



# Combined effects of saline irrigation and genotype on the growth, grain yield and mineral concentration of durum wheat in hot arid areas

Ayesha Rukhsar<sup>a,b</sup>, Osama Kanbar<sup>c</sup>, Henda Mahmoudi<sup>c</sup>, Salima Yousfi<sup>a,b</sup>, José L. Araus<sup>a,b</sup>, Maria D. Serret<sup>a,b,\*</sup>

<sup>a</sup> Section of Plant Physiology, University of Barcelona, Barcelona 08028, Spain

<sup>b</sup> AGROTECNIO (Center of Research in Agrotechnology), Lleida 25198, Spain

<sup>c</sup> International Center for Biosaline Agriculture (ICBA), P.O. Box 14660, Dubai, United Arab Emirates

## ARTICLE INFO

### Keywords:

Salinity  
Durum wheat  
Mineral concentration  
Yield  
Nitrogen concentration  
Stable isotopes

## ABSTRACT

Durum wheat cultivation in many parts of the Middle East is viable only under irrigation, often with saline water. This study evaluated the effects of salinity, season, and genotype on durum wheat grain yield and quality. Ten durum wheat genotypes were grown for two consecutive seasons under different irrigation salinities (2.6, 10, and 15 dSm<sup>-1</sup>) in sandy soils at the International Center for Biosaline Agriculture (Dubai, UAE). Various traits were evaluated, including grain yield (GY), biomass, plant height, number of spikes per plant, thousand grain weight (TGW), chlorophyll content, and grain isotope composition. Salinity reduced GY, agronomic traits, and chlorophyll content, while increasing  $\delta^{13}\text{C}$  and sodium (Na) concentration in grains. The season effect significantly impacted GY, biomass, TGW, and some mineral concentrations, potentially due to heat waves during grain filling. The genotypic effect was significant for GY, agronomic traits, and concentrations of nitrogen and most minerals. A negative phenotypic correlation was found between GY and both Na and  $\delta^{13}\text{C}$ , suggesting that better water status and lower Na accumulation were linked to genotypes with improved performance. However, there was no negative trade-off across genotypes between grain yield and concentrations of most minerals. Moreover, the accumulation of N and several nutrients (P, Mg, Mn, Fe, Zn, Cu, S) in grains followed a similar pattern, with positive correlations observed. We conclude that genotypic variability is crucial to improving yield and modulating mineral content in durum wheat grown under saline irrigation in hot arid areas.

## 1. Introduction

Durum wheat (*Triticum turgidum* L. subsp. *durum* (Desf) Husn.) is a prominent cereal crop cultivated extensively in many regions of the world, particularly around the Mediterranean basin, encompassing Southern Europe, North Africa, and West Asia (Turki et al., 2023). Notably, the countries situated in the Mediterranean basin are the primary consumers and importers of durum wheat-based commodities, including flour, pasta, and semolina (Xynias et al., 2020) as well as couscous, burgul and frik (Boggini et al., 2012). In fact, durum wheat is recognised for its high digestibility and nutritional composition, making it a suitable food for humans (Saini et al., 2022). Ongoing climate change, marked by increasing temperatures and evapotranspiration, and a trend of decreasing rainfall, is negatively impacting the productivity of durum wheat. Support irrigation has long been considered an effective way to mitigate the effects of climate change on crops such as durum

wheat, which have traditionally been cultivated under rainfed conditions. However, while supplemental irrigation is essential under arid/semi-arid conditions (Soni et al., 2021), it can exacerbate soil salinity (Bouras et al., 2019; Huang et al., 2019). Additionally, the increasing demand for water for non-agricultural activities, including urbanisation, industry, and services, is reducing the availability of water for agriculture. This is further compounded by the declining quality of available water due to the use of reclaimed water and the lowering of the water table from over-pumping (Horriche and Benabdallah, 2020). In this context, the use of durum wheat varieties best adapted to saline water irrigation is considered a crucial approach for improving wheat production in arid areas. Durum wheat is conventionally classified as a salinity-tolerant herbaceous crop with a salinity threshold of 5.9 dS/m according to FAO classification (De Santis et al., 2021). Nevertheless, salinity can still challenge the cultivation of durum wheat, which is less salt tolerant than bread wheat (Martínez-Moreno et al., 2022) and has

\* Corresponding author at: Section of Plant Physiology, University of Barcelona, Barcelona 08028, Spain.

E-mail address: [dserret@ub.edu](mailto:dserret@ub.edu) (M.D. Serret).

<https://doi.org/10.1016/j.eja.2025.127585>

Received 22 December 2024; Received in revised form 25 February 2025; Accepted 2 March 2025

Available online 12 March 2025

1161-0301/© 2025 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

even lower tolerance than barley (Munns et al., 2006).

Salinity is a two-phase plant stress. Initially it produces water stress, followed in the longer term by ionic stress, which accelerates senescence (Munns and Tester, 2008). The water stress component of salinity causes a decrease in growth and stomatal closure, subsequently affecting photosynthesis (Hnilickova et al., 2021) and disrupting nitrogen assimilation (Yousfi et al., 2010, 2012). The ionic stress component increases the toxicity associated with accumulation of salt ions in the cells and the consequent imbalance in ionic ratios (Zhang et al., 2019), thereby accelerating senescence. The decrease in stomatal conductance caused by salinity can be indirectly assessed through increases in the carbon isotope composition ( $\delta^{13}\text{C}$ ) of plant dry matter. In addition, the impact of salinity on nitrogen assimilation is reflected by decreases in nitrogen isotope composition ( $\delta^{15}\text{N}$ ) and the total nitrogen content of the plant matter (Yousfi et al., 2009, 2010, 2012). The ionic component of saline stress can be assessed through the loss of photosynthetic pigments, particularly chlorophyll (Abdehpour and Ehsanzadeh, 2019; Javaid et al., 2019; Khattabi et al., 2022; Yousfi et al., 2010), and changes in the dry matter content and ratios of sodium or magnesium to potassium and calcium (El-Lethy et al., 2013, Yousfi et al., 2012).

Besides yield, salinity may also affect the quality of grains, including their size, protein content, and mineral composition (Ashraf, 2014; De Santis et al., 2021; Turki et al., 2024). Salt stress can lead to decreased grain size and a subsequent increase in protein content per unit of dry matter (Francois et al., 1986; Katerji et al., 2005). Salinity stress may influence mineral accumulation in different ways, including health-related grain micronutrients such as Fe, Zn, and Mn (Masoni et al., 2007). Changes in mineral concentration in grains in response to salinity are not necessarily an indirect consequence of changes in grain size. The presence of  $\text{Na}^+$  and  $\text{Cl}^-$  ions can lead to a nutritional imbalance in the plant due to their antagonistic actions, resulting in reduced absorption of  $\text{K}^+$ ,  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{NH}_4^+$ , and  $\text{NO}_3^-$  (Hu and Schmidhalter, 2005). Additionally, the osmotic effect associated with salinity may cause water stress, decreasing the transpiration-related accumulation of some minerals, while simultaneously favouring the accumulation of compatible solutes, contributing to osmotic adjustment (Nadeem et al., 2022). Moreover, EL Sabagh et al. (2021) have reported that one of the effects of high salinity levels in wheat grain is an ionic imbalance that can lead to differential accumulation of minerals. Furthermore, the water used for irrigation also has an effect on the mineral content, depending on the composition and level of salinity of the irrigation water. The nature of the fertiliser is also a factor to consider, particularly in sandy soils from arid environments, where the addition of manure may represent an additional source of salinity (Rezzouk et al., 2020). Therefore, the mineral content in grains will depend on a complex set of factors: the water stress effect induced by the saline water (Yadav et al., 2015), the ionic imbalance caused by increased levels of Na and Cl (EL Sabagh et al., 2021), together with the other ions diluted in the irrigation water (Yadav et al., 2015). This scenario may become even more complex depending on the compost and chemical fertilisers applied.

Improving the salt stress tolerance of durum wheat varieties is a key strategy to ensure consistent agricultural outputs in arid and semiarid areas (Nakayama et al., 2022), since salinity is a prominent abiotic stress that imposes significant limitations on wheat productivity (Majeed and Muhammad, 2019; Awaad et al., 2020; Moustafa et al., 2021) and grain quality (Nadeem et al., 2020; De Santis et al., 2021). In this regard, a better understanding of the interactions between genotypic performance and the level of salinity is required, and may help the development of high-throughput phenotyping techniques under real (i.e., field) conditions (Araus and Cairns, 2014; Araus et al., 2022). The durum wheat germplasm developed in recent years by ACSAD (Arab Center for the Studies of Arid Zones and Drylands) and ICARDA (International Center for Agricultural Research in the Dry Areas) for the drought and heat conditions prevailing in the Mediterranean basin and Middle East is an asset that is worthwhile exploring for genetic tolerance to irrigation with saline water. However, it is not only the quantities of durum wheat

produced that are crucial in arid areas, the quality of the wheat grains is also an important criterion. In fact, limited information is available regarding the effect of salt stress on micronutrient accumulation in durum wheat grains (De Santis et al., 2021). Considering the significant impact of environmental conditions on mineral concentrations in grains, it is imperative to expand research efforts to include arid and semi-arid regions as well as soils with alkaline pH levels (Caldelas et al., 2023). For this reason, the objective of the current study is the evaluation of durum wheat genotypes under arid growing conditions and irrigation with saline water in terms of both production and grain quality and the potential genotype, salinity and season interactions.

This study compares the performance of seven durum wheat genotypes developed from ACSAD (Table 1) alongside three well-known Syrian varieties. Of the latter, two were released by ICARDA, namely “SHAM 3”, which is considered drought tolerant and adapted to arid zones, and “SHAM 5”, which is described as genotype tolerant to drought (Almeselmani et al., 2011), and the third variety is “Hawrani” (also termed Hourani), which is a traditional durum wheat variety that is versatile in terms of culinary uses and described as tolerant to drought (Table 1). The experimental field trials were conducted during two consecutive seasons (2020–2021 and 2021–2022) in the United Arab Emirates (UAE), which is one of the world’s driest regions, characterised by very low or frequently absent rainfall, high temperatures often reaching  $50^\circ\text{C}$ , poor sandy soils, and saline water irrigation. The selection of durum wheat genotypes with the ability to tolerate the saline water irrigation, as well as the extreme soil and climatic conditions of the UAE is a crucial breeding strategy to improve wheat production and ensure crop sustainability in arid areas. Therefore, this study aimed to identify the durum wheat genotype that is most tolerant to the specific UAE environmental and agronomic conditions, and to evaluate the grain quality of durum wheat genotypes in arid areas. The originality of this work lies in its comprehensive nature, assessing in real (i.e. field) conditions the relative importance of irrigation salinity, season and genotype variability on durum wheat performance under the hot arid conditions and sandy soils prevailing at the UAE. Specifically, the study focused on grain yield and agronomic components, as well as on grain quality (nitrogen and the concentration of essential and non-essential mineral concentrations), together with a set of physiological indicators

**Table 1**

Provenance, origin and agronomic performance under the arid Mediterranean drought conditions of Syria and the southern and eastern Mediterranean basin of the ten durum wheat varieties used in this study.

Genotype	Provenance/ Origin	Tolerant/ Susceptible to drought	Source
ACSAD 357	ACSAD - Syria	Susceptible	Kanbar, ICBA personal communication
ACSAD 1105	ACSAD - Syria	Tolerant	Almeselmani et al. (2011)
ACSAD 1229	ACSAD - Syria	Tolerant	Ali Saleh (2017) and Almeselmani et al. (2012)
ACSAD 1289	ACSAD - Syria	Susceptible	Kanbar, ICBA personal communication
ACSAD 65	ACSAD - Syria	Moderately susceptible	Almeselmani et al. (2011)
ACSAD 1107	ACSAD - Syria	Tolerant	Ali Saleh (2017)
ACSAD 1187	ACSAD - Syria	Tolerant	Kanbar, ICBA personal communication
SHAM 3	ICARDA - Syria	Tolerant	Almeselmani et al. (2011, 2012)
SHAM 5	ICARDA - Syria	Tolerant	Almeselmani et al. (2011, 2012)
Hawrani	Local variety - Syria	Tolerant	Almeselmani et al. (2011)

ACSAD, The Arab Center for the Studies of Arid Zones and Drylands; ICARDA, The International Center for Agricultural Research in the Dry Areas, ICBA, The International Center for Biosaline Agriculture.

of plant adaptation to the environmental conditions. These indicators are the carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope compositions and Na accumulation in grains, together with the chlorophyll content of the flag leaf, which may help to define the ideotypic characteristics associated with genotypic performance under different irrigation salinities, and therefore have potential to serve as phenotyping characteristics. In summary, the study focused on the following questions: (i) measuring the relative effects of saline irrigation and genetic variation on durum wheat yield and quality, (ii) identifying genotypes that are more resilient to salinity in terms of yield and/or quality, (iii) establishing phenotypic selection criteria, and (iv) evaluating potential trade-offs between grain yield and quality.

## 2. Materials and methods

### 2.1. Plant material and growth conditions

Trials were carried out during two consecutive seasons at the field facilities of the International Center for Biosaline Agriculture (ICBA) in Dubai, UAE ( $25^{\circ}05'49''\text{ N}$  and  $55^{\circ}23'25''\text{ E}$ ). The soils at the ICBA experimental fields are sandy in texture (98 % sand, 1 % silt, and 1 % clay), calcareous (50–60 %  $\text{CaCO}_3$  equivalents), porous (45 % porosity), and moderately alkaline (pH 8.22) with very low organic matter (<0.5 %). The saturation percentage of the soil was 26, indicating very high drainage capacity, and the electrical conductivity of its saturated extract (ECe) was  $1.2\text{ dS m}^{-1}$ . Ten different genotypes of durum wheat (*Triticum turgidum* L. subsp. *durum* (Desf) Husn.) were cultivated during the 2020–2021 and 2021–2022 seasons under the specific climatic conditions of the UAE (Fig. 1). The first cropping season experienced several heat waves during anthesis and the early stages of grain filling

(Fig. S1). The genotypes tested were “ACSAD 65”, “ACSAD 357”, “ACSAD 1105”, “ACSAD 1107”, “ACSAD 1229”, “ACSAD 1187”, “ACSAD 1289”, “SHAM 3”, “SHAM 5”, and “Hawrani”. Most of them are considered tolerant to the drought conditions of the southern and eastern Mediterranean basin (Table 1). Plot size was  $2\text{ m}^2$ , with 4 rows per plot and 25 cm distances between rows. On each row, plants were planted at 20 cm intervals, with five seeds in each hole, totalling a density of  $100\text{ seeds m}^{-2}$ . A drip irrigation system with drippers at 20 cm intervals was used. The resulting planting density is due to the use of drip irrigation, which is commonly practised in the UAE. For all three irrigation treatments, approximately 550 mm of water was applied per crop season. Irrigation was conducted three times a day (morning, noon, and evening) with a daily volume of  $2.5\text{ l m}^{-2}$  from planting until the onset of stem elongation (approximately two months later). Following this, the irrigation volume was increased to  $5\text{ l m}^{-2}$  per day until grain maturity. This adjustment was made to meet the increased evapotranspirative demand associated with crop growth and the rising temperatures during this period.

