concentration inside the growing grain, Na accumulation in the grain may have an osmotic role in the movement of water from the xylem into the phloem at the grain's sink end. Nevertheless, these results support the idea that the osmotic role of the inflorescence may be even more important than the vegetative parts of the plant. Indeed, osmotic adjustment is an adaptive mechanism that helps plants cope with water stress, particularly in the spikes of cereals (Tambussi et al., 2007), which under stress conditions are the main photosynthetic contributors to grain filling (Sanchez-Bragado et al., 2020). Sodium may be exported to the grain from the ear bracts rather than from the vegetative tissues. However, our results contrast with previous studies which concluded that effective Na exclusion in vegetative tissues is associated with salt tolerance in barley (Tester and Davenport, 2003; Jadidi et al., 2022).

The consistent positive association between GY and grain Na concentration across genotypes, under both saline and control conditions (Fig. 3), points to a potential physiological link between Na accumulation and yield that is functional under a wide range of salinity conditions. The potential role of Na accumulation in grains favoring it for osmotic adjustment is further supported by a strong and negative relationship of Na with δ^1 ^3C across genotypes under both control and saline conditions (Fig. 4). In contrast, the relationship between the grain K/Na balance and yield was less consistent, and grain K alone showed no clear association with yield. This overall pattern, also supported by path analysis (Fig. 6), indicates a robust connection between Na accumulation in the grain and reduced δ^1 ^3C under both environments. These findings suggest that higher-yielding genotypes maintain greater stomatal openness, resulting in lower δ^1 ^3C values, while accumulating Na, as a mechanism for osmotic adjustment. Besides osmotic adjustment, the occurrence of higher Na accumulation coupled with lower δ^1 ^3C may be explained by tissue tolerance in barley. Barley genotypes can tolerate elevated Na levels through efficient compartmentalization of Na ions within leaf cells (Munns and Gilliham, 2015), using Na as a low-cost osmolyte (Houston et al., 2020), likely due to mechanisms such as vacuolar sequestration or cellular compartmentalization of Na in vegetative tissues (Munns et al., 2012) to maintain cell turgor and avoid toxicity. In fact, the three highest-yielding lines under both control and

irrigation salinity conditions (ACSAD 1746, ACSAD 1230 and Furat 4; genotypes 4, 8 and 10 in Fig. 3), were those with the highest Na concentrations in the grain. In support of this finding, Houston et al. (2020) provided compelling evidence challenging the long-held assumption that low Na accumulation in the grain and shoots is essential for salinity tolerance in barley. Their study showed that biomass and yield can be maintained in barley lines with grain Na concentrations traditionally considered detrimental. Specifically, genotypes carrying a particular allele of the high-affinity K transporter gene *HvHKT1;5*, which regulates Na transport, accumulated significantly higher Na levels in the grain while sustaining biomass production. The authors concluded that natural allelic variation in *HvHKT1;5* plays a key role in regulating Na^+ homeostasis in barley grain under both saline and non-saline conditions. They further suggest that a specific amino acid variant, proline at position 189 (P189), may alter the *HvHKT1;5* protein structure, potentially leading to its degradation before plasma membrane insertion. This would reduce Na retrieval from the xylem during bulk flow, increasing grain Na accumulation. These findings indicate that elevated Na concentration in tolerant genotypes is not necessarily harmful, and that Na exclusion may not be the primary mechanism of salinity tolerance in barley. It should be noted, nevertheless, that the observed association between grain Na concentration, yield, and $\delta^{13}C$ in this study is correlative in nature. Further mechanistic investigations are therefore required to determine whether Na accumulation in the grain plays a functional role as an osmolyte under these conditions. In summary our results are in line with the higher salinity tolerance of barley compared with other cereals. Indeed, a recent study in durum wheat under similar growing conditions reported that GY was negatively correlated across genotypes, not only with $\delta^{13}C$, but also with Na concentration (Rukhsar et al., 2025).

Leaf chlorophyll content did not emerge as a relevant trait to explain genotypic differences (Table 3), suggesting that chlorophyll content per unit area is not a primary indicator of genotypic performance under the conditions tested. This contrasts with the conclusions of Munns and James, (2003), proposing LC as a reliable screening criterion for salinity tolerance in wheat breeding programs (Munns and James, 2003).