In the first season, seeds were sown on December 6, 2020, and in the second season on December 6, 2021. The agronomic conditions were similar for both crop seasons. After sowing, the soil was covered with mesh to protect it from birds. Once the plants emerged (approximately 10 days later the first season and one week later the second season), the cover was removed. For plant protection, a pesticide against aphids was sprayed about two weeks after sowing, and weeds were removed by hand around the middle of January (first season) and late December and late January (second season). Additionally, a net to protect against birds during grain filling was installed on February 6, 2021, and on February 15, 2022. Salinity treatments began one month after planting, once the crop was well established. Until then, all plots were irrigated with fresh water ( $2.6\text{ dS m}^{-1}$ ) to secure germination, further seedling emergence, and therefore proper establishment of the crop, which is crucial for it to endure saline conditions (Iqbal et al., 1998). From that point, three levels of salinity were applied in the irrigation water:  $2.6\text{ dS m}^{-1}$  (Control),  $10\text{ dS m}^{-1}$  (Salinity 1), and  $15\text{ dS m}^{-1}$  (Salinity 2). The sodium (Na), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) concentrations in the supplied irrigation water (fresh and saline water) are reported in Table S1. The experimental design for the two crop seasons followed a randomised complete block design, with three levels of salinity ( $2.6\text{ dS m}^{-1}$ ,  $10\text{ dS m}^{-1}$ , and  $15\text{ dS m}^{-1}$ ), 10 durum wheat genotypes, and three replicates per genotype and salinity level. A total of 180 plots were studied across the two crop seasons. A predefined animal compost (Table S1) was applied before planting at a rate of  $50\text{ Mg ha}^{-1}$ . A granular NPK (12–12–17) fertiliser also containing traces of different minerals (Table S1) was supplied at a rate of  $100\text{ kg ha}^{-1}$  during the tillering stage. For the first crop season, chlorophyll content was measured in the flag leaf using a chlorophyll meter (SPAD, Minolta, Japan) on February 15, 2021, and on March 29, 2021 the number of spikes per plant and plant height were measured. Harvesting took place on April 17 for plants subjected to the  $15\text{ dS m}^{-1}$  salinity treatment and on May 1 for the other two irrigation treatments ( $10$  and  $2.6\text{ dS m}^{-1}$ ). Additionally, total shoot biomass (SB), grain yield (GY), and thousand grain weight (TGW) were assessed after the harvest. For the second season, chlorophyll measurement took place on February 22, 2022. Plant height and the number of spikes per plant were measured on March 25, 2022, and harvesting took place on April 20 for the  $15\text{ dS m}^{-1}$  treatment and on May 3 for the other two irrigation treatments. Additionally, total shoot biomass (SB), grain yield (GY), and thousand grain weight (TGW) were assessed as in the first season.

### 2.2. Stable isotope composition and nitrogen concentration

Grain samples were dried at  $60\text{ }^{\circ}\text{C}$  until constant weight and 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 the measurement of total N concentration and the stable

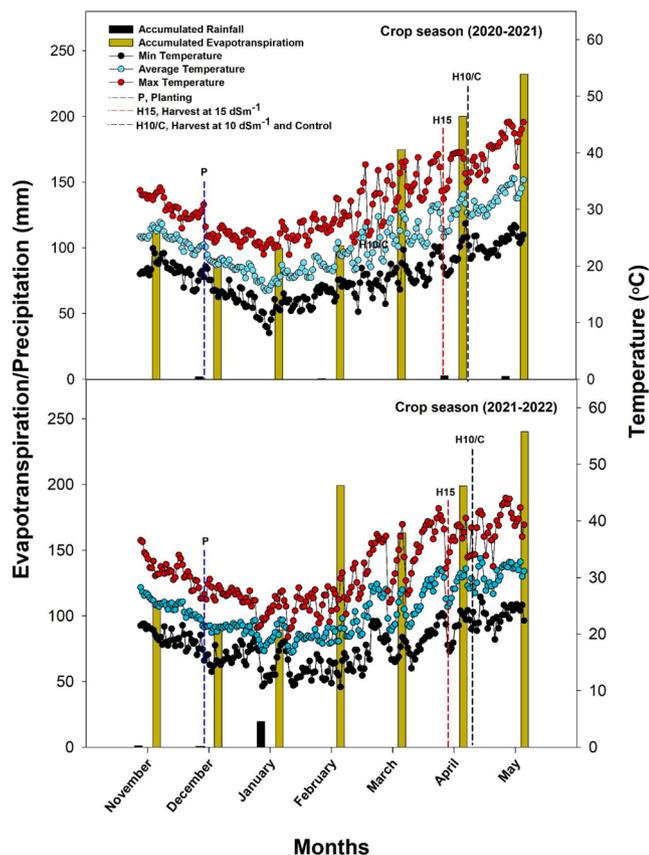


Fig. 1. The monthly accumulated precipitation, potential evapotranspiration, and the minimum, maximum and average daily temperatures during the growing period of durum wheat in the two crop seasons.

carbon ( $^{13}\text{C}/^{12}\text{C}$ ) and nitrogen ( $^{15}\text{N}/^{14}\text{N}$ ) ratios using an elemental analyser (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) (EA-IRMS) operating in continuous flow mode and performed at the Scientific Facilities of the University of Barcelona. The  $^{13}\text{C}/^{12}\text{C}$  ratios (R) of plant material were expressed in  $\delta$  notation (Coplen, 2008) as carbon isotope composition ( $\delta^{13}\text{C}$ ):  $\delta^{13}\text{C} (\text{‰}) = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$ , where sample refers to plant material and standard to Pee Dee Belemnite (PDB) calcium carbonate. International isotope secondary standards of known  $^{13}\text{C}/^{12}\text{C}$  ratios (IAEA CH7, polyethylene foil; IAEA CH6, sucrose; USGS 40, L glutamic acid) were used with an analytical precision of 0.1 ‰. The same  $\delta$  notation was used to represent the  $^{15}\text{N}/^{14}\text{N}$  ratio expression ( $\delta^{15}\text{N}$ ), but with the standard referring to  $\text{N}_2$  in air. For nitrogen, the international isotope secondary standards IAEA N1, IAEA N2, IAEA N3, and USGS40 were used with a precision of 0.3 ‰.

### 2.3. Mineral analyses

To determine the mineral concentration in the grain, 100 mg of wheat flour was weighed in Teflon® beakers and digested in 2 ml  $\text{HNO}_3$  and 1 ml  $\text{H}_2\text{O}_2$  at 90 °C overnight at the ionomics service of the CEBAS (Centro de Edafología y Biología Aplicada, del Segura) Murcia, Spain. Digests were diluted in 30 ml of MilliQ water (18.2  $\Omega$ ) and refrigerated until analysis. The mineral concentration in the digests was determined by Induced Coupled Plasma Optical Emission Spectrometry (ICP-OES) for calcium (Ca), iron (Fe), potassium (K), magnesium (Mg), sodium (Na), phosphorus (P), sulphur (S), nickel (Ni), and aluminium (Al) (Optima 8300, Perkin Elmer, Waltham, MA, USA) and for silicon Si (Optima 3200rl, Perkin Elmer); and by Induced Coupled Plasma Mass Spectrometry (ICP-MS, Elan6000, Perkin Elmer) for copper (Cu), manganese (Mn), rubidium (Rb), molybdenum (Mo), strontium (Sr), titanium (Ti) and zinc (Zn). For every 11 samples, a procedural blank and an aliquot of certified reference materials were analysed in the same manner. The reference materials were BCR-60 (aquatic plant, Joint Research Centre (JRC), Brussels, Belgium), BCR-62 (olive leaves, JRC), and BCR-279 (sea lettuce, JRC). Recoveries were 90–94 % for Cu, Mn, Rb, and Zn relative to the certified values. The digestion beakers were acid-washed and rinsed in Milli-Q water before use. The quality of the acids was 69–70 % Baker Instra-Analyzed Reagent 9598.34 (Thermo Fisher Scientific, Waltham, MA, USA) for  $\text{HNO}_3$ , and 30 % Suprapur 1.07298.1000 (Merck, Darmstadt, Germany) for  $\text{H}_2\text{O}_2$ . Plastic tubes and caps were rinsed three times in the digest before filling them for analysis.

### 2.4. Statistical analysis

All the agronomic, physiological and analytical traits evaluated in this study were subjected to factorial analyses of variance (ANOVAs) to assess the effects of salinity, genotype, season and all their interactions. Means were compared using Tukey's honestly significant difference (HSD) test to detect differences in salinity and genotypes. The crop season, salinity level, and genotype were considered as fixed factors, while all measured agro-physiological variables were treated as dependent factors. The relative importance of each of the effects (salinity, season, genotype and the respective interactions) as sources of variability for each trait was assessed as the portion of the total variability in the mean squares of the combined analyses of variance. In addition, to verify the efficacy of the model used in this study, the partial estimation squared (PES) and observed power (OP) were calculated for all variables measured (Tables S2 and S3). The dependent variables included all agro-physiological variables and mineral concentrations, while salinity, genotype, and season were the independent variables. Small values of PES indicate that the variable contributes minimally to the model, while larger values indicate a stronger contribution. Higher partial estimation squared values reflect a greater proportion of variation explained by the model effect, with a maximum value of 1. The

observed power (OP) represents the probability of correctly rejecting the null hypothesis (which posits no difference between groups) based on the observed effect size, sample size, and significance level. A typical desired power level is 0.80, while higher OP values, such as 0.90, indicate stronger statistical evidence, up to a maximum of 1. This study demonstrated high values of PES and OP effects of salinity, genotype, season, and their interactions for most of the traits considered (Tables S2 and S3). Furthermore, to explore the associations between traits, a bivariate Pearson correlation and correlation heat map was employed. Additionally, a principal component analysis (PCA) was conducted using grain yield, biomass, leaf chlorophyll content,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , thousand grain weight, and the concentrations in the grains of nitrogen and all minerals to distinguish between genotype groups under all growing conditions combined. Path analysis (Li, 1975) was also performed to draft a mechanistic model relating key physiological traits with either grain yield or total biomass at maturity. The goodness of fit for the path model was assessed using the Comparative Fit Index (CFI) (Arbuckle, 1997). Statistical analyses were carried out using IBM SPSS Statistics Version 25.0 (SPSS Inc., Chicago, IL, USA). Figures were generated using Sigma-Plot 11.0 for Windows (Systat Software Inc., Point Richmond, CA, USA). The correlation heat map and the PCA analyses were created using the Past (Paleontological STatistics) program.

## 3. Results

### 3.1. Effect of salinity, genotype and season on yield and agronomic components

Salinity significantly decreased grain yield (GY), shoot biomass (SB), thousand grain weight (TGW), plant height, and the number of spikes

**Table 2**

Effect of salinity, genotypes and season on the plant height, the number of spikes per plant, the biomass, the thousand grain weight (TGW) and the grain yield of durum wheat genotypes. The values of each irrigation condition are the mean  $\pm$  SE of 60 measurements (10 genotypes, three replicates per genotype and two seasons). The values for each season are the mean  $\pm$  SE of 90 measurements (10 genotypes, three replicates per genotype and three irrigation conditions). 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.

	Plant height (cm)	Spikes plant <sup>-1</sup>	Biomass (Mg ha <sup>-1</sup> )	TGW (g)	Grain Yield (Mg ha <sup>-1</sup> )
<b>Irrigation</b>					
Control (2.6 dS m <sup>-1</sup> )	60.64 <sup>a</sup> $\pm 0.96$	3.56 <sup>a</sup> $\pm 0.09$	6.18 <sup>a</sup> $\pm 0.35$	41.63 <sup>a</sup> $\pm 0.58$	2.19 <sup>a</sup> $\pm 0.14$
Salinity 1 (10 dS m <sup>-1</sup> )	60.72 <sup>a</sup> $\pm 0.79$	3.39 <sup>a</sup> $\pm 0.07$	3.65 <sup>b</sup> $\pm 0.14$	33.71 <sup>b</sup> $\pm 0.65$	1.32 <sup>b</sup> $\pm 0.05$
Salinity 2 (15 dS m <sup>-1</sup> )	55.92 <sup>b</sup> $\pm 0.59$	2.73 <sup>b</sup> $\pm 0.06$	2.58 <sup>c</sup> $\pm 0.09$	29.17 <sup>c</sup> $\pm 0.59$	0.85 <sup>c</sup> $\pm 0.05$
<b>Season</b>					
2020–2021	62.88 $\pm 0.66$	3.29 $\pm 0.06$	3.58 $\pm 0.17$	32.66 $\pm 0.83$	1.05 $\pm 0.06$
2021–2022	55.31 $\pm 0.45$	3.16 $\pm 0.08$	4.70 $\pm 0.29$	37.01 $\pm 0.53$	1.86 $\pm 0.10$
<b>Level of significance</b>					
Salinity (S)	905.70***	23.00***	410.73***	4774.00***	55.41***
Genotype (G)	884.39***	4.47 <sup>ns</sup>	165.36***	1502.27***	19.38***
Season (Se)	2575.61***	0.80 <sup>ns</sup>	56.29***	852.62***	29.58***
S x G	613.29**	7.00 <sup>ns</sup>	85.00***	327.26**	9.26***
S x Se	142.12**	1.29 <sup>ns</sup>	73.00***	241.00***	9.15***
G x Se	362.35**	1.82 <sup>ns</sup>	33.04***	572.55***	4.47**
S x G x Se	523.86**	6.41 <sup>ns</sup>	29.59 <sup>ns</sup>	269.60***	3.91 <sup>ns</sup>

per plant (Table 2). Specifically, compared to the control, salinity reduced grain yield by approximately 40 % under 10 dSm<sup>-1</sup> and 62 % at 15 dSm<sup>-1</sup>. Shoot Biomass (SB) also declined by about 41 % and 58 % under 10 dSm<sup>-1</sup> and 15 dSm<sup>-1</sup>, respectively (Table 2). However, the reduction in TGW was less pronounced (Table 2), with decreases of 19 % (10 dSm<sup>-1</sup>) and 30 % (15 dSm<sup>-1</sup>). Comparing across seasons, differences were observed in all agronomic traits, except for the number of spikes per plant (Table 2). The genotypic effect was significant for all traits, except for the number of spikes per plant (Table 2). Double interactions between salinity (S), genotype (G) and season (Se) were significant for all traits, except the number of spikes per plant. However, the triple interaction (S x G x Se) was significant only for plant height and TGW (Table 2). Except for plant height, the main factor affecting variability in GY and the other agronomic traits was irrigation, followed by genotype, which in both cases had an effect around three times lower than irrigation. “Hawrani” and “ACSAD 1229” were the best-performing genotypes in terms of grain yield and biomass (Table 3). Conversely, “ACSAD 357” and “ACSAD 1187” exhibited the lowest grain yield and biomass (Table 3). Regarding TGW, “ACSAD 65” and “ACSAD 1229” showed the highest values, whereas “ACSAD 1187” and “ACSAD 1289” had the lowest values (Table 3). “ACSAD 65” and “ACSAD 1229” were also the tallest plants, while “ACSAD 1289” and “ACSAD 1105” were the shortest. The intra-treatment comparisons highlighted significant genotype differences in grain yield under Salinity 1 (10 dSm<sup>-1</sup>), while under control conditions the differences were significant but weaker, and no differences were found under the high levels of Salinity 2

**Table 3**

Effect of genotype on plant height, the number of spikes per plant, biomass, thousand grain weight (TGW) and the grain yield of durum wheat genotypes. The values of each genotype are the mean of 18 measurements ± SE (three levels of salinity, 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 for genotypes under all growing conditions combined. The probabilities (ns, not significant; \*p < 0.050; \*\*p < 0.010; \*\*\*p < 0.001) are shown for genotypic differences under all growing conditions combined and under each level of salinity.

Genotype	Plant height (cm)	Spikes plant <sup>-1</sup>	Biomass (Mg ha <sup>-1</sup> )	TGW (g)	Grain Yield (Mg ha <sup>-1</sup> )
ACSAD 65	62.18 <sup>a</sup> ± 1.70	3.17 <sup>a</sup> ± 0.15	4.31 <sup>bcd</sup> ± 0.43	39.00 <sup>a</sup> ± 1.19	1.74 <sup>abc</sup> ± 0.21
ACSAD 357	57.30 <sup>bc</sup> ± 1.26	3.46 <sup>a</sup> ± 0.19	2.00 <sup>e</sup> ± 0.27	35.73 <sup>bc</sup> ± 1.62	0.78 <sup>e</sup> ± 0.10
ACSAD 1105	57.64 <sup>bc</sup> ± 0.97	3.44 <sup>a</sup> ± 0.19	4.30 <sup>bcd</sup> ± 0.53	37.00 <sup>b</sup> ± 1.58	1.49 <sup>bcd</sup> ± 0.22
ACSAD 1107	59.02 <sup>ab</sup> ± 1.89	3.18 <sup>a</sup> ± 0.15	4.33 <sup>bcd</sup> ± 0.41	35.30 <sup>c</sup> ± 1.13	1.29 <sup>d</sup> ± 0.16
ACSAD 1229	62.20 <sup>a</sup> ± 1.61	3.22 <sup>a</sup> ± 0.16	4.89 <sup>ab</sup> ± 0.48	37.08 <sup>b</sup> ± 1.54	1.84 <sup>ab</sup> ± 0.20
ACSAD 1187	57.85 <sup>bc</sup> ± 0.96	3.10 <sup>a</sup> ± 0.16	3.41 <sup>d</sup> ± 0.24	30.55 <sup>d</sup> ± 1.16	1.17 <sup>de</sup> ± 0.13
ACSAD 1289	54.64 <sup>c</sup> ± 0.88	3.48 <sup>a</sup> ± 0.17	3.68 <sup>cd</sup> ± 0.43	30.60 <sup>d</sup> ± 1.46	1.34 <sup>cd</sup> ± 0.20
SHAM 3	59.98 <sup>ab</sup> ± 1.55	3.09 <sup>a</sup> ± 0.17	4.05 <sup>bcd</sup> ± 0.39	36.64 <sup>bc</sup> ± 1.54	1.47 <sup>bcd</sup> ± 0.15
SHAM 5	60.57 <sup>ab</sup> ± 1.55	3.09 <sup>a</sup> ± 0.09	4.55 <sup>bc</sup> ± 0.76	35.77 <sup>bc</sup> ± 1.58	1.47 <sup>bcd</sup> ± 0.26
Hawrani	59.60 <sup>ab</sup> ± 2.05	3.07 <sup>a</sup> ± 0.14	5.87 <sup>a</sup> ± 0.84	31.00 <sup>d</sup> ± 2.24	1.96 <sup>a</sup> ± 0.30
<b>Level of significance</b>					
All growing conditions	***	ns	***	***	***
Control (2.6 dS m <sup>-1</sup> )	ns	ns	***	***	*
Salinity 1 (10 dS m <sup>-1</sup> )	ns	ns	***	**	***
Salinity 2 (15 dS m <sup>-1</sup> )	ns	ns	**	**	ns

(Table 3). Genotypic differences in biomass and TGW were significant under both control and saline conditions (Table 3). However, no differences were found between genotypes for plant height or the number of spikes per plant under control and salinity conditions (Table 3). Under both 10 dSm<sup>-1</sup> and control, “Hawrani” and “ACSAD 65” were the most productive genotypes (Fig. S2A), followed by “ACSAD 1229”. However, “ACSAD 357” was the least productive genotype under both control and 10 dSm<sup>-1</sup>. Furthermore, under both salinity levels, “ACSAD 65” and “Hawrani” exhibited the highest and the lowest values for TGW, respectively (Fig. S2B).

### 3.2. Impact of salinity, genotype and season on nitrogen concentration and isotope signatures

Salinity significantly increased the carbon isotope composition (δ<sup>13</sup>C); however, no differences were found in the nitrogen concentration (N) or nitrogen isotope composition (δ<sup>15</sup>N) of grains between treatments (Table 4). Leaf chlorophyll content (LC) also decreased significantly under salinity (Table 4). The season effect was significant only for N and LC. (Table 4). The genotypic effect was highly significant for δ<sup>13</sup>C, δ<sup>15</sup>N, N, and LC (Table 4). Interactions were significant for all the traits except for G x Se and S x Se x G in LC (Table 4). The main factor effect was attributed to irrigation in the case of δ<sup>13</sup>C and leaf chlorophyll content, while the genotypic effect was significant but lower for both traits. The genotypic effect was the main factor affecting δ<sup>15</sup>N and nitrogen concentration.

“ACSAD 1187” and “ACSAD 1105” exhibited the lowest δ<sup>13</sup>C values (Table 5), followed by Hawrani, while the highest δ<sup>13</sup>C values were observed in “ACSAD 357” and “ACSAD 1107”. Hawrani also presented the highest N concentration and δ<sup>15</sup>N values (Table 5). The highest leaf chlorophyll content was recorded in “SHAM 5” and “ACSAD 1107”, while “ACSAD 1229” and “SHAM 3” displayed the lowest values (Table 5). Comparing genotypes within each treatment, the difference

**Table 4**

Effect of salinity, genotype and season on the grain carbon isotope composition (δ<sup>13</sup>C), grain nitrogen isotope composition (δ<sup>15</sup>N), grain nitrogen concentration (N) and the leaf chlorophyll of durum wheat genotypes. The values from each irrigation condition are the mean ± SE of 60 measurements (10 genotypes, three replicates per genotype and two seasons). The values for each season are the mean ± SE of 90 measurements (10 genotypes, three replicates per genotype and three irrigation conditions). 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.

	δ <sup>13</sup> C (‰)	δ <sup>15</sup> N (‰)	N (%)	Leaf chlorophyll (SPAD units)
<b>Irrigation</b>				
Control (2.6 dS m <sup>-1</sup> )	-27.65 <sup>c</sup> ± 0.11	7.43 <sup>a</sup> ± 0.09	2.46 <sup>a</sup> ± 0.03	40.00 <sup>a</sup> ± 0.46
Salinity 1 (10 dS m <sup>-1</sup> )	-26.65 <sup>b</sup> ± 0.10	7.57 <sup>a</sup> ± 0.07	2.47 <sup>a</sup> ± 0.04	39.00 <sup>b</sup> ± 0.30
Salinity 2 (15 dS m <sup>-1</sup> )	-26.31 <sup>a</sup> ± 0.11	7.42 <sup>a</sup> ± 0.11	2.52 <sup>a</sup> ± 0.04	36.62 <sup>c</sup> ± 0.24
<b>Season</b>				
2020–2021	-26.85 ± 0.08	7.41 ± 0.06	2.29 ± 0.02	37.38 ± 0.21
2021–2022	-26.89 ± 0.13	7.53 ± 0.09	2.67 ± 0.03	39.23 ± 0.36
<b>Level of significance</b>				
Salinity (S)	58.31***	0.92 <sup>ns</sup>	0.52 <sup>ns</sup>	372.29***
Genotype (G)	39.68***	32.76***	2.62***	106.16**
Season (Se)	0.06 <sup>ns</sup>	0.67 <sup>ns</sup>	6.21***	153.74***
S x G	14.35***	13.69***	1.78***	173.39**
S x Se	48.16***	1.69**	0.90***	93.33***
G x Se	15.01***	3.60*	2.72***	66.10 <sup>ns</sup>
S x G x Se	9.14***	25.63***	2.00***	100.63 <sup>ns</sup>

**Table 5**

Effect of genotypes on the grain carbon isotope composition ( $\delta^{13}\text{C}$ ), the grain nitrogen isotope composition ( $\delta^{15}\text{N}$ ), the grain nitrogen concentration (N) and the leaf chlorophyll of durum wheat genotypes. The values of each genotype are the mean of 18 measurements  $\pm$  SE (three levels of salinity, 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 for genotypes under all growing conditions combined. The probabilities (ns, not significant; \* $p < 0.050$ ; \*\* $p < 0.010$ ; \*\*\* $p < 0.001$ ) are shown for genotypic differences under all growing conditions combined and under each level of salinity.

Genotype	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	N (%)	Leaf chlorophyll (SPAD units)
ACSAD 65	-26.96 <sup>bcd</sup> $\pm 0.25$	7.04 <sup>de</sup> $\pm 0.15$	2.60 <sup>ab</sup> $\pm 0.05$	37.81 <sup>ab</sup> $\pm 0.80$
ACSAD 357	-25.51 <sup>a</sup> $\pm 0.39$	8.16 <sup>a</sup> $\pm 0.16$	2.36 <sup>de</sup> $\pm 0.04$	38.14 <sup>ab</sup> $\pm 0.84$
ACSAD 1105	-27.14 <sup>cd</sup> $\pm 0.19$	6.76 <sup>e</sup> $\pm 0.32$	2.45 <sup>cd</sup> $\pm 0.11$	38.27 <sup>ab</sup> $\pm 0.89$
ACSAD 1107	-26.75 <sup>b</sup> $\pm 0.22$	7.59 <sup>bc</sup> $\pm 0.04$	2.34 <sup>e</sup> $\pm 0.07$	39.29 <sup>ab</sup> $\pm 0.64$
ACSAD 1229	-27.11 <sup>cd</sup> $\pm 0.16$	7.69 <sup>abc</sup> $\pm 0.03$	2.34 <sup>e</sup> $\pm 0.05$	37.27 <sup>b</sup> $\pm 0.47$
ACSAD 1187	-27.20 <sup>d</sup> $\pm 0.19$	7.67 <sup>bc</sup> $\pm 0.07$	2.47 <sup>cd</sup> $\pm 0.05$	39.00 <sup>ab</sup> $\pm 0.65$
ACSAD 1289	-26.89 <sup>bc</sup> $\pm 0.20$	7.44 <sup>bc</sup> $\pm 0.05$	2.61 <sup>ab</sup> $\pm 0.06$	38.04 <sup>ab</sup> $\pm 0.57$
SHAM 3	-26.95 <sup>bcd</sup> $\pm 0.20$	7.05 <sup>de</sup> $\pm 0.18$	2.41 <sup>de</sup> $\pm 0.09$	37.29 <sup>b</sup> $\pm 0.66$
SHAM 5	-27.06 <sup>cd</sup> $\pm 0.20$	7.29 <sup>cd</sup> $\pm 0.16$	2.54 <sup>bc</sup> $\pm 0.07$	39.72 <sup>a</sup> $\pm 0.76$
Hawrani	-27.12 <sup>cd</sup> $\pm 0.07$	8.06 <sup>ab</sup> $\pm 0.06$	2.70 <sup>a</sup> $\pm 0.02$	38.29 <sup>ab</sup> $\pm 0.57$
<b>Level of significance</b>				
All growing conditions	***	***	***	**
Control (2.6 dS m <sup>-1</sup> )	ns	ns	**	ns
Salinity 1 (10 dS m <sup>-1</sup> )	***	***	ns	ns
Salinity 2 (15 dS m <sup>-1</sup> )	***	***	*	ns

was highly significant for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  under Salinity 1 (10 dS m<sup>-1</sup>) and 2 (15 dS m<sup>-1</sup>), while no difference was found under control conditions (Table 5). Moreover, differences between genotypes in N concentration were observed under control and Salinity 2 (15 dS m<sup>-1</sup>). Under 10 dS m<sup>-1</sup> and 15 dS m<sup>-1</sup> salinity levels, "ACSAD 357" exhibited the highest values of  $\delta^{13}\text{C}$ , whereas "Hawrani" showed the lowest  $\delta^{13}\text{C}$  (Fig. S2D). Additionally, "ACSAD 357" and "Hawrani" displayed the highest  $\delta^{15}\text{N}$  under both salinities (Fig. S2E). Regarding N concentration, "ACSAD 65" and "Hawrani" exhibited the highest levels under both salinities (Fig. S2F).

**3.3. Salinity, genotype and season effects on the mineral nutrients**

Salinity significantly increased the grain concentration of Mn and S under both Salinity 1 (10 dS m<sup>-1</sup>) and Salinity 2 (15 dS m<sup>-1</sup>) (Table 6). However, the concentration of K, Ca, Mg and Zn increased under Salinity 1, while no significant differences were observed between the control and Salinity 2 (Table 6), except for Zn, which decreased under salinity 2. Moreover, no differences were found in P or Fe concentrations between control and the two salinity levels, while Cu decreased under Salinity 2 compared to the control, with no difference observed between control and Salinity 1. The season had a significant effect on the levels of all the essential minerals analysed. Additionally, significant genotypic variability was observed for all the essential minerals analysed (Table 6). The double interactions between salinity (S), genotype (G), and season (Se) and the triple interaction S x G x Se were significant for all essential minerals, except in a few cases (Table 6). The genotypic effect for all the essential minerals was stronger than the effect due to irrigation.

**Table 6** Effect of salinity, genotype and season on the essential mineral concentration in the grain of durum wheat genotypes. The values of each irrigation condition are the mean  $\pm$  SE of 60 measurements (10 genotypes, three replicates per genotype and two seasons). The values for each season are the mean  $\pm$  SE of 90 measurements (10 genotypes, three replicates per genotype and three irrigation conditions). 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.