In contrast, longer crop duration was positively associated with SB across genotypes under both control and saline conditions (Fig. 5), with a similar, though non-significant, trend observed for GY. This pattern suggests that later-maturing genotypes benefit from an extended period of vegetative growth, allowing greater biomass accumulation (Fig. 6). This relationship was evidenced by the genotypes ACSAD 1746 and ACSAD 1230, which together with extended growth cycles, displayed the highest SB and GY, supporting their physiological adaptation to saline environments. Stay-green, implying longer active crop duration, is considered a valuable trait in barley breeding programs due to its role in enhancing drought resilience and supporting yield stability across diverse environments (Brunner et al., 2024). Additionally, under saline conditions the path model reveals a significant positive relationship between grain N concentration and DM, suggesting that genotypes with longer growth cycles tend to accumulate more N in the grain, possibly reflecting enhanced N uptake or remobilization efficiency over the extended growing period. Together, these results point to crop duration as a key trait mediating genotypic differences in biomass production under both irrigated and saline conditions. In contrast to our findings, Mansour et al. (2021) grew barley in an arid region with saline soils (7.72 dS m^{-1}) and under irrigation salinity levels ranging between 5 and 11 dS m^{-1}, reported higher yield in early-maturing genotypes, which minimize exposure to prolonged salinity stress. However, the study of Mansour et al. (2021) did not clearly indicate the periodicity and amount of irrigation, whereas in our study, the irrigation was periodic until maturity while the soil exhibited good drainage because of its sandy texture. Therefore, growing conditions in the study of Mansour et al. (2021) are more in line with favoring an escape strategy. Similarly, under Mediterranean rainfed conditions, selecting for shorter growth duration has been widely implemented in barley breeding programs to facilitate escape from terminal stress (Voltas et al., 1999). By contrast, in our study the early-maturing genotype ACSAD 60 exhibited reduced SB and GY under both control and saline conditions (Fig. 5). Although ACSAD 60 has been previously characterized as salinity tolerant under Syrian conditions (Table 1), its poor performance in the UAE setting suggests limited adaptation to the saline irrigation and high-temperature stress typical of the region. However, despite its lower GY, ACSAD 60 maintained a higher TGW under both control and saline conditions, in contrast to ACSAD 1746 and ACSAD 1230, which, while high-yielding, exhibited the lowest TGW (Fig. 5). This may indicate a trade-off in which these genotypes allocate limited assimilates toward filling a greater number of grains, resulting in reduced TGW. In contrast, Furat 4, a line from GCSAR, was the only genotype to exhibit both high GY and high TGW under both conditions, underscoring its superior adaptation and agronomic potential under the arid and saline conditions of the UAE.

4.4. *N metabolism in response to salinity: N concentration and $\delta^{15}N$ in the grain*

It is reported that salinity stress significantly alters nitrogen metabolism in barley, including nitrogen uptake, retranslocation, and isotopic fractionation (Domergue et al., 2022). In our study, salinity increased $\delta^{15}N$ and N concentration in barley grain. In the case of $\delta^{15}N$, increases may reflect changes in nitrogen uptake, assimilation and retranslocation, such as increased reliance on ammonium or organic nitrogen forms under salt stress (Robinson et al., 2000; Yousfi et al., 2012). However, the salinity-induced increase in grain N concentration is likely not a direct physiological response to salt stress per se, but rather a concentration effect driven by the concurrent reduction in grain size, as supported by the negative relationship observed between TGW and N concentration (Fig. 1). As grains become smaller under salinity, the same or similar amount of N is distributed across less biomass, resulting in apparently higher N concentration per unit dry weight. An increase in grain protein concentration under salinity has been reported in barley by Hussain et al. (2022a), although the magnitude was considerably larger than observed here, which may partly reflect differences in the severity of the salinity treatments applied. Notably, those authors did not report TGW, making it difficult to assess whether the protein increase they observed was similarly driven by a grain size effect or represented an enhancement of N accumulation in the grain.

Total N concentration showed strong positive correlations with several essential mineral nutrients, including K, Ca, Mg, Mn, P, Fe, Zn and S under all growing conditions combined (Fig. 1). Rukhsar et al. (2025), working in durum wheat under similar growing conditions as in this study, also reported positive relationships of N with several nutrients (P, Mg, Mn, Fe, Zn, Cu, S) in grain, which are not just explained by the small decrease (around 5%) in TGW caused by salinity. In addition, total N also correlated positively with some of the minerals across genotypes within control and salinity (Supplementary Table S7). These relationships highlight a potential link between nitrogen assimilation and mineral nutrient accumulation, likely influenced by the enzymatic processes involved in nitrogen metabolism (Hamnér et al., 2017). De Santis et al. (2021) underscored the crucial importance of micronutrients in plant nutrition, noting their structural role in enzyme function and nitrogen metabolism (Shah et al., 2017). Hu and Chu (2020) explained that nitrogen metabolism and phosphorus absorption are interconnected, contributing to nutritional balance, which is vital for enhancing nutrient accumulation in plants. Similarly, Fatholahi et al. (2022) observed a positive correlation between nitrogen availability and phosphorus concentration in grain. Clarkson et al. (1989) indicated that sulfur plays a role in nitrogen uptake and is a fundamental component of enzymes involved in nitrogen-related processes (Scherer, 2008). Although $\delta^{15}N$ exhibits a similar pattern to nitrogen (Yousfi et al., 2012) and was positively associated with minerals, the

underlying biochemical mechanisms driving $\delta^{15}N$ variation are not yet fully understood (Cernusak et al., 2009; Tcherkez, 2011).

Considerable genotypic variability in N concentration and $\delta^{15}N$ was observed in our study (Table 3, Supplementary Table S4), highlighting the potential of these traits for genotype selection under salinity. Similarly, Hussain et al. (2022b) reported $\delta^{15}N$ variability in barley under UAE field conditions and saline irrigation. High variation in both traits has also been documented in durum wheat under the arid and saline conditions of the UAE (Rukshar et al., 2025), as well as under salinity stress in Tunisia (Chamekh et al., 2016) and in pot studies (Yousfi et al., 2012). In fact, $\delta^{15}N$ and N concentration have been proposed as valuable physiological markers for differentiating genotypic responses to salinity (Yousfi et al., 2012). In line with this, our study found that genotypes with enriched $\delta^{15}N$ values also exhibited higher nitrogen concentration values, suggesting the involvement of genotype-specific nitrogen assimilation or remobilization strategies under saline and arid conditions.