Irrigation	Mineral concentration (mg kg <sup>-1</sup> )									
	K	Ca	Mg	P	Fe	Mn	Zn	Cu	S	S
Control (2.6 dS m <sup>-1</sup> )	6369.46 <sup>b</sup> $\pm 148.42$	759.76 <sup>b</sup> $\pm 24.48$	1680.47 <sup>ab</sup> $\pm 34.88$	5828.21 <sup>a</sup> $\pm 93.37$	35.58 <sup>b</sup> $\pm 1.21$	22.11 <sup>b</sup> $\pm 0.57$	82.00 <sup>b</sup> $\pm 1.67$	6.31 <sup>a</sup> $\pm 0.20$	1672.12 <sup>c</sup> $\pm 35.95$	1283811.60 <sup>***</sup>
Salinity 1 (10 dS m <sup>-1</sup> )	6702.38 <sup>a</sup> $\pm 69.37$	829.06 <sup>a</sup> $\pm 16.59$	1716.03 <sup>a</sup> $\pm 14.41$	5955.31 <sup>a</sup> $\pm 47.18$	35.74 <sup>a</sup> $\pm 1.01$	23.84 <sup>a</sup> $\pm 0.43$	85.16 <sup>a</sup> $\pm 1.29$	6.13 <sup>a</sup> $\pm 1.60$	1796.78 <sup>b</sup> $\pm 21.59$	1825632.87 <sup>***</sup>
Salinity 2 (15 dS m <sup>-1</sup> )	6276.34 <sup>b</sup> $\pm 38.50$	785.37 <sup>b</sup> $\pm 14.52$	1656.91 <sup>b</sup> $\pm 23.55$	5903.71 <sup>a</sup> $\pm 77.12$	35.87 <sup>a</sup> $\pm 1.06$	24.33 <sup>a</sup> $\pm 0.74$	78.86 <sup>c</sup> $\pm 1.21$	5.17 <sup>b</sup> $\pm 1.24$	1891.09 <sup>a</sup> $\pm 31.37$	894136.41 <sup>****</sup>
Season	6597.19 $\pm 103.75$	811.33 $\pm 16.82$	1635.89 $\pm 18.342$	5762.53 $\pm 64.87$	33.71 $\pm 0.89$	21.81 $\pm 0.37$	76.90 $\pm 0.94$	5.51 $\pm 0.13$	1718.69 $\pm 21.42$	1219.88 <sup>***</sup>
2020-2021	6278.73 $\pm 79.12$	768.24 $\pm 14.31$	1747.62 $\pm 21.95$	6036.87 $\pm 53.69$	37.85 $\pm 0.83$	25.29 $\pm 0.53$	87.79 $\pm 1.11$	6.30 $\pm 0.15$	1862.27 $\pm 28.48$	4371.89 <sup>***</sup>
2021-2022	5392535.20 <sup>***</sup>	135576.54 <sup>***</sup>	95747.55 <sup>*</sup>	421657.19 <sup>ns</sup>	2.67 <sup>ns</sup>	1.46.88 <sup>***</sup>	1219.88 <sup>***</sup>	46.07 <sup>***</sup>	1283811.60 <sup>***</sup>	1825632.87 <sup>***</sup>
Level of significance	26031936.41 <sup>***</sup>	1594852.58 <sup>***</sup>	1233159.91 <sup>***</sup>	12334339.90 <sup>***</sup>	1824.23 <sup>***</sup>	1177.47 <sup>***</sup>	4371.89 <sup>***</sup>	133.02 <sup>***</sup>	1825632.87 <sup>***</sup>	1825632.87 <sup>***</sup>
Salinity (S)	4703042.45 <sup>***</sup>	423893.72 <sup>***</sup>	423893.72 <sup>***</sup>	3111512.41 <sup>***</sup>	829.05 <sup>***</sup>	463.28 <sup>***</sup>	5020.58 <sup>***</sup>	25.79 <sup>***</sup>	894136.41 <sup>****</sup>	894136.41 <sup>****</sup>
Genotype (G)	15848737.40 <sup>***</sup>	269698.07 <sup>***</sup>	686354.16 <sup>**</sup>	5692931.74 <sup>ns</sup>	1150.02 <sup>ns</sup>	441.88 <sup>***</sup>	1433.62 <sup>*</sup>	12.17 <sup>**</sup>	1124825.33 <sup>***</sup>	1124825.33 <sup>***</sup>
Season (Se)	11904734.09 <sup>***</sup>	562005.29 <sup>***</sup>	181311.79 <sup>**</sup>	1207598.13 <sup>ns</sup>	587.26 <sup>***</sup>	337.01 <sup>***</sup>	271.66 <sup>*</sup>	18.80 <sup>**</sup>	801850.09 <sup>***</sup>	801850.09 <sup>***</sup>
S x G	28173400.94 <sup>***</sup>	237607.83 <sup>***</sup>	273604.84 <sup>ns</sup>	4764049.57 <sup>*</sup>	410.58 <sup>ns</sup>	174.57 <sup>***</sup>	1815.92 <sup>***</sup>	44.10 <sup>***</sup>	466989.58 <sup>*</sup>	466989.58 <sup>*</sup>
S x Se	12014078.60 <sup>**</sup>	341635.82 <sup>***</sup>	386475.96 <sup>ns</sup>	4153810.13 <sup>ns</sup>	2703.45 <sup>***</sup>	382.23 <sup>***</sup>	1515.25 <sup>*</sup>	18.42 <sup>***</sup>	1381297.56 <sup>***</sup>	1381297.56 <sup>***</sup>
S x G x Se										

K, potassium; Ca, calcium; Mg, magnesium; P, phosphorus; Fe, iron; Mn, manganese; Zn, zinc; Cu, copper; S, sulphur.

Concerning genotypic variability, “Hawrani” exhibited the highest concentration of K, P and Mn (Table 7). Additionally, “Hawrani” also displayed the highest Cu concentration and the highest level of Zn. “ACSAD 1289” exhibited the highest values of S followed by “Hawrani” (Table 7). Moreover, “SHAM 5” and “ACSAD 1289” displayed the highest Ca concentrations, while “ACSAD 1289” and “ACSAD 1105” exhibited the highest Fe concentrations. Significant differences between genotypes were observed for all essential minerals under each treatment, except for P, Fe, and S under control conditions, and Zn under both control and Salinity 1 (Table 7). Under control conditions, “Hawrani” and “ACSAD 1289” had the highest concentration of Ca, Mg, Mn, and Cu, while the highest K values were found in “Hawrani”, followed by “ACSAD 357” (Figs. S3A, B, C, D and H). Conversely, “ACSAD 65” and “ACSAD 1107” exhibited the lowest K, Ca, Mg, and Mn concentrations, while “ACSAD 1229” together with “ACSAD 357” showed the lowest Cu values (Figs. S3A, B, C, D and H). Under 10 dSm<sup>-1</sup> growing conditions, “SHAM 3” and “SHAM 5” exhibited the highest levels of K, but “ACSAD 65” and “ACSAD 1229” displayed the lowest concentrations (Fig. S3A). “SHAM 5” and “ACSAD 1105” had the highest levels of Ca, whereas “ACSAD 65” and “ACSAD 1229” had the lowest levels (Fig. S3B). Additionally, “Hawrani” and “ACSAD 1289” exhibited the highest levels of Mn, P, and S, while the lowest Mn and P concentrations were observed in “ACSAD 357” and the lowest S concentration were found in “ACSAD 1107” (Figs. S3D, E and I). Moreover, “ACSAD 1289” and “ACSAD 1105” had the highest levels of Mg and Fe, with “ACSAD 1229” possessing the lowest values for both minerals (Figs. S3C and F). Regarding Cu concentrations, “Hawrani” and “ACSAD 1107” had the highest levels and “ACSAD 357” had the lowest (Fig. S3H). Furthermore, under high salinity (15 dSm<sup>-1</sup>), “Hawrani” and “ACSAD 1187” exhibited the highest K concentrations (Fig. S3A), and “ACSAD 1229” and “SHAM 3” had the lowest. The highest levels of Ca and Cu were found in

“Hawrani” and “ACSAD 1289” (Figs. S3B and H), whereas “ACSAD 1229” along with “ACSAD 65” had the lowest Ca, and “ACSAD 357” the lowest Cu. Additionally, “Hawrani” and “ACSAD 1105” possessed the highest Mg, Mn, P and S levels (Figs. 2SC, D, E and I) and “ACSAD 1229” and “ACSAD 357” exhibited the lowest values for these nutrients. Regarding the Fe and Zn concentrations, “ACSAD 1105” and “ACSAD 1107” had the highest Fe levels and “Hawrani” and “ACSAD 1107” had the highest Zn. In contrast, “ACSAD 1229” had the lowest values for both minerals (Figs. S3F and G).

#### 3.4. Salinity, genotype and season effects on the non-essential minerals

For the non-essential minerals, in comparison to the control, salinity significantly increased Na concentration by 47 % and 71 % under 10 dSm<sup>-1</sup> and 15 dSm<sup>-1</sup>, respectively (Table 8). However, the Rb concentration decreased under salinity, and no differences were found between control and salinity for Si, Mo, Al, Ti, Sr, and Ni (Table 8). The season had a significant effect only on Na, Mo and Rb (Table 8). Significant genotypic effects were observed for Na, Mo, Al, Rb, Sr and Ni, while no genotypic differences were found for Si or Ti (Table 8). Significant differences were found for most of the non-essential minerals in the double and the triple interactions between salinity (S), genotype (G), and season (Se) (Table 8). Except for Rb, the genotypic effect was the most prominent for all the non-essential minerals, including Na.

The genotypes “ACSAD 357” and “ACSAD 1289” displayed the highest Na concentration (Table 9). “Hawrani” exhibited the highest levels of Si and “ACSAD 1105” had the highest Al (Table 9). “ACSAD 1289” displayed the highest Mo levels, while “ACSAD 65” possessed the highest Rb level (Table 9). The intra-treatment comparison revealed significant genotypic differences in Na and Rb under both salinity levels, whereas no differences were observed under control conditions

**Table 7**

Effect of genotypes on the essential mineral concentration in grains of durum wheat genotypes. The values of each genotype are the mean of 18 measurements ± SE (three levels of salinity, 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 for genotypes under all growing conditions combined. The probabilities (ns, not significant; \* $p < 0.050$ ; \*\* $p < 0.010$ ; \*\*\* $p < 0.001$ ) are shown for genotypic differences under all growing conditions combined and under each level of salinity.

Mineral concentration (mg kg <sup>-1</sup> )									
	K	Ca	Mg	P	Fe	Mn	Zn	Cu	S
<b>Genotype</b>									
ACSAD 65	5817.42 <sup>c</sup> ± 142.06	557.79 <sup>d</sup> ± 23.93	1602.70 <sup>c</sup> ± 43.64	5713.58 <sup>cd</sup> ± 120.48	33.44 <sup>bc</sup> ± 2.05	22.50 <sup>cd</sup> ± 1.32	76.64 <sup>d</sup> ± 1.75	5.48 <sup>c</sup> ± 0.18	1720.64 <sup>bc</sup> ± 51.34
ACSAD 357	6610.45 <sup>b</sup> ± 164.95	806.53 <sup>abcd</sup> ± 32.54	1600.08 <sup>c</sup> ± 33.19	5806.41 <sup>bcd</sup> ± 101.32	35.12 <sup>bc</sup> ± 0.63	19.57 <sup>e</sup> ± 0.50	81.38 <sup>bcd</sup> ± 1.76	4.34 <sup>d</sup> ± 0.22	1727.21 <sup>bc</sup> ± 30.59
ACSAD 1105	6372.66 <sup>bc</sup> ± 198.77	872.83 <sup>a</sup> ± 31.79	1767.06 <sup>ab</sup> ± 47.97	6021.96 <sup>abc</sup> ± 162.46	43.61 <sup>a</sup> ± 3.54	24.01 <sup>bc</sup> ± 1.44	87.47 <sup>bc</sup> ± 2.04	5.85 <sup>bc</sup> ± 0.17	1826.49 <sup>ab</sup> ± 70.23
ACSAD 1107	6120.15 <sup>bc</sup> ± 230.72	754.95 <sup>cd</sup> ± 27.91	1603.12 <sup>c</sup> ± 33.21	5746.66 <sup>cd</sup> ± 109.51	36.76 <sup>abc</sup> ± 1.37	22.27 <sup>cd</sup> ± 0.91	88.31 <sup>ab</sup> ± 2.58	6.93 <sup>a</sup> ± 0.22	1745.67 <sup>bc</sup> ± 59.55
ACSAD 1229	6061.62 <sup>bc</sup> ± 127.57	715.79 <sup>c</sup> ± 22.21	1579.16 <sup>c</sup> ± 32.30	5481.48 <sup>d</sup> ± 101.77	30.81 <sup>c</sup> ± 0.67	20.62 <sup>de</sup> ± 0.48	75.51 <sup>d</sup> ± 2.01	4.89 <sup>d</sup> ± 0.19	1616.73 <sup>c</sup> ± 43.29
ACSAD1187	6620.50 <sup>b</sup> ± 192.93	840.99 <sup>a</sup> ± 29.51	1707.50 <sup>abc</sup> ± 33.38	6002.53 <sup>abcd</sup> ± 96.19	34.35 <sup>bc</sup> ± 1.48	22.43 <sup>cd</sup> ± 0.81	78.29 <sup>cd</sup> ± 2.42	5.53 <sup>c</sup> ± 0.23	1788.40 <sup>abc</sup> ± 46.95
ACSAD 1289	6605.34 <sup>b</sup> ± 185.19	887.75 <sup>a</sup> ± 32.73	1819.58 <sup>a</sup> ± 48.67	6325.96 <sup>ab</sup> ± 177.34	38.56 <sup>ab</sup> ± 1.62	24.86 <sup>b</sup> ± 0.86	84.92 <sup>bc</sup> ± 2.55	6.83 <sup>a</sup> ± 0.31	1953.69 <sup>a</sup> ± 73.03
SHAM 3	6458.26 <sup>b</sup> ± 183.84	754.38 <sup>cd</sup> ± 22.03	1661.81 <sup>bc</sup> ± 40.29	5752.60 <sup>cd</sup> ± 120.85	33.81 <sup>bc</sup> ± 1.07	24.05 <sup>bc</sup> ± 0.73	81.41 <sup>bcd</sup> ± 3.19	6.13 <sup>b</sup> ± 0.38	1698.05 <sup>bc</sup> ± 51.61
SHAM 5	6503.95 <sup>b</sup> ± 161.21	874.79 <sup>a</sup> ± 29.77	1709.15 <sup>abc</sup> ± 79.26	5731.93 <sup>cd</sup> ± 138.84	36.94 <sup>abc</sup> ± 3.01	24.74 <sup>b</sup> ± 1.04	80.70 <sup>bcd</sup> ± 3.17	5.69 <sup>bc</sup> ± 0.33	1870.65 <sup>ab</sup> ± 67.86
Hawrani	7309.82 <sup>a</sup> ± 286.96	860.59 <sup>a</sup> ± 24.11	1801.67 <sup>ab</sup> ± 23.56	6391.03 <sup>a</sup> ± 86.55	34.32 <sup>bc</sup> ± 0.97	29.81 <sup>a</sup> ± 0.56	92.66 <sup>a</sup> ± 2.01	7.12 <sup>a</sup> ± 0.25	1945.42 <sup>a</sup> ± 39.93
<b>Level of significance</b>									
All growing conditions	***	***	***	***	***	***	***	***	***
Control (2.6 dS m <sup>-1</sup> )	*	**	*	ns	ns	***	ns	**	ns
Salinity 1 (10 dS m <sup>-1</sup> )	**	***	***	***	*	***	ns	***	**
Salinity 2 (15 dS m <sup>-1</sup> )	***	***	***	***	*	***	***	***	**

K, potassium; Ca, calcium; Mg, magnesium; P, phosphorus; Fe, iron; Mn, manganese; Zn, zinc; Cu, copper; S, sulphur.

**Table 8**

Effect of salinity, genotype and season on the non-essential mineral concentration in the grain of durum wheat genotypes. The values of each irrigation condition are the mean  $\pm$  SE of 60 measurements (10 genotypes, three replicates per genotype and two seasons). The values for each season are the mean  $\pm$  SE of 90 measurements (10 genotypes, three replicates per genotype and three irrigation conditions). 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.