4.5. Grain mineral concentration: salinity, seasonal and genotypic effects

Salinity stress altered the mineral nutrient composition of barley grain, enhancing the accumulation of several macronutrients (K, Ca, S) and micronutrients (Zn, Mn), which are known to support abiotic stress tolerance through roles in enzymatic activity and nitrogen metabolism (Shah et al., 2017). Moreover, the increase in the grain concentration of micronutrients such as Zn and Mn may have clear nutritional implications (Rukshar et al., 2025). However, the magnitude of increases in all these minerals (less than 10%) in response to salinity (Tables 4, 5) suggest rather a passive increase in concentration of these minerals associated with the decrease in TGW caused by salinity (Table 2), and in fact, negative correlations between TGW and minerals (particularly K, Mg, Mn, P, Ca, S) across salinities and seasons were rather strong (Fig. 1). In contrast to barley, when durum wheat was grown under similar conditions, the concentration of most minerals increased under intermediate salinity, but further decreased at high salinity; this is despite the observation that TGW strongly decreased as salinity increased (Rukhsar et al., 2025). Again, such differences in the pattern between barley and durum wheat are coherent with the differential tolerance to salinity of both species. However, in the present study, Cu concentrations decreased slightly, while Mg and P levels remained relatively stable under saline conditions, despite the fact that TGW decreased, suggesting that salinity even had a negative influence on the accumulation of these particular elements. These patterns likely reflect ion-specific uptake regulation under salt stress, potentially influenced by competition from elevated Na levels. Supporting this, Hassan et al. (1970) observed a decline in grain Cu but stable Mg concentrations in barley under saline soils, highlighting the differential sensitivity to salinity of nutrient uptake pathways. Furthermore, Mo concentrations increased strongly in response to salinity, with a 125% rise at 15 dSm^{-1} , even when the total concentration of Mo was 300–400 times lower than Na, which does not support a role for Mo as an osmolyte. In addition, the negative relationship between Mo and grain yield (Supplementary Fig. S3) suggests that Mo accumulation reflects the severity of salt stress imposed on the plant rather than a direct toxic effect from Mo itself. The positive association between Mo and $\delta^{13}C$ (Supplementary Fig. S3) further supports this interpretation, as increased Mo accumulation coincided with greater stomatal limitation. Moreover, the strong positive association between Mo and Na accumulation in barley grain (Supplementary Fig. S3) suggests that increasing Na loading under salinity was accompanied by proportional increases in Mo, indicating that Mo enrichment in barley grain was primarily driven by the intensity of the salinity stress. Mo has been implicated in salinity stress mitigation through its role in enhancing the activity of Mo-dependent enzymes, including nitrate reductase, aldehyde oxidase, and xanthine dehydrogenase, which collectively reduce oxidative damage in plant tissues (Babenko et al., 2015). However, for this mineral, the genotypic effect was not significant. Seasonal variation also significantly influenced the concentrations of essential minerals in the grain. Although TGW was approximately 15% lower in the second season compared to the first, the concentrations of several minerals including K, Ca, Mg, and Fe increased by about 30%, while other elements showed increases ranging from 10% to 20%. This may be attributed to environmental factors (Caldelas et al., 2023) combined with a grain-size dilution effect observed in the first season. The genotypic effect was stronger than the salinity effect for grain minerals. However, apart from Mn, Zn, and Cu, the season effect was greater (Table 4). In the case of durum wheat under similar growing conditions, genotype was the main factor affecting mineral concentration for all the essential minerals assayed, while salinity and even season had a lesser effect. Caldelas et al. (2023) also concluded that genotype was the main driver of Ca, K, and Mg concentration in the grain of bread wheat grown under semiarid conditions.

As expected, salinity altered ion balance by promoting Na accumulation and shifted the Na/K ratio across roots, shoots, and grains. This pattern suggests a typical response in barley under salt stress, where increasing salinity levels lead to greater Na uptake and redistribution within the plant, consistent with known salt-accumulation behavior. This trend is consistent with previous findings (Ghonaim et al., 2023; Hussain et al., 2022a), where increased Na concentrations in the shoots of barley genotypes were reported under saline irrigation. However, in our study the increase in Na in relative terms was far higher in the grain than in the shoot. Moreover, while no genotypic effect was found for Na accumulation in roots and shoots, the genotypic effect on grain Na concentration was higher than the effect of irrigation salinity. These results indirectly support genotype-specific responses to Na accumulation in the grain and are in line with the positive genotypic correlations of grain Na with GY discussed above.

4.6. Breeding implications for salinity stress in arid zones

Consistent with earlier reports in barley (Hammami et al., 2016; Mansour et al., 2021; Hussain et al., 2022a,b), our findings confirm substantial genotypic variability in barley GY performance under salinity stress. Genotypes such as ACSAD 1746, ACSAD 1230, and Furat 4 consistently maintained higher GY and SB under both control and saline irrigation conditions, suggesting the involvement of tolerance mechanisms such as osmotic adjustment, as described by Munns et al. (2006). Notably, despite accumulating higher Na in grain under salinity, these genotypes sustained greater GY and SB, implying mechanisms of tissue tolerance through Na compartmentalization and the potential use of Na as an osmolyte.

It is noteworthy that these three genotypes have previously been classified as drought tolerant under Syrian agro-environments characterized by harsh rainfed conditions (Table 1). The results of our study, conducted under the high temperatures, evapotranspirative conditions and the sandy soils of the UAE, together with periodic irrigation with different levels of saline water, extend the tolerance of these genotypes to a broader range of arid environments and salinity. However, while ACSAD 1230 is reported as having a long cycle (Saleh and Almahasned, 2023), in our study this genotype and the other two lines exhibited an intermediate crop duration. By contrast, ACSAD 1630 and ACSAD 1713, characterized as drought susceptible under Mediterranean rainfed conditions (Saleh and Almhasned, 2023), exhibited the highest DM and intermediate GY in our study. Therefore, there is no direct correspondence between the agronomic performance under drought (Table 1) and salinity conditions.

Concerning mineral concentration, the top-yielding genotypes (ACSAD 1746, ACSAD 1230, and Furat 4) exhibited lower mineral concentrations in the grain, compared to the less productive genotypes. Such differences are consistent with the findings by Caldelas et al. (2023) in bread wheat, who reported that lower-yielding varieties often display elevated mineral concentrations, likely due to the mineral dilution effect observed in plants with higher TGW. However, the

exception in our study is ACSAD 1811, which besides yielding around 20% less than the most productive genotypes, combined a higher TGW with elevated grain nutrient concentrations, indicating a genotype-specific capacity for efficient nutrient assimilation under arid and saline conditions. Sharqi et al. (2023) also reported that ACSAD 1811 exhibited higher TGW and grain protein concentration compared to other barley genotypes under arid conditions in Iraq. Moreover, the grain of ACSAD 1811 accumulated up to 74 mg kg^{-1} of Zn, a mineral with high nutritional value (Cakmak, 2008). According to Mazhar et al. (2023), grain Zn concentrations in cereals above 50 mg kg^{-1} are considered optimal for enhancing human health and nutrient deficiencies. ACSAD 1811 also possessed the highest concentration of Fe, an essential micronutrient critical for human health and nutrition (Zulfiqar et al., 2024). Similarly, the genotypes ACSAD 1630 exhibited the highest level of Mg. In this context, Broadley and White (2010) reported that the Mg concentration in food crops is becoming an important global issue in food quality and human nutrition.

5. Conclusions

Saline irrigation significantly impaired barley agronomic performance, with GY and SB more severely affected than TGW. The increase in δ^1 ^{3}C with only minor decreases in LC indicates that the negative effect of salinity operates primarily through water stress rather than ion toxicity or accelerated senescence. Genotypic variability was a core driver of barley salt tolerance with grain Na and δ^1 ^{3}C being key phenotypic indicators. Moreover, genotype was the dominant driver for grain quality, even when some trade-offs existed between yield and grain nitrogen and mineral content. The identified genotypes ACSAD 1746, ACSAD 1230, and Furat 4 were the most salt-tolerant highest-yielding varieties, suitable for breeding in arid, saline areas, while presenting intermediate grain mineral values. Finally, given the correlational nature of our study, the main conclusions need further confirmation through more mechanistic studies. This is the case, for example, for Na accumulation in grains as a positive phenotypic trait, which deserves further research including the analysis of osmolytes in reproductive tissues.

CRediT authorship contribution statement

José L. Araus: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Maria D. Serret:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Data curation, Conceptualization. **Mahmoud Henda:** Visualization, Validation, Supervision, Methodology, Investigation, Conceptualization. **Salima Yousfi:** Writing – review & editing, Writing – original draft, Visualization, Software, Investigation, Data curation. **Eider Zearreta Urien:** Methodology, Data curation. **Osama Kanbar:** Visualization, Validation, Supervision, Methodology, Investigation, Conceptualization. **Ayesha Rukhsar:** Writing – original draft, Methodology, Data curation.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agwat.2026.110469.

Data availability

Data will be made available on request.

References

Ali Saleh, R., 2015. The Annual Technical Report 2015- The Arab Center for the Studies of Arid Zones and Dry Lands (ACSAD). Library/ACSAD.ORG. ⟨https://acsad.org/en/library/⟩.

Al-khalaf, K.N., 2021. Identification and isolation of some genes responsible for improving osmotic stress tolerance in some barley (*Hordeum vulgare* L.) genotypes. International System for Agricultural Science and Technology (AGRIS). Food and Agriculture Organization of the United Nations (FAO).

Al-khalaf, K.N., Lawand, S., Al-mahasneh, H., 2022. Genetic relationshipbetween some barley genotypes (*Hordeum vulgare* L.) using SSR technique (microsatellite). Iraqi J. Agric. Sci. 53, 890–900.

Amin, A.Y., Safwat, G., El-Emary, G., 2010. Development of doubled haploid wheat genotypes using chromosome eliminating technique and assessment under salt stress. J. Am. Sci. 6, 139–148.

Araus, J.L., 2004. The problem of sustainable water use in the Mediterranean and research requirements for agriculture. Ann. Appl. Biol. 144, 259–272.

Araus, J.L., Slafer, G.A., Reynolds, M.P., Royo, C., 2002. Plant breeding and drought in C_3 cereals: what should we breed for? Ann. Bot. 89, 925–940.