Mineral concentration (mg kg <sup>-1</sup> )								
	Na	Si	Mo	Al	Rb	Ti	Sr	Ni
<b>Irrigation</b>								
Control (2.6 dS m <sup>-1</sup> )	595.75 <sup>c</sup> $\pm$ 63.28	76.24 <sup>a</sup> $\pm$ 8.58	1.42 <sup>±</sup> 0.36	8.75 <sup>a</sup> $\pm$ 0.49	2.48 <sup>a</sup> $\pm$ 0.09	1.07 <sup>a</sup> $\pm$ 0.15	13.07 <sup>±</sup> 0.57	0.41 <sup>a</sup> $\pm$ 0.05
Salinity 1 (10 dS m <sup>-1</sup> )	873.44 <sup>b</sup> $\pm$ 56.70	68.90 <sup>a</sup> $\pm$ 3.25	1.37 <sup>a</sup> $\pm$ 0.21	9.66 <sup>a</sup> $\pm$ 0.67	2.01 <sup>b</sup> $\pm$ 0.05	0.92 <sup>a</sup> $\pm$ 0.10	13.03 <sup>a</sup> $\pm$ 0.25	0.32 <sup>a</sup> $\pm$ 0.01
Salinity 2 (15 dS m <sup>-1</sup> )	1019.67 <sup>a</sup> $\pm$ 40.49	72.62 <sup>a</sup> $\pm$ 4.21	1.54 <sup>a</sup> $\pm$ 0.27	8.77 <sup>a</sup> $\pm$ 0.41	1.84 <sup>c</sup> $\pm$ 0.06	0.85 <sup>a</sup> $\pm$ 0.10	13.39 <sup>a</sup> $\pm$ 0.29	0.31 <sup>a</sup> $\pm$ 0.04
<b>Season</b>								
2020.2021	965.59 $\pm$ 38.90	71.01 $\pm$ 3.72	2.13 $\pm$ 0.32	9.23 $\pm$ 0.54	1.88 $\pm$ 0.05	1.10 $\pm$ 0.12	13.30 $\pm$ 0.28	0.33 $\pm$ 0.02
2021–2022	683.22 $\pm$ 47.68	83.26 $\pm$ 5.63	1.17 $\pm$ 0.05	8.99 $\pm$ 0.29	2.38 $\pm$ 0.07	0.96 $\pm$ 0.07	13.27 $\pm$ 0.36	0.36 $\pm$ 0.03
<b>Level of significance</b>								
Salinity (S)	5405272.15***	1479.73 <sup>ns</sup>	1.15 <sup>ns</sup>	43.98 <sup>ns</sup>	12.69***	1.51 <sup>ns</sup>	3.89 <sup>ns</sup>	0.35 <sup>ns</sup>
Genotype (G)	9955648.92***	11887.170 <sup>ns</sup>	60.88***	390.82***	4.17***	5.139 <sup>ns</sup>	726.88***	3.04***
Season (Se)	3106406.96***	979.35 <sup>ns</sup>	13.72***	11.69 <sup>ns</sup>	9.62***	0.18 <sup>ns</sup>	0.05 <sup>ns</sup>	0.01 <sup>ns</sup>
S x G	889264.44***	16599.09 <sup>ns</sup>	47.54**	415.85**	7.542***	9.69 <sup>ns</sup>	195.69***	0.97 <sup>ns</sup>
S x Se	5789335.14***	11099.88**	23.38***	206.26***	6.82***	4.14**	31.24***	0.05 <sup>ns</sup>
G x Se	2597055.64***	11577.32 <sup>ns</sup>	51.91***	153.88 <sup>ns</sup>	8.57***	14.10***	150.37***	0.66 <sup>ns</sup>
S x G x Se	907192.32***	18484.61 <sup>ns</sup>	62.70***	556.17***	8.83***	9.44 <sup>ns</sup>	150.25***	2.72**

Na, sodium; Si, silicon, Mo, molybdenum; Al, aluminium; Rb, rubidium; Ti, titanium; Sr, strontium, Ni, nickel.

**Table 9**

Effect of salinity on the non-essential mineral concentration in the grain of durum wheat genotypes. The values of each genotype are the mean of 18 measurements (three levels of salinity, 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 for genotypes under all growing conditions combined. The probabilities (ns, not significant; \* $p < 0.050$ ; \*\* $p < 0.010$ ; \*\*\* $p < 0.001$ ) are shown for genotypic differences under all growing conditions combined and under each level of salinity.

	Mineral concentration (mg kg <sup>-1</sup> )							
	Na	Si	Mo	Al	Rb	Ti	Sr	Ni
<b>Genotype</b>								
ACSAD 65	355.65 <sup>h</sup> $\pm$ 62.70	55.68 <sup>b</sup> $\pm$ 6.07	1.23 <sup>b</sup> $\pm$ 0.08	5.62 <sup>b</sup> $\pm$ 0.54	2.52 <sup>a</sup> $\pm$ 0.12	0.65 <sup>a</sup> $\pm$ 0.10	8.95 <sup>g</sup> $\pm$ 0.44	0.22 <sup>b</sup> $\pm$ 0.01
ACSAD 357	1320.23 <sup>a</sup> $\pm$ 121.28	65.68 <sup>ab</sup> $\pm$ 3.62	1.33 <sup>b</sup> $\pm$ 0.21	9.04 <sup>ab</sup> $\pm$ 0.59	2.14 <sup>bc</sup> $\pm$ 0.12	0.88 <sup>a</sup> $\pm$ 0.07	13.93 <sup>bc</sup> $\pm$ 0.26	0.32 <sup>b</sup> $\pm$ 0–01
ACSAD 1105	857.97 <sup>de</sup> $\pm$ 84.22	72.46 <sup>ab</sup> $\pm$ 6.73	1.29 <sup>b</sup> $\pm$ 0.99	11.54 <sup>a</sup> $\pm$ 1.89	2.26 <sup>b</sup> $\pm$ 0.12	1.32 <sup>a</sup> $\pm$ 0.35	12.53 <sup>de</sup> $\pm$ 0.27	0.28 <sup>b</sup> $\pm$ 0.02
ACSAD 1107	824.37 <sup>e</sup> $\pm$ 83.52	72.81 <sup>ab</sup> $\pm$ 7.71	1.11 <sup>b</sup> $\pm$ 0.14	9.57 <sup>a</sup> $\pm$ 0.83	1.90 <sup>c</sup> $\pm$ 0.11	0.93 <sup>a</sup> $\pm$ 0.15	12.35 <sup>ef</sup> $\pm$ 0.42	0.44 <sup>ab</sup> $\pm$ 0.10
ACSAD 1229	765.01 <sup>ef</sup> $\pm$ 72.90	76.52 <sup>ab</sup> $\pm$ 11.61	1.18 <sup>b</sup> $\pm$ 0.14	8.26 <sup>ab</sup> $\pm$ 0.88	1.95 <sup>cd</sup> $\pm$ 0.16	1.03 <sup>a</sup> $\pm$ 0.21	11.19 <sup>f</sup> $\pm$ 0.44	0.26 <sup>b</sup> $\pm$ 0.01
ACSAD1187	680.95 <sup>g</sup> $\pm$ 63.83	80.17 <sup>ab</sup> $\pm$ 8.77	1.01 <sup>b</sup> $\pm$ 0.11	9.42 <sup>a</sup> $\pm$ 0.57	2.26 <sup>b</sup> $\pm$ 0.12	0.96 <sup>a</sup> $\pm$ 0.16	14.07 <sup>bc</sup> $\pm$ 0–46	0.29 <sup>b</sup> $\pm$ 0.02
ACSAD 1289	1096.47 <sup>b</sup> $\pm$ 111.21	64.79 <sup>ab</sup> $\pm$ 4.61	2.95 <sup>a</sup> $\pm$ 0.88	10.28 <sup>a</sup> $\pm$ 0.90	1.90 <sup>d</sup> $\pm$ 0.15	1.32 <sup>a</sup> $\pm$ 0.27	17.25 <sup>a</sup> $\pm$ 0.19	0.69 <sup>a</sup> $\pm$ 0.17
SHAM 3	590.26 <sup>g</sup> $\pm$ 50.35	73.77 <sup>ab</sup> $\pm$ 7.13	1.06 <sup>b</sup> $\pm$ 0.10	8.19 <sup>ab</sup> $\pm$ 0.59	2.13 <sup>bcd</sup> $\pm$ 0.21	0.89 <sup>a</sup> $\pm$ 0.22	12.85 <sup>cde</sup> $\pm$ 0.25	0.34 <sup>b</sup> $\pm$ 0.03
SHAM 5	971.09 <sup>e</sup> $\pm$ 81.51	112.03 <sup>a</sup> $\pm$ 22.04	1.61 <sup>b</sup> $\pm$ 0.88	8.28 <sup>ab</sup> $\pm$ 0.56	1.92 <sup>cd</sup> $\pm$ 0.17	1.06 <sup>a</sup> $\pm$ 0.25	13.69 <sup>cd</sup> $\pm$ 0.34	0.40 <sup>b</sup> $\pm$ 0.04
Hawrani	953.80 <sup>cd</sup> $\pm$ 103.38	90.28 <sup>a</sup> $\pm$ 12.56	1.82 <sup>ab</sup> $\pm$ 0.11	10.35 <sup>a</sup> $\pm$ 1.10	1.98 <sup>cd</sup> $\pm$ 0.15	1.12 <sup>a</sup> $\pm$ 0.30	15.12 <sup>b</sup> $\pm$ 0.37	0.23 <sup>b</sup> $\pm$ 0.01
<b>Level of significance</b>								
All growing conditions	***	ns	***	***	***	ns	***	***
Control (2.6 dS m <sup>-1</sup> )	ns	ns	ns	ns	ns	ns	***	*
Salinity 1 (10 dS m <sup>-1</sup> )	***	**	*	ns	**	ns	***	***
Salinity 2 (15 dS m <sup>-1</sup> )	***	ns	ns	ns	***	ns	***	ns

Na, sodium; Si, silicon, Mo, molybdenum; Al, aluminium; Rb, rubidium; Ti, titanium; Sr, strontium, Ni, nickel.

(Table 9). Differences in Si and Mo were noted under 10 dSm<sup>-1</sup>, although these were weaker. No genotypic differences were found for Al or Ti under any of the three growing conditions. Sr concentrations exhibited significant genotypic variability across all three conditions, while Ni exhibited weaker but still significant genotypic differences under control conditions and stronger genotypic differences under 10 dSm<sup>-1</sup> salinity (Table 9).

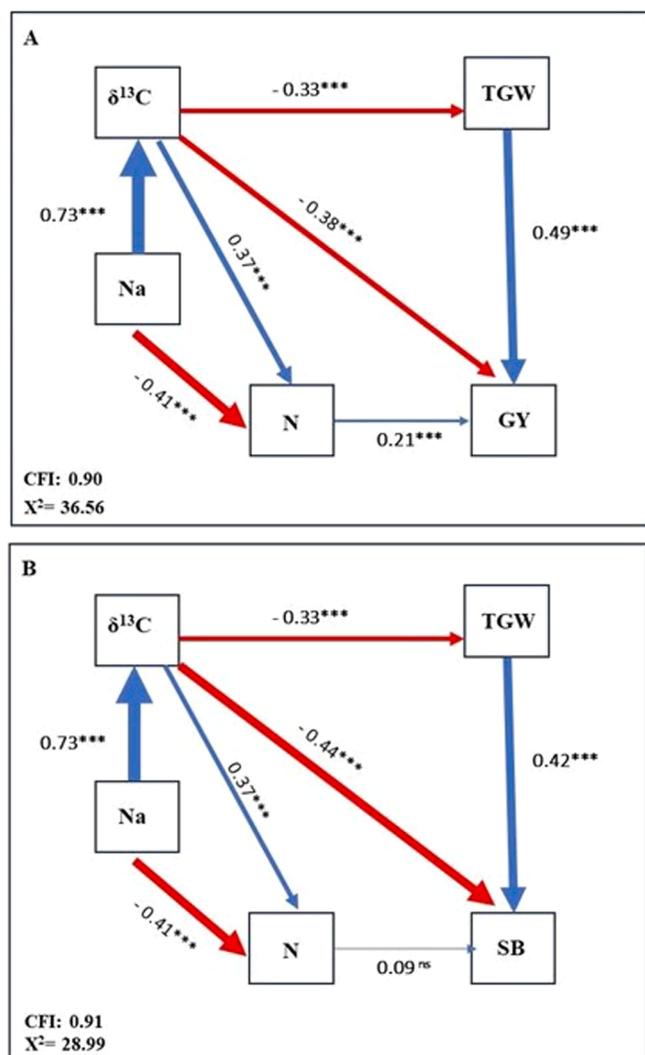
### 3.5. Relationships between agronomic and physiological traits across growing conditions

Combining all growing conditions and seasons,  $\delta^{13}\text{C}$  exhibited a negative correlation with GY, TGW, SB and LC (Fig. S4), with the highest correlation coefficients shown by GY ( $r = -0.57$ ;  $p < 0.001$ ) and SB ( $r = -0.63$ ;  $p < 0.001$ ). Additionally, the GY was positively correlated with SB, TGW, LC (Fig. S4), and a weaker positive correlation was found between GY and N (Fig. S4). Nevertheless,  $\delta^{15}\text{N}$  did not show a significant correlation with GY, TGW, LC, N or  $\delta^{13}\text{C}$  (Fig. S4). A conceptual

model was proposed through path analysis, which distinguished direct acclimation responses in grain yield (Fig. 2A) and total aerial biomass (Fig. 2B) related to salinity conditions (via Na) and their subsequent effects on water status and photosynthesis (via  $\delta^{13}\text{C}$ ), as well as grain weight (via TGW) and quality (via N in grains). The two models provided an acceptable fit to the data ( $\text{CFI} \geq 0.9$  and  $P > 0.05$  for both path analyses). In both models, Na had a strong positive effect on  $\delta^{13}\text{C}$  and a negative effect on grain N concentration. Conversely,  $\delta^{13}\text{C}$  had a positive effect on N grain but a negative effect on TGW as well as grain yield (GY) and biomass. Additionally, the TGW had a positive effect on GY and biomass. Finally, the effect of grain N on GY was low and its effect on biomass was negligible.