Araus, J.L., Villegas, D., Aparicio, N., García del Moral, L.F., El Hani, S., Rharrabti, Y., Ferrio, J.P., Royo, C., 2003. Environmental factors determining carbon isotope discrimination and yield in durum wheat under Mediterranean conditions. Crop. Sci. 43, 170–180.

Ashraf, M., 2014. Stress-Induced Changes in Wheat Grain Composition and Quality. Crit. Rev. Food Sci. Nutr. 54, 1576–1583.

Ashraf, M., Shahzad, S.M., Imtiaz, M., Rizwan, M.S., 2018. Salinity effects on nitrogen metabolism in plants-focusing on the activities of nitrogen metabolizing enzymes: A review. J. Plant. Nutr. 41, 1065–1081.

Babenko, O.N., Brychkova, G., Sagi, M., 2015. Molybdenum application enhances adaptation of crested wheatgrass to salinity stress. Acta Physiol. Plant 37, 14.

Blum, A., 2017. Osmotic adjustment is a prime drought stress adaptive engine in support of plant production. Plant. Cell. Environ. 40, 4–10.

Boussora, F., Triki, T., Bennani, L., Bagues, M., Sihem Ben Ali, S., Ferchichi, A., K., Guasmi, F., 2024. Mineral accumulation, relative water content and gas exchange are the main physiological regulating mechanisms to cope with salt stress in barley. Sci. Rep. 14, 14931.

Broadley, M.R., White, P.J., 2010. Eats roots and leaves. Can edible horticultural crops address calcium, magnesium and potassium deficiencies? Proc. Nutr. Soc. 69, 601–612.

Brunner, S.M., Dinglasan, E., Baraibar, S., Alahmad, S., Katsikis, C., van der Meer, S., Godoy, J., Moody, D., Smith, M., Hickey, L., Robinson, H., 2024. Characterizing stay-green in barley across diverse environments: unveiling novel haplotypes. Theor. Appl. Genet 137, 120.

Cakmak, I., 2008. Enrichment of cereal grains with zinc: agronomic or genetic biofortification. Plant. Soil 302, 1–17.

Caldelas, C., Rezzouk, F.Z., Aparicio Gutiérrez, N., Diez–Fraile, M.M., Araus Ortega, J.L., 2023. Interaction of genotype, water availability, and nitrogen fertilization on the mineral content of wheat grain. Food Chem. 404, 134565.

Cernusak, L.A., Winter, K., Turner, B.L., 2009. Plant δ^{15}N correlates with the transpiration efficiency of nitrogen acquisition in tropical trees. Plant. Physiol. 151, 1667–1676.

Chamekh, Z., Ayadi, A., Karmous, C., Boudabbous, K., Trifa, Y., Amara, H., Yousfi, S., Serret, M.D., Araus, J.L., 2016. Comparative effect of salinity on growth, grain yield, water use efficiency, δ^{13}C and δ^{15}N of landraces and improved durum wheat varieties. Plant. Sci. 251, 44–53.

Clarkson, D.T., Saker, L.R., Purves, J.V., 1989. Depression of nitrate and ammonium transport in barley plants with diminished sulphate status. Evidence of co-regulation of nitrogen and sulphate intake. J. Exp. Bot. 40, 953–963.

Coplen, T.B., 2008. Explanatory glossary of terms used in expression of relative isotope ratios and gas ratios. IUPAC Recomm. 2008. Int. Union Pure Appl. Chem. Inorg. Chem. Div. Comm. Isot. Abundances At. Weights.

De Santis, M.A., Soccio, M., Laus, M.N., Flagella, Z., 2021. Influence of drought and salt stress on durum wheat grain quality and composition: A review. Plants 10 (12), 2599.

Domergue, J.B., Lalande, J., Beucher, D., Satour, P., Abadie, C., Limami, A.M., Tcherkez, G., 2022. Experimental evidence for seed metabolic allometry in barrel medic (*Medicago truncatula* Gaertn.). Inter. J. Mol. Sci. 23, 8484.

El Sabagh, A., Hossain, A., Islam, M.S., Barutcular, C., Hussain, S., Hasanuzzaman, M., Akram, T., Mubeen, M., Nasim, W., Fahad, S., Kumar, N., Meena, R.S., Kızılgeçi, F., Yıldırım, M., Ratnasekera, D., Saneoka, H., 2019. Drought and salinity stresses in barley: Consequences and mitigation strategies. Aust. J. Crop Sci. 13, 810–820.

Eleuch, L., Rezgui, S., Slim Amara, H., Daaloul, A., El Hassni, M., El Hadrami, I., 2005. Effect of salt treatment on the expression of phenolics and peroxidase activity assessed in two barley cultivars Ascad 1230 and Arig 8. J. Agron. 4, 196–202.

El-Hendawy, S.E., Hu, Y., Sakagami, J.I., Schmidhalter, U., 2011. Screen. Egypt. wheat genotypes salt Toler. Early Growth Stages Int. J. Plant. Prod. 5, 239–256.
El-Lethy, S.R., Abdelhamid, M.T., Reda, F., 2013. Effect of potassium application on wheat (*Triticum aestivum* L.) cultivars grown under salinity stress. World. Appl. Sci. J. 26, 840–850.
FAO, 2024. The global status of salt-affected soils. Food and Agriculture Organization of the United Nations, Rome.
Faraj, H., Saleh, J., AL- Janieer, F., 2023. Analysis of variance and correlation coefficient of grain yield and its components in some barley genotypes under rainfed conditions. Arab Cent. Stud. Arid Zones Dry. Lands 16, 118–129.
Farquhar, G.D., Richards, R.A., 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. Aus. J. Plant. Physiol. 11, 539–552.
Farquhar, G.D., Ehleringer, J.R., Hubick, K.T., 1989. Carbon isotope discrimination and photosynthesis. Annu. Rev. Plant. Physiol. Plant. Mol. Biol. 40, 503–537.
Fatholahi, S., Ehsanzadeh, P., Karimmojeni, H., 2022. Post-anthesis photosynthetic attributes and NPK status of standard and emmer wheats respond differently to nitrogen supply. J. Plant. Nutr. 46, 2131–2143.
Francois, L.E., Maas, E.V., Donovan, T.J., Youngs, V.L., 1986. Effect of salinity on grain yield and quality, vegetative growth, and germination of semi-dwarf and durum wheat. Agron. J. 78, 1053–1058.
Ghafoor, K., AL-Juhaimi, F., Ozcan, M.M., Jahurul, M.H.A., 2015. Some nutritional characteristics and mineral contents in barley (*Hordeum vulgare* L.) seeds cultivated under salt stress. Qual. Assur. Saf. Crops Foods 7, 363–368.
Ghonaim, M.M., Attya, A.M., Aly, H.G., Mohamed, H.I., Omran, A.A., 2023. Agro-morphological, biochemical, and molecular markers of barley genotypes grown under salinity stress conditions. Bmc. Plant. Biol. 23, 526.
González, A., Martin, I., Ayerbe, L., 1999. Barley yield in water-stress conditions. fluence Preco osmotic Adjust. stomatal Conducta Field Crops Res. 62, 23–34.
González, A., Martın, I., Ayerbe, L., 2008. Yield and osmotic adjustment capacity of barley under terminal water-stress conditions. J. Agro. Crop. Sci. 194, 81–91.
Hammami, Z., Sbei, H., Kadri, K., Jmel, Z., Sahli, A., Belhaj Fraj, M., Naser, H., Teixeira da Silva, J.A., Trifa, Y., 2016. Evaluation of performance of different barley genotypes irrigated with saline water in South Tunisian Saharan conditions. Environ. Exp. Biol. 14, 15–21.
Hammami, Z., Qureshi, A.S., Sahli, A., Gau reteau, A., Chamekh, Z., Ben Azaiez, F.E., Ayadi, S., Trifa, Y., 2020. Modeling the effects of irrigation water salinity on growth, yield and water productivity of barley in three contrasted environments. Agronomy 10, 1459.
Hammami, Z., Jallouli, S., Ayadi, S., Trifa, Y., 2026. Impact of soil and climate on barley (*Hordeum vulgare* L.) salinity tolerance in diverse arid and saline conditions. Sci. Rep. 16, 869.
Hamnér, K., Weih, M., Eriksson, J., Kirchmann, H., 2017. Influence of nitrogen supply on macro- and micronutrient accumulation during growth of winter wheat. Field Crops Res. 213, 118–129.
Hassan, N.,A.K., Drew, J.V., Knudsen, D., Olson, R.A., 1970. Influence of soil salinity on production of dry matter and uptake and distribution of nutrients in barley and corn: I. Barley (*Hordeum vulgare* L). Agron. J. 62, 43–45.
Houston, K., Qiu, J., Wege, S., Hrmova, M., Oakey, H., Qu, Y., Smith, P., Situmorang, A., Macaulay, M., Flis, P., Bayer, M., Roy, S., Halpin, C., Russell, J., Schreiber, M., Byrt, C., Gilliham, M., Salt, D.E., Waugh, R., 2020. Barley sodium content is regulated by natural variants of the Na^+ transporter *HvHKT1;5*. Commun. Biol. 31, 258.
Hu, B., Chu, C., 2020. Nitrogen–phosphorus interplay: old story with molecular tale. New. Phytol. 225, 1455–1460.
Hussain, M.I., Khan, Z.I., Farooq, T.H., Al Farraj, D.A., Elshikh, M.S., 2022b. Comparative plasticity responses of stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), ion homeostasis, and yield attributes in barley exposed to saline environment. Plants 11, 1516.
Hussain, M.I., Al-Dakheel, A.J., Chaudhry, U.K., Khan, M.I., AlHaithloul, H.A.S., Alghanem, S.M., Alaklabi, A., 2022a. Morpho-physiological response of barley to assess genotypic differences of salinity tolerance under hyper-arid climate. Agric. Water Manag 272, 106045.
Isla, R., Aragues, R., Royo, A., 1998. Validity of various physiological traits as screening criteria for salt tolerance in barley. Field Crops Res. 58, 97–107.
Jadidi, O., Etminan, A., Azizi-Nezhad, R., Ebrahimi, A., Pour-Aboughadareh, A., 2022. Physiological and molecular responses of barley genotypes to salinity stress. Genes 13, 2040.
Jiang, Q., Roche, D., Monaco, T.A., Durham, S., 2006. Gas exchange, chlorophyll fluorescence parameters and carbon isotope discrimination of 14 barley genetic lines in response to salinity. Field Crops Res. 96, 269–278.
Katerji, N., Van Hoorn, J.W., Fares, C., Hamdy, A., Mastrorilli, M., Oweis, T., 2005. Salinity effect on grain quality of two durum wheat varieties differing in salt tolerance. Agric. Water Manag 75, 85–91.
Mahmood, T., Abdullah, M., Ahmar, S., Yasir, M., Iqbal, M.S., Yasir, M., Ur Rehman, S., Ahmed, S., Rana, R.M., Ghafoor, A., Nawaz Shah, M.K., Du, X., Mora-Poblete, F., 2020. Incredible role of osmotic adjustment in grain yield sustainability under water scarcity conditions in wheat (*Triticum aestivum* L.). Plants 15 (9), 1208.
Mansour, E., Moustafa, E.S.A., Abdul-Hamid, M.I.E., Ash-shormillesy, S.M.A.I., Merwad, A.-R.M.A., Wafa, H.A., Igartua, E., 2021. Field responses of barley genotypes across a salinity gradient in an arid Mediterranean environment. Agric. Water Manag. 258, 107206.
Masoni, A., Ercoli, L., Mariotti, M., Arduini, I., 2007. Post-anthesis accumulation and remobilization of dry matter, nitrogen and phosphorus in durum wheat as affected by soil type. Eur. J. Agron. 26, 179–186.