### 3.6. Relationships of minerals with agronomic and physiological traits

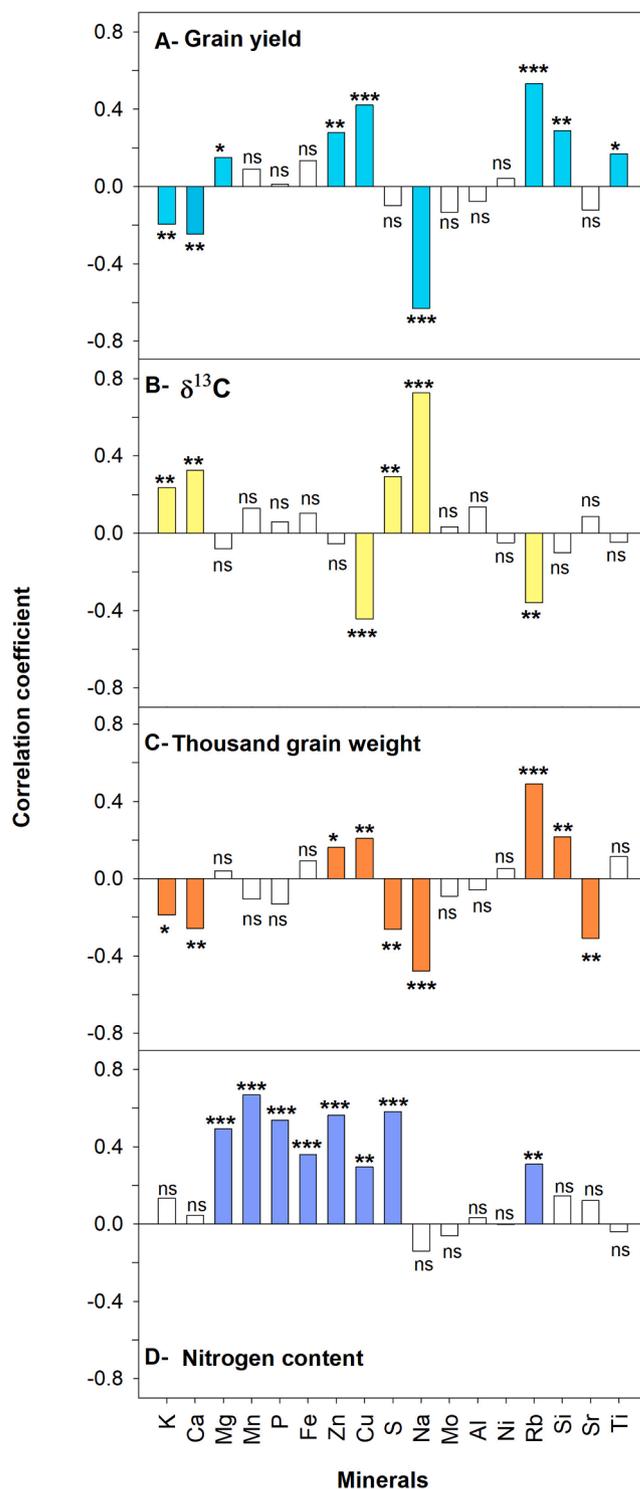
Combining all growing conditions and seasons, a negative correlation was found between Na and GY (Fig. 3 and S4), TGW (Fig. 3 and S4), LC and SB (Fig. S4), with the highest correlation coefficients observed



**Fig. 2.** Path analyses conducted on the ten durum wheat 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 ( $\delta^{13}\text{C}$ , Na concentration in grains), a grain quality trait (grain N), and agronomic yield components (TGW) on (A) shoot biomass (SB) at maturity and (B) grain yield. 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 comparative fit index (CFI), are presented at the bottom right of each panel. A CFI value greater than 0.9 is considered indicative of a good fit, particularly for small sample sizes. Statistical significance levels are indicated as ns, not significant and  $***p < 0.001$ .

for GY ( $r = -0.63$ ;  $p < 0.001$ ). Moreover, under control conditions, Na correlated negatively (strongly) with GY, while the correlation with N was weaker and no significant correlation was found with TGW (Table 10). Under  $10 \text{ dSm}^{-1}$ , Na was strongly negatively correlated with GY, TGW and N, and no correlation was found between Na and all these traits under  $15 \text{ dSm}^{-1}$  (Table 10). Additionally, Na correlated strongly and positively with  $\delta^{13}\text{C}$  under all growing conditions combined ( $r = 0.73$ ;  $p < 0.001$ ) (Fig. 3 and S4), as well as under control and both 10 and  $15 \text{ dSm}^{-1}$  (Table 10). Na correlated positively with K, Ca, S, Al, Sr (Fig. S4) and negatively with Rb and Cu (Fig. S4).

Under all growing conditions combined, both K and Ca were correlated negatively with grain yield and TGW (Fig. 3 and S4) and positively with  $\delta^{13}\text{C}$ , but there was no correlation with N (Fig. 3 and S4). Additionally, K and Ca correlated negatively with GY under control and 10



**Fig. 3.** Correlation coefficients of the relationship between mineral concentration and grain yield (A); the carbon ( $\delta^{13}\text{C}$ ) isotope composition (B); the thousand grain weight (C) and nitrogen concentration (D). K, potassium; Ca, calcium; Mg, magnesium; P, phosphorus; Fe, iron; Mn, manganese; Zn, zinc; Cu, copper; S, sulphur. Na, sodium; Si, silicon, Mo, molybdenum; Al, aluminium; Rb, rubidium; Ti, titanium; Sr, strontium, Ni, nickel. The correlation was evaluated across 180 points (the combination of ten genotypes, three replicates per genotype, three levels of salinity and two crop seasons). Levels of significance are shown: ns, not significant;  $*p < 0.050$ ;  $**p < 0.010$ ;  $***p < 0.001$ .

**Table 10**

Relationship between mineral concentration and grain yield (GY), thousand grain weight (TGW), carbon ( $\delta^{13}\text{C}$ ) isotope composition and nitrogen content (N). Data used are the individual values of each genotype under each growing condition. The table only shows minerals that correlate with at least one of the parameters (GY, TGW,  $\delta^{13}\text{C}$  and N) and under one of the three growing conditions.

	K	Ca	Mg	Mn	P	Fe	Zn	Cu	S	Na	Rb	Si	Sr
<b>Control (2.6 dS m<sup>-1</sup>)</b>													
GY	-0.305*	-0.283*	0.074 <sup>ns</sup>	0.106 <sup>ns</sup>	-0.033 <sup>ns</sup>	0.258*	0.257*	0.383**	0.041 <sup>ns</sup>	-	0.445**	0.217 <sup>ns</sup>	-0.179 <sup>ns</sup>
TGW	-	-0.298*	-	-	-0.211 <sup>ns</sup>	0.148 <sup>ns</sup>	0.023 <sup>ns</sup>	-	-	-0.167 <sup>ns</sup>	0.156 <sup>ns</sup>	0.126 <sup>ns</sup>	-0.536**
$\delta^{13}\text{C}$	0.225 <sup>ns</sup>	0.397**	0.104 <sup>ns</sup>	0.174 <sup>ns</sup>	-	-	-	0.124 <sup>ns</sup>	0.118 <sup>ns</sup>	0.807**	-	-0.065 <sup>ns</sup>	0.126 <sup>ns</sup>
N	0.191 <sup>ns</sup>	-	0.153 <sup>ns</sup>	0.057 <sup>ns</sup>	0.402**	0.065 <sup>ns</sup>	0.251 <sup>ns</sup>	0.348**	0.305*	-0.302*	0.554**	0.140 <sup>ns</sup>	0.218 <sup>ns</sup>
		0.041 <sup>ns</sup>	0.454**	0.463**		0.289*	0.480**	0.356**			0.572**		
<b>Salinity 1 (10 dS m<sup>-1</sup>)</b>													
GY	-0.270*	-	0.168 <sup>ns</sup>	0.475***	0.298*	-	0.432**	0.376**	0.323*	-	-	0.269*	-0.304*
TGW	-	0.357**	0.081 <sup>ns</sup>	0.099 <sup>ns</sup>	0.009 <sup>ns</sup>	0.233 <sup>ns</sup>	0.358**	0.214 <sup>ns</sup>	0.121 <sup>ns</sup>	-	0.082 <sup>ns</sup>	0.115 <sup>ns</sup>	-0.603**
$\delta^{13}\text{C}$	0.353**	-0.276*	-	-	0.039 <sup>ns</sup>	0.003 <sup>ns</sup>	0.012 <sup>ns</sup>	-	0.003 <sup>ns</sup>	0.492***	0.236 <sup>ns</sup>	0.154 <sup>ns</sup>	0.154 <sup>ns</sup>
N	0.291*	0.193 <sup>ns</sup>	0.103 <sup>ns</sup>	0.169 <sup>ns</sup>	0.577***	-	0.780**	0.342**	0.704***	0.602**	0.204 <sup>ns</sup>	-0.039 <sup>ns</sup>	0.021 <sup>ns</sup>
	-	-0.256*	0.425**	0.653**		0.002 <sup>ns</sup>		0.560**		0.511***	0.113 <sup>ns</sup>		-0.279*
<b>Salinity 2 (15 dS m<sup>-1</sup>)</b>													
GY	0.022 <sup>ns</sup>	0.105 <sup>ns</sup>	0.363**	0.525***	0.200 <sup>ns</sup>	0.433**	0.278*	-	0.416**	-0.030 <sup>ns</sup>	0.451***	0.326*	0.063 <sup>ns</sup>
TGW	-	-0.258*	0.011 <sup>ns</sup>	0.145 <sup>ns</sup>	-0.160 <sup>ns</sup>	0.273*	0.011 <sup>ns</sup>	0.083 <sup>ns</sup>	0.027 <sup>ns</sup>	0.155 <sup>ns</sup>	0.440***	0.247 <sup>ns</sup>	-0.374**
$\delta^{13}\text{C}$	0.376**	0.157 <sup>ns</sup>	0.105 <sup>ns</sup>	0.223 <sup>ns</sup>	0.141 <sup>ns</sup>	0.394**	0.276*	0.337**	-	0.304*	0.505***	0.247 <sup>ns</sup>	0.089 <sup>ns</sup>
N	0.084 <sup>ns</sup>	0.450***	0.764***	0.810***	0.721***	0.741***	0.630***	0.419**	0.808***	0.207 <sup>ns</sup>	0.712***	0.355**	0.361**
	0.454***							0.213 <sup>ns</sup>					

K, potassium; Ca, calcium; Mg, magnesium; Mn, manganese; P, phosphorus; Fe, iron; Zn, zinc; Cu, copper; S, sulphur; Na, sodium; Rb, rubidium; Si, silicon and Sr, strontium.

dSm<sup>-1</sup> (Table 10). A negative correlation was found between TGW and both K and Ca under 10 and 15 dSm<sup>-1</sup>, whereas under control, TGW correlated negatively with Ca alone (Table 10). Nitrogen was correlated positively with K and Ca under 15 dSm<sup>-1</sup>, and negatively with Ca under 10 dSm<sup>-1</sup>. Mg was positively correlated with N (strongly) and GY (weakly), while no significant correlation was found between  $\delta^{13}\text{C}$  and Mg under all growing conditions combined (Fig. 3 and S4). Furthermore, Mg also correlated positively and strongly with N under control and both 10 and 15 dSm<sup>-1</sup>, while a correlation (positive and weaker) with GY was only found under 15 dSm<sup>-1</sup> (Table 10).

Regarding Mn, P and Fe, a strong and positive correlation was observed with N, whereas no correlation was found between GY,  $\delta^{13}\text{C}$  and TGW with these minerals (Fig. 3 and S4). Mn was correlated positively and strongly with N under control and both 10 and 15 dSm<sup>-1</sup>, while a positive correlation with this mineral and GY was found only under both salinity levels (Table 10). P was also strongly and positively correlated with N under control, 10 and 15 dSm<sup>-1</sup>, and a weak and positive correlation was also found between P and GY under 15 dSm<sup>-1</sup> (Table 10). Fe was correlated positively with GY and N under control conditions, while under 15 dSm<sup>-1</sup> a positive correlation was observed between Fe and GY, TGW,  $\delta^{13}\text{C}$  and N (strong in this last case), and no correlation was found under 10 dSm<sup>-1</sup> (Table 10). Likewise, under all growing conditions combined, Zn was correlated positively with N (strongly), GY, and TGW, while no significant correlation with  $\delta^{13}\text{C}$  was found (Fig. 3 and S4). Moreover, Zn was positively correlated with N (strongly) and GY under control, 10 and 15 dSm<sup>-1</sup>, while positive correlations of this mineral were only found with  $\delta^{13}\text{C}$  and TGW under 15 dSm<sup>-1</sup> and 10 dSm<sup>-1</sup>, respectively (Table 10). In the case of Cu, it was correlated negatively with  $\delta^{13}\text{C}$  and positively with N, GY and TGW under all growing conditions plotted together (Fig. 3 and S4). However, Cu was correlated positively with GY and N under control and 10 dSm<sup>-1</sup>,

while a negative correlation was found between Cu and  $\delta^{13}\text{C}$  under control, 10 dSm<sup>-1</sup> and 15 dSm<sup>-1</sup>, and with TGW under 15 dSm<sup>-1</sup> alone (Table 10). A strong and positive correlation was found between S and N (Fig. 3 and S4), and similarly S was also correlated positively with  $\delta^{13}\text{C}$  and negatively with TGW. At the same time, S was strongly and positively correlated with N under control and both salinities, and with GY (also positively) under 10 and 15 dSm<sup>-1</sup> (Table 10). However, no significant correlation was found between S and TGW under a given level of salinity, and a positive correlation was found with  $\delta^{13}\text{C}$  only under 15 dSm<sup>-1</sup> (Table 10).

The minerals Mo, Al and Ni were not correlated with GY,  $\delta^{13}\text{C}$ , TGW or N across growing conditions and seasons (Fig. 3 and S4). However, Rb was correlated positively with GY, SB, TGW and N and negatively with  $\delta^{13}\text{C}$  (Fig. 3 and S4). Additionally, Rb was correlated positively with GY and N under control and 15 dSm<sup>-1</sup>, and with TGW (positively) under 15 dSm<sup>-1</sup> alone (Table 10). However, a negative correlation was found between Rb and  $\delta^{13}\text{C}$  under control. Si also correlated positively with GY, SB and TGW when combining all growing conditions and seasons (Fig. 3 and S4). Under 10 and 15 dSm<sup>-1</sup>, Si was correlated positively but weakly with GY, but a positive correlation with N was only found under 15 dSm<sup>-1</sup> (Table 10). Regarding Sr, no significant correlation was found between Sr and GY,  $\delta^{13}\text{C}$  and N with all growing conditions combined (Fig. 3 and S4), while a negative correlation was found with TGW (Fig. 3 and S4). Similarly, Sr was correlated negatively with TGW under control, 10 dSm<sup>-1</sup> and 15 dSm<sup>-1</sup> (Table 10), negatively with GY under 10 dSm<sup>-1</sup> alone, and with N under both 10 dSm<sup>-1</sup> (negatively) and 15 dSm<sup>-1</sup> (positively). Ti was correlated positively but weakly with GY and SB under all growing conditions (Fig. 3 and S4), while no significant correlation was found under each growing condition separately. Leaf chlorophyll content (LC) was positively correlated with Zn, Cu, Rb, and Si (Fig. S4) and negatively with Na concentration. On the other hand,

$\delta^{15}\text{N}$  displayed negative correlations with Mg, Mn, Fe and Rb (Fig. S4).

### 3.7. Physiological basis of genotypic differences in GY and minerals

Since Na and  $\delta^{13}\text{C}$  of grains were the physiological traits best correlated with GY across genotypes, growing conditions and seasons (Fig. S4), a phenotypic correlation of these traits was investigated. For this purpose, the genotypic means across salinities and seasons and under each crop season separately were calculated for the 10 genotypes and the Pearson relationships assessed (Fig. 4 and S5). Both Na and  $\delta^{13}\text{C}$  were negatively correlated with GY. Further, PCA analysis was conducted for genotype differentiation (Fig. 5), analysing control and salinity data together, and analysing agronomic performance (Fig. 5A) as well as the accumulation of essential (Fig. 5B) and non-essential (Fig. 5C) minerals. The first PCA model (Fig. 5A), which included grain yield, shoot biomass, thousand grain weight, nitrogen concentration, leaf chlorophyll content,  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$ , explained approximately 69 % of the total genotypic variation (42 % for the first component and 27 % for the second). This model distinctly separated the genotypes, with “Hawrani” (the most productive genotype) and “ACSAD 357” (the least productive) positioned at opposite extremes. Genotypes with high to medium agronomic performance, such as “ACSAD 65”, “ACSAD 1229”, “ACSAD 1105”, and “SHAM 3”, were clustered together. Conversely, the less productive genotypes like “ACSAD 1187”, “ACSAD 1289”, “ACSAD 1107”, and “SHAM 3” were grouped together. The second PCA model (Fig. 5B), which focused on the accumulation of essential minerals, accounted for around 74 % of the total genotypic variation (60 % for the first component and 14 % for the second). In this analysis, the genotypes with higher nutrient concentration, comprising “Hawrani”, “ACSAD 1289”, “ACSAD 1105”, “ACSAD 1107”, “SHAM 3”, and “SHAM 5”, were clustered together. However, genotypes with lower nutrient levels, such as “ACSAD 65”, “ACSAD 357”, “ACSAD 1229”, and “ACSAD 1187”, formed distinct groups. The third PCA model (Fig. 5C), which included non-essential minerals, explained about 67 % of the genotypic variation (45 % for the first component and 22 % for the second). “ACSAD 65”, which had the lowest Na and Al concentration, was placed separately from the other genotypes. Meanwhile, “Hawrani”, “SHAM 5”, “ACSAD 1105”, and “ACSAD 1289” (genotypes with higher Al and Sr accumulation) were grouped together. Genotypes with lower accumulation of Al

and Sr, such as “ACSAD 357”, “SHAM 3”, “ACSAD 1229”, “ACSAD 1107”, and “ACSAD 1187”, were clustered together.

## 4. Discussion

### 4.1. Saline irrigation and durum wheat growth and yield

Salinity significantly decreased the grain yield of durum wheat genotypes, as well as biomass, thousand grain weight, plant height, and the number of spikes per plant. Thus, grain yield was negatively correlated with grain Na concentration when all growing conditions were combined (Fig. 3 and S4). This is consistent with Munns and Tester (2008), who reported that salinity negatively affects crop growth and yield due to salinity-induced water stress and sodium toxicity. Moreover, saline water irrigation has been shown to reduce the number of spikes (Frank et al., 1987) and grain weight (Abbas et al., 2013), which ultimately affects grain yield (Shahid et al., 2018; Sorour et al., 2019). Husain et al. (2003) reported that salinity at a level of  $15 \text{ dSm}^{-1}$  caused a reduction in durum wheat grain yield by approximately 90 %. This finding aligns with the general agreement in the literature that high salinity levels severely harm wheat production. In contrast, while our study observed a mean reduction of approximately 40 % ( $10 \text{ dSm}^{-1}$ ) and 62 % ( $15 \text{ dSm}^{-1}$ ), a substantial genotypic variability in tolerance to severe salinity existed. Additionally, we found that the decrease in GY in our study is more likely due to the decrease in TGW than the number of spikes per plant, because no difference was observed in the number of spikes per plant between the control and  $10 \text{ dSm}^{-1}$ , and the correlation between the GY and the TGW ( $r = 0.62$ ;  $p < 0.001$ ) was stronger than the correlation between GY and the number of spikes per plant ( $r = 0.20$ ;  $p < 0.01$ ). The path analysis, which links the effect of Na on GY and biomass through TGW (Fig. 2), rather than through spikes per plant (data not shown), provides further support for the conclusions above. Considering the high growing temperatures, and the fact that all three of the treatments received fresh water during the first month of cultivation, the number of reproductive tillers per plant and their maximum plant height were already determined in part before the salinity treatments started. Contrastingly, grain formation (and particularly grain filling) occurred when plants were already subjected to different saline conditions, therefore ensuring a greater effect on grain weight from the

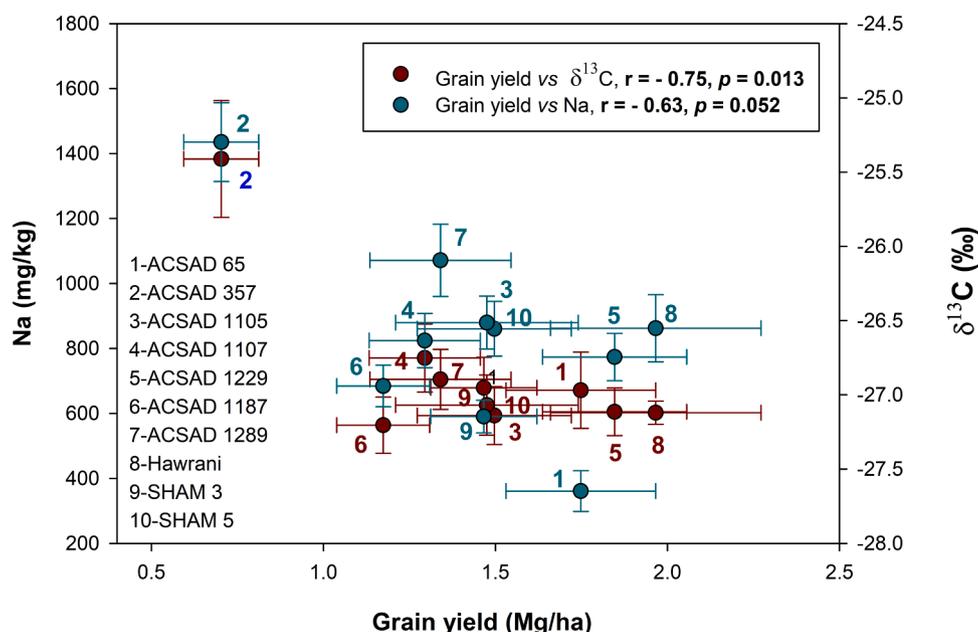
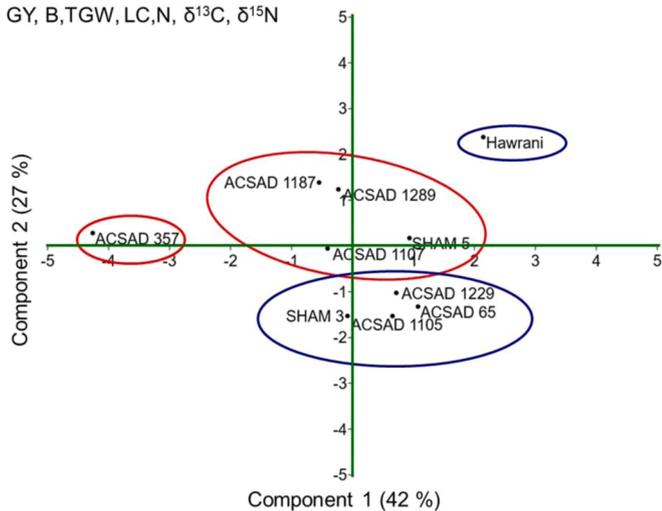
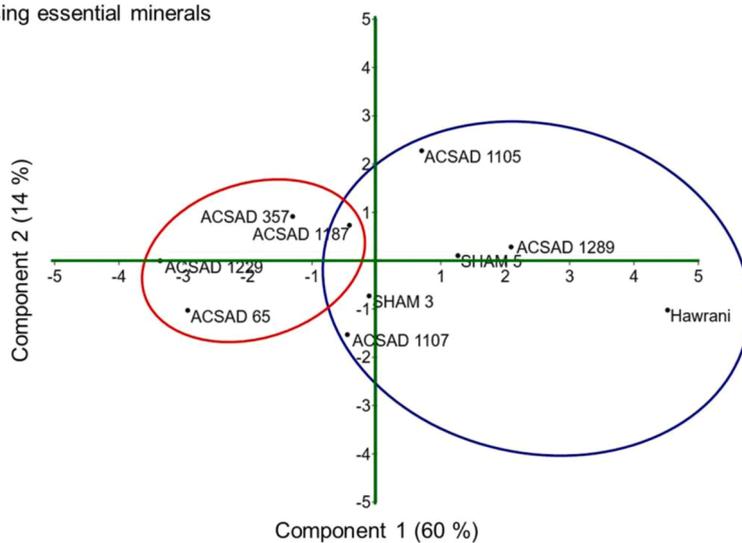


Fig. 4. The relationship of the grain yield with the sodium content (Na) (left y-axis) and the carbon isotope composition ( $\delta^{13}\text{C}$ ) (right y-axis) across the ten genotypes. For each genotype, the value plotted is the mean  $\pm$  SE of 18 values (corresponding to the three replicates per salinity condition, the three levels of salinity and the two crop seasons).

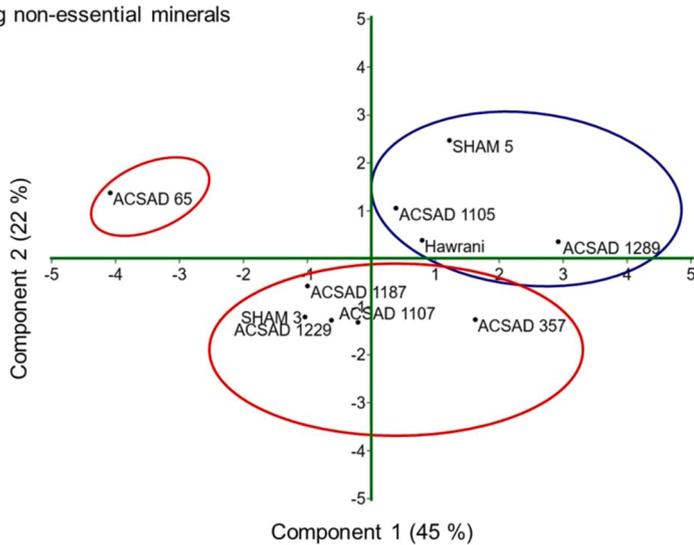
A- PCA using GY, B, TGW, LC, N,  $\delta^{13}C$ ,  $\delta^{15}N$



B- PCA using essential minerals



C- PCA using non-essential minerals



(caption on next page)

**Fig. 5.** Principal component analysis (PCA) for genotype differentiation combining all growing conditions (Control, Salinity 1 and Salinity 2). Parameters included are: (A) grain yield, shoot biomass, thousand grain weight, nitrogen concentration, leaf chlorophyll content, and the carbon and nitrogen isotope compositions; (B) the grain concentrations of essential minerals (K, potassium; Ca, calcium; Mg, magnesium; P, phosphorus; Fe, Iron; Mn, manganese; Zn, zinc; Cu, copper; S, sulphur); and (C) the grain concentrations of non-essential minerals (Na, sodium; Si, silicon; Mo, molybdenum; Al, aluminium; Rb, rubidium; Ti, titanium; Sr, strontium, Ni, nickel). Data for each genotype are the mean of 6 measurements (three replicates per salinity condition and 2 crop seasons). The blue circles indicate genotypes with high performance, while the red ones represent genotypes with low performance.

treatment than plant height or the number of spikes per plant. In this context, [Javed et al. \(2003\)](#) reported that salinity effects were most pronounced on yield components undergoing development during salt stress. Moreover, the effect of salinity is progressive in the sense that over the short term, irrigation with low quality water may palliate the water stress induced by the high evapotranspiration due to heat and arid conditions. [Akram et al. \(2002\)](#) and [Kamkar et al. \(2004\)](#) also noted that salinity primarily reduces grain yield through a severe reduction in grain weight. In the present work, shoot biomass decreased by 58 % under 10 dSm<sup>-1</sup>, aligning with the approximately 50 % decreases reported in previous studies at similar salinity levels ([Ayers, Westcott, 1989](#); [Yousfi et al., 2009](#)).

The seasonal effect was significant for most agronomic traits, regardless of the saline irrigation conditions. Specifically, grain yield, total aerial biomass, and thousand grain weight (TGW) were lower in the first season compared to the second, while plant height was higher in the first season. Spikes followed a similar trend, although the differences were not statistically significant. This pattern suggests that during the first season the crop suffered a stress, independent of the salinity conditions, during the later stages of the crop cycle. Repeated heat stress events, with temperatures reaching nearly 40°C around anthesis and early grain filling in the first season ([Fig. 1](#) and [S1](#)), may have been the cause ([Wardlaw et al., 2002](#); [Barnabás et al., 2008](#)).

#### 4.2. Salinity and genotypically mediated physiological effects on grain yield

Grain yield was negatively correlated with grain Na concentration, not only when all growing conditions were combined ([Fig. 3](#) and [S4](#)) or under given levels of salinity ([Table 10](#)), but also across genotypic means ([Fig. 4](#) and [S5](#)). This agrees again with [Munns and Tester \(2008\)](#), who reported a negative relationship between sodium concentration in leaves and grain yield across durum wheat genotypes. In our results, a negative correlation was observed between Na concentration in grains and GY. These negative correlations, and particularly the phenotypic correlation ([Fig. 4](#)), indicate that Na accumulation affects durum wheat genotypes differently, with genotypes exhibiting lower levels of Na in grains being the most productive. Na concentration in grains could serve as a useful phenotypic selection trait when breeding durum wheat for better adaptation to saline irrigation, particularly because it can be analysed in stored samples, alongside other routine analyses.

Leaf chlorophyll content on an area basis, as measured with the chlorophyll meter, also decreased under salinity but in a minor (10 dSm<sup>-1</sup>) to a moderate (15 dSm<sup>-1</sup>) level. The low decrease in leaf chlorophyll content due to salt toxicity in our study may be attributed to increased leaf thickness or mesophyll cell packing as a response to water stress, leading to constant chlorophyll build-up ([Munns et al., 2010](#); [Yousfi et al., 2009](#)). Nevertheless, leaf chlorophyll content in this study was positively correlated with grain yield, biomass, and TGW, but in a weaker manner than the corresponding negative correlations of Na concentration and  $\delta^{13}\text{C}$  with the same traits ([Fig. S4](#)). While leaf chlorophyll content has been proposed as a screening criterion for wheat breeding under salinity conditions ([Munns and James, 2003](#)), in the current study the phenotypic relationship across the ten genotypes for the LC against GY was not significant ( $r = -0.03$ ;  $p = 0.92$ ).

Salinity increased the  $\delta^{13}\text{C}$  of durum wheat grain, consistent with previous results reported in durum wheat and barley ([Chamekh et al., 2017](#); [Isia et al., 1998](#); [Condon et al., 2002](#); [Araus et al., 2003](#); [Yousfi](#)

[et al., 2009, 2010](#)). The increase in the  $\delta^{13}\text{C}$  of grain may be due to a decrease in stomatal conductance, reflecting the induction of water stress (due to the effect of salt stress). Moreover, a high genotypic variability in  $\delta^{13}\text{C}$  was found in our study ([Table 4](#)). In this regard, genotypic variability in  $\delta^{13}\text{C}$  has been previously reported in durum wheat leaves ([Yousfi et al., 2012](#)) and grains ([Chamekh et al., 2017](#)) as a response to salinity. The range of grain  $\delta^{13}\text{C}$  values in our study is comparable to those of durum wheat subjected to saline irrigation in other locations ([Chamekh et al., 2017](#)). The negative relationship between grain  $\delta^{13}\text{C}$  and grain yield under all growing conditions combined ([Fig. S4](#)) has been extensively reported for combined differences in water availability ([Araus et al., 2013](#); [Elazab et al., 2015](#)) as well as combined differences in salinity ([Chamekh et al., 2016](#); [Borzouei et al., 2020](#)). Such a relationship from combining different saline conditions is consistent with the main effects of salinity, which are decreases in GY through water stress in the short term and then decreases due to stomatal limitation of photosynthesis ([Munns et al., 2006](#); [Chaves et al., 2009](#)). Thus, the path analysis in our study further supports the idea that the effects of Na on GY and biomass are mediated through changes in stomatal conductance, which were assessed in a time-integrated manner using the  $\delta^{13}\text{C}$  of grains ([Fig. 2](#)). It is likely that the other effect of salt-induced water stress is a decrease in cell expansion and then plant growth, which may subsequently affect canopy photosynthesis ([Munns et al., 2006](#)). Season did not have a significant effect on the  $\delta^{13}\text{C}$  of grains, despite the fact that GY, biomass, and TGW were lower in the first season under all salinity conditions. The lack of differences may be attributed to the increased contribution of pre-anthesis assimilates to grain filling under heat stress ([Barnabás et al., 2008](#)).