Merah, O., Monneveux, P., 2015. Contribution of different organs to grain filling in durum wheat under Mediterranean conditions I. Contribution of post-anthesis photosynthesis and remobilization. J. Agron. Crop Sci. 201, 344–352.
Munns, R., Gilliham, M., 2015. Salinity tolerance of crops – what is the cost? N. Phytol. 208, 668–673.
Munns, R., James, R.A., 2003. Screening methods for salinity tolerance: a case study with tetraploid wheat. Plant. Soil 253, 201–218.
Munns, R., James, R.A., Läuchli, A., 2006. Approaches to increasing the salt tolerance of wheat and other cereals. J. Exp. Bot. 57, 1025–1043.
Munns, R., James, R., Sirault, X., Furbank, R., Jones, H., 2010. New phenotyping methods for screening wheat and barley for beneficial responses to water deficit. J. Exp. Bot. 61, 3499–3507.
Munns, R., James, R., Xu, B., Athman, A., Conn, S.J., Jordans, C., Byrt, C.S., Hare, R.A., Tyerman, S.D., Tester, M., Plett, D., Gilliham, M., 2012. Wheat grain yield on saline soils is improved by an ancestral Na^+ transporter gene. Nat. Biotechnol. 30, 360–364.
Oweis, T., Pala, M., Ryan, J., 1998. Stabilizing rainfed wheat yields with supplemental irrigation and nitrogen in a Mediterranean-type climate. Agron. J. 90, 672–681.
Passioura, J.B., 2002. Soil conditions and plant growth. Plant. Cell. Environ. 25, 311–318.
Peñuelas, J., Isla, R., Filella, I., Araus, J.L., 1997. Visible and near-infrared reflectance assessment of salinity effects on barley. Crop. Sci. 37, 198–202.
Prasad, R., Majumdar, K., Shivay, Y.S., Kapil, U., 2016. Minerals in Plant and Human Nutrition and Health. International Plant Nutrition Institute, Peachtree Corners, GA, USA.
Rezzouk, F.Z., Shahid, M.A., Elouafi, I.A., Zhou, B., Araus, J.L., Serret, M.D., 2020. Agronomic performance of irrigated quinoa in desert areas: Comparing different approaches for early assessment of salinity stress. Agric. Water Manag 240, 106205.
Robinson, D., Handley, L.L., Scrimgeour, C.M., Gordon, C., Forster, B.P., Ellis, R.P., 2000. Using stable isotope natural abundances ($\delta^{15}N$ and $\delta^{13}C$) to integrate the stress responses of wild barley (*Hordeum spontaneum* C. Koch.) genotypes. J. Exp. Bot. 51, 41–50.
Rukhsar, A., Kanbar, O., Mahmoudi, H., Yousfi, S., Araus, J.L., Serret, M.D., 2025. Combined effects of saline irrigation and genotype on the growth, grain yield, and mineral concentration of durum wheat in hot arid areas. Eur. J. Agro 168, 127585.
Saini, H.S., Aspinall, D., 1982. Abnormal sporogenesis in wheat (*Triticum aestivum* L.) induced by short periods of high temperature. Ann. Bot. 49, 835–846.
Saleh, J., Almahasneh, H., 2023. Evaluation the Variation in Water Use Efficiency Among ACSAD-Genotypes of Barley (*Hordeum vulgare* L.). Arab. J. Arid. Environ. 16, 58–69.
Sanchez-Bragado, R., Kim, J.W., Rivera-Amado, C., Molero, G., Araus, J.L., Savin, R., Slafer, G.A., 2020. Are awns truly relevant for wheat yields? A study of performance of awned/awnless isogenic lines and their response to source–sink manipulations. Field Crops Res. 254, 107827.
Scherer, H.W., 2008. Impact of sulfur on N_2 fixation of legumes. In: Khan, N.A., Singh, S. (Eds.), Sulfur Assimilation and Abiotic Stress in Plants. Springer, Berlin/Heidelberg, pp. 43–54.
Shah, J.M., Bukhari, S.A.H., Zeng, J.B., Quan, X.Y., Ali, E., Muhammad, N., Zhang, G.P., 2017. Nitrogen (N) metabolism related enzyme activities, cell ultrastructure and nutrient contents as affected by N level and barley genotype. J. Integr. Agric. 16, 190–198.
Shah, S.H., Houborg, R., McCabe, M.F., 2017. Response of chlorophyll, carotenoid and SPAD-502 measurement to salinity and nutrient stress in wheat (*Triticum aestivum* L.). Agronomy 7, 61.
Shaheen, R., Hood-Nowotny, R.C., 2005. Effect of drought and salinity on carbon isotope discrimination in wheat cultivars. Plant. Sci. 168, 901–909.
Sharqi, O.R., Anees, A.H., Ali, H.S., 2023. Evaluation of the productive traits of genotypes of barley (*Hordeum vulgare* L.) by the effect of seeding rate. In: IOP Conference Series: Earth and Environmental Science, 1262. IOP Publishing, 052031.
Slafer, G.A., Savin, R., Sadras, V.O., 2014. Coarse and fine regulation of wheat yield components in response to genotype and environment. Field Crops Res 157, 71–83.
Tambussi, E.A., Bort, J., Araus, J.L., 2007. Water use efficiency in C3 cereals under Mediterranean conditions: a review of physiological aspects. Ann. Appl. Biol. 150, 307–321.
Tcherkez, G., 2011. Natural $^{15}N/14N$ isotope composition in C_3 leaves: are enzymatic isotope effects informative for predicting the ^{15}N-abundance in key metabolites? Func. Plant. Biol. 38, 1–12.
Tester, M., Davenport, R., 2003. Na^+ tolerance and Na^+ transport in higher plants. Ann. Bot. 91, 503–527.
Turki, N., Shehzad, T., Elbok, S., Kazutoshi, O., 2024. The impact of salinity on the productivity and quality of durum and bread wheat. J. OASIS Agric. Sustain. Dev. 6, 56–60.
Uddling, J., Gelang-Alfredsson, J., Piikki, K., Pleijel, H., 2007. Evaluating the relationship between leaf chlorophyll concentration and SPAD-502 chlorophyll meter readings. Photosynth. Res. 91, 37–46.
USDA-FAS, 2026. World Barley Production. (United States Department of Agriculture Foreign Agricultural Service). USDA Foreign Agricultural Service, Washington, DC (Accessed: May 2026).
Voltas, J., Romagosa, I., Lafarga, A., Armesto, A.P., Sombrero, A., Araus, J.L., 1999. Genotype by environment interaction for grain yield and carbon isotope discrimination of barley in Mediterranean Spain. Aus. J. Agric. Res. 50, 1263–1271.
Yadav, A.K., Yadav, P.K., Vinod, P., Abha, T., Yadav, S.S., 2015. Effect of Saline Water Irrigation on the Yield and Mineral Composition of Crops in Rice-Wheat Cropping System. J. Indian. Soc. Soil. Sci. 63, 276–282.
Yousfi, S., Serret, M.D., Voltas, J., Araus, J.L., 2010b. Effect of salinity and water stress during the reproductive stage on growth, ion concentrations, $\Delta^{13}C$, and $\delta^{15}N$ of durum wheat and related amphiploids. J. Exp. Bot. 61, 3529–3542.

Yousfi, S., Serret, M.D., Araus, J.L., 2010a. A comparative effect of salinity and drought on growth, ion concentration and $\delta^{13}C$ and $\delta^{15}N$ in barley. Asp. Appl. Biol. 105, 73–81.

Yousfi, S., Serret, M.D., Márquez, A.J., Voltas, J., Araus, J.L., 2012. Combined use of $\delta^{13}C$, $\delta^{18}O$ and $\delta^{15}N$ tracks nitrogen metabolism and genotypic adaptation of durum wheat to salinity and water deficit. New. Phytol. 194, 230–244.

Yousfi, S., Shahid, M., Thushar, S., Ferreira, J.P., Serret, M.D., Araus, J.L., 2025. Effect of irrigation salinity on yield and quality of seeds in different quinoa genotypes. Agric. Water Manag 312, 109413.

Zeeshan, M., Lu, M., Sehar, S., Holford, P., Wu, F., 2020. Comparison of biochemical, anatomical, morphological, and physiological responses to salinity stress in wheat and barley genotypes deferring in salinity tolerance. Agronomy 10, 127.

Zhang, R., Yang, P., Liu, S., Wang, C., Liu, J., 2022. Evaluation of the methods for estimating leaf chlorophyll content with SPAD chlorophyll meters. Remote Sens 14, 5144.

Zhang, S., Gan, Y., Xu, B., 2019. Mechanisms of the IAA and ACC-deaminase producing strain of Trichoderma longibrachiatum T6 in enhancing wheat seedling tolerance to NaCl stress. Plant. Biol. 19, 22.

Zulfiqar, U., Ayub, A., Hussain, S., Ahmad, M., Rehman, A., Ishfaq, M., Fraz, M., Shabaan, M., Hong Yong, J.W., 2024. Iron biofortification in cereal crops: Recent progress and prospects. Food Energy Secur 13, e547.