In the present work,  $\delta^{13}\text{C}$  was also negatively correlated with grain yield, either under control conditions ( $r = -0.51$ ;  $p < 0.001$ ) or under 10 dSm<sup>-1</sup> salinity ( $r = -0.33$ ;  $p < 0.010$ ), which agrees with previous results under irrigation with fresh water ([Araus et al., 2003, 2013](#)) and saline water ([Chamekh et al., 2017](#)). These negative relationships support the notion that genotypic differences in yield under saline conditions are related to the ability to avoid water stress effects, keeping stomata more open and therefore contributing to higher rates of photosynthesis and lower canopy temperatures ([Cabrera-Bosquet et al., 2011](#); [Yousfi et al., 2009, 2010, 2012](#)), resulting in an increased yield. Moreover, the phenotypic relationship between  $\delta^{13}\text{C}$  and GY using the mean values (across salinities, replicates and seasons) for the ten genotypes was also negative ( $r = -0.75$ ,  $p = 0.013$ ). Therefore, tolerant genotypes are able to sustain higher stomatal conductance and/or photosynthetic capacity over the long term under salt stress and exhibit lower  $\delta^{13}\text{C}$ . In addition, the present study showed a positive correlation between  $\delta^{13}\text{C}$  and Na concentration under all growing conditions combined, as well as under each level of salinity ([Figs. 2, 3, S4](#) and [Table 10](#)). This suggested that the ability to maintain more open stomata is also related to lower accumulation of sodium in durum wheat, which agrees with earlier work where both  $\delta^{13}\text{C}$  and Na concentration have been analysed in leaves rather than mature grains ([Rivelli et al., 2002](#); [Yousfi et al., 2010, 2012](#)).

#### 4.3. Salinity and genotypically mediated physiological effects on nitrogen concentration

There was no correlation between TGW and grain N concentration across genotypes and treatments ([Fig. S4](#)). However, a high level of salinity (15 dSm<sup>-1</sup>) tended to increase N concentration, although this

was not statistically significant (Table 4). Previous studies have reported that salinity increases grain protein concentration in durum wheat (Francois et al., 1986) and other wheat species (Abdehpour and Ehsanzadeh, 2024). In contrast, other research suggests that the presence of Na in soil interferes with nitrogen absorption, leading to lower protein content in wheat grains due to nutritional imbalance (EL Sabagh et al., 2021). In our study, path analysis revealed a direct negative effect of Na on grain N concentration, likely due to ion imbalance. The positive effect of Na on N concentration was indirect, mediated through an increase in  $\delta^{13}\text{C}$  and reflecting water stress (Fig. 2). As a result of these opposing mechanisms, salinity had no clear effect on N concentration in grains.

The grain N concentration was positively correlated with GY under all growing conditions combined (Fig. S4), as well as under control conditions ( $r = 0.35$ ;  $p < 0.010$ ), and each of the two salinities ( $r = 0.48$   $p < 0.001$  under  $10 \text{ dSm}^{-1}$  and  $r = 0.487$ ;  $p < 0.001$  under  $15 \text{ dSm}^{-1}$ ). The path analysis in our study also supports a positive association between grain N concentration and grain yield (Fig. 2). Manure was the primary source of nitrogen available to the plants in the sandy soils of our trials, supplemented with application of chemical fertiliser after planting. In line with this, application of poultry manure (Arshad et al., 2024) or an increase in N fertilisation (Ahanger et al., 2019) or P-fertilisation (Bouras et al., 2023) improved the N uptake of wheat plants under saline conditions. Season had an impact on grain N concentration, with the more stressed first season exhibiting lower nitrogen concentration, despite having lower TGW compared to the second season. The negative effect of heat stress on N translocation from the leaves to the grains during grain filling has been documented previously (Barnabás et al., 2008; Ullah et al., 2022). In the absence of factors that abruptly stop grain filling, nitrogen accumulates in the grains throughout the grain filling period (Araus and Tapia, 1987), particularly during its initial phase (Martre et al., 2003).

Furthermore, no differences between salinity and control were found for grain  $\delta^{15}\text{N}$  in our study. Previous studies under controlled conditions and a nutrient solution as the only source of nitrogen have reported  $\delta^{15}\text{N}$  as being significantly decreased in response to increasing saline conditions (Yousfi et al., 2009, 2012, 2013, Chamekh et al., 2016). The lack in our study of any effect of salinity on  $\delta^{15}\text{N}$  may be due to the fact that plants were grown under high levels of nitrogen fertiliser. Under conditions of abundant nitrogen, plants incorporate both  $^{14}\text{N}$  and  $^{15}\text{N}$  more equally, leading to reduced isotopic fractionation against  $^{15}\text{N}$  (Handley and Raven, 1992). Furthermore, the grain  $\delta^{15}\text{N}$  values in our study were higher (around 7.5 ‰) than those obtained by Chamekh et al. (2016), who used only chemical fertiliser as the nitrogen source and determined grain  $\delta^{15}\text{N}$  values of around 4 ‰ in durum genotypes grown under salinity, while our findings correspond with increases in the  $\delta^{15}\text{N}$  of the grains following manuring (Serret et al., 2008). However, we also found a high genotypic difference in both the N and  $\delta^{15}\text{N}$  of grains, in accordance with previous reports from grains subjected to soil salinity under Mediterranean conditions (Chamekh et al., 2016). In this context, a negative correlation was found between N and  $\delta^{13}\text{C}$  under  $15 \text{ dSm}^{-1}$  ( $r = -0.31$ ;  $p < 0.010$ ), indicating that under salinity, tolerant genotypes exhibited lower  $\delta^{13}\text{C}$  (i.e. higher stomatal conductance) and higher N uptake, in agreement with Yousfi et al. (2012). Nevertheless, a positive correlation was found between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  under  $12 \text{ dSm}^{-1}$  ( $r = 0.44$ ;  $p < 0.001$ ), demonstrating that the reduction in stomatal conductance (reflected in higher  $\delta^{13}\text{C}$ ) in the susceptible genotypes was not related to  $^{15}\text{N}$  discrimination. In contrast to our study, different authors have reported that reduced stomatal conductance under salinity, due to either salinity (Yousfi et al., 2012) or water stress (Farquhar et al., 1980, Smart and Bloom, 2001), should lead to a reduction in the loss of ammonia and nitrous oxide, therefore decreasing  $\delta^{15}\text{N}$  in the plant. The results of the current study revealed that different genotypes have different mechanism for N assimilation and N isotopic fractionation.

#### 4.4. Salinity and genotypically mediated effects on mineral concentration

Saline water irrigation significantly increased the Na concentration in grains (Table 8). These results align with Chamekh et al. (2016), who found similar increases in durum wheat grains. In the same way, Bouras et al. (2023) and Yousfi et al. (2010), (2012) reported an increase in leaf Na concentration in bread and durum wheat under salinity stress. Francois et al. (1986) noted that salinity elevated the leaf Na concentration. Indeed, in the present work, exposure to  $10 \text{ dSm}^{-1}$  salinity increased the grain concentrations of K, Ca, Mg, Mn, and Zn, but no difference was observed in Fe and P between control and saline conditions.

The results of our study showed that grain concentrations for different elements (K, Ca, Mg, P, Cu, Fe and S) are comparable to those obtained by Caldelas et al. (2023) in bread wheat grown under Mediterranean rainfed conditions and different N fertiliser applications. However, regardless of the saline conditions, the concentration of Zn in our study was about 80 mg/kg, which is far higher than the values reported by Mazhar et al. (2023) in bread wheat grains under saline conditions and with and without application of ZnO nanoparticles ( $45.7 \text{ mg kg}^{-1}$  and  $18.5 \text{ mg kg}^{-1}$ , respectively). Mazhar et al. (2023) reported that a Zn concentration of more than 50 mg/kg in cereal grains is generally desirable to achieve an optimal beneficial impact on human health and combat malnutrition. Season affected the concentration of all minerals studied in the grains. Except for K and Ca, which slightly decreased, the concentrations of all other minerals increased during the second season, regardless of the increase in TGW. This pattern was similar to that of grain nitrogen concentration, suggesting a common underlying mechanism (Waters et al., 2009; Hammer et al., 2017). Heat stress thus appears to influence the mineral nutrition of wheat grains, generally leading to a decline in the concentration of micronutrients, particularly Fe, Zn, and Mn (Guzmán et al., 2016; Wang and Liu, 2021). Among the non-essential minerals, Rb followed a pattern similar to nitrogen, increasing in the second season, while Na and Mo decreased, with no differences observed for the other minerals.

Genotypic variability existed in terms of mineral accumulation in grains as a consequence of salinity but such genotypic differences were not primarily driven by differences in grain weight caused by salinity. In fact, the only minerals exhibiting a negative relationship with TGW were Na and, to a much lesser extent, S, Sr, K Ca and Cu, when combining all growing conditions (Fig. 3 and S4) and within given salinity levels (Table 10). In this sense, Caldelas et al. (2023) reported a negative correlation between TGW and Ca, Cu and S concentrations in bread wheat. These authors also reported that none of the highest-yielding varieties in their study stood out for their highly nutritious grains, whereas varieties with lower yields showed the highest mineral concentrations. Indeed, Karaköy et al. (2012) reported a mineral dilution effect in plants that produce larger seeds. However, similar to TGW, GY in our study only correlated negatively with Na and, to lower degree, Sr, K and Ca under control and  $10 \text{ dSm}^{-1}$  conditions, while GY displayed positive correlations with Cu, Mg, and even Zn, Fe and S under all growing condition combined, as well as under control and given levels of salinity (Fig. 3, Table 10). We suggest that this positive relationship is due to the high availability of these minerals in the soil, resulting from the fertilisation practices used, specifically the application of both organic manure and the chemical fertiliser enriched in Mg, S, Fe and Zn (Table S1). Accordingly, Shahid et al. (2016) reported that the application of manure significantly increased the concentrations of Fe, Zn and Cu in soil. Moreover, the specific NKP chemical fertiliser used in the study was especially fortified with different micronutrients (Table S1).

Additionally, this study revealed that there was no significant variation between control and salinity conditions in the quantities of other non-essential minerals or even those considered as pollutants (Si, Mo, Al, Ti, Sr and Ni) (Table 8). Therefore, the saline irrigation conditions in this study did not increase the level of potential pollutants in durum wheat grains. Furthermore, only Rb decreased significantly under salinity, and

in fact, grain yield, shoot biomass and the TGW displayed a positive correlation with Rb concentration under all growing conditions combined and within given salinity levels (Fig. 3, S4 and Table 10). Moreover, genotypes with higher yield, biomass and TGW possessed higher levels of Rb. In addition, Rb displayed a negative correlation with Na, suggesting that a stronger agronomic performance is related to a greater accumulation of Rb in durum wheat grains. Indeed, El-Sheikh et al. (1967) reported a beneficial effect of Rubidium that suggests its essentiality in ensuring maximal growth. The benefits of Rb may be mediated through increases in the activity of some enzyme systems as a result of an adequate cation balance between K and Rb (Page and Di Cera, 2006).

#### 4.5. Carbon and nitrogen metabolism linked to mineral concentration

Understanding the link between photosynthetic carbon and nitrogen metabolism and mineral concentration across different irrigation salinities provides a valuable insight into the environmental mechanisms and genotypic variability affecting mineral concentration in grains. This study examined the relationships of the grain concentration of different minerals to  $\delta^{13}\text{C}$ , which is an indicator of the effect of saline-induced water stress on photosynthetic carbon metabolism (Farquhar and Richards, 1984), while the total N concentration and  $\delta^{15}\text{N}$  of grains behave as an indicator of the response of nitrogen metabolism to salinity (Yousfi et al., 2012). Thus,  $\delta^{13}\text{C}$  correlated positively with K and Ca and negatively with Cu and Rb. Similarly, Caldelas et al. (2023) reported for bread wheat that grain  $\delta^{13}\text{C}$  correlated positively with K, and negatively with Mg, Mn, and P. These authors concluded that the negative correlation of  $\delta^{13}\text{C}$  with these minerals suggests that higher transpiration (i.e. lower  $\delta^{13}\text{C}$ ) contributes to a greater accumulation of minerals through bulk flow. In the case of K and Ca, the positive correlation with  $\delta^{13}\text{C}$  indicated that salinity stress increased their grain concentrations. Nevertheless, the increase is not mediated through a concentration effect due to smaller grains. Although TGW was negatively correlated with K and Ca, the strength of the correlation was marginal. Tareq et al. (2011) found moderate (between 10 % and 20 %) increases in K, and Ca concentrations in bread wheat grains in response to salinity. However, in another study with bread wheat (Nadeem et al., 2020), salinity decreased the uptake of K and Ca, along with that of other minerals (P, Fe, Mg and Zn) in grains. In fact, in our study the highest salinity (15 dSm<sup>-1</sup>) reversed the increase in many of the minerals. Rose et al. (2015) reported for bread wheat under field conditions that the grain concentrations of Ca and K increased in response to water stress, while other minerals (Mg, Mn, P, Fe, Cu and Zn) were unaffected by drought stress. These authors concluded that differences among nutrients in phloem mobility, post-anthesis uptake and grain loading patterns do not fully explain their differential responses to drought stress in terms of grain nutrient concentration (Rose et al., 2015). In summary, our results demonstrated a dual response to salinity for most of the minerals analysed. Concentrations increased at intermediate salinity levels, likely due to a water-stress effect, while concentrations tended to decrease at the highest salinity tested, probably due to nutrient imbalances associated with Na (EL Sabagh et al., 2021).

The total nitrogen concentration in grains exhibited positive correlations with Mn, Mg, P, S, Zn, Fe, Cu, and Rb (Fig. 3, Table 10), under all growing conditions and both control and salinity conditions. These results suggest a linkage between nitrogen assimilation and mineral accumulation under the growing conditions and fertilisation settings of this study. Likewise, De Santis et al. (2021) highlighted the essential role of micronutrients in plant nutrition, emphasising their structural involvement in enzyme activity and nitrogen metabolism (Shah et al., 2017). Clarkson et al. (1989) indicated that sulphur is associated with N uptake, and it is a key component of enzyme activities involved in N metabolism (Scherer, 2008). Hu and Chu (2020) added that N metabolism and phosphorus uptake interacts together, creating a nutritional balance and this interaction is important for improving plant nutrient levels. In this sense, Fatholahi et al. (2022) have reported a positive

association between N availability and P concentration in grains.

Concerning Zn, Shin et al. (2017) reported that numerous transcription factors act as essential regulators of the plant N response, among which zinc proteins are included. Moreover, Iqbal et al. (2018) reported that Cu, as a micronutrient, had a role in reducing the harmful impacts of salinity on plants through an increase in the level of amino acids under salinity. Therefore, the strong correlation between nitrogen and nutrient concentration observed in our study may be attributed to enzyme activities linked to nitrogen metabolism and fertilisation practices in arid regions. Lopez-Bellido et al. (2004) reported that genotypic variability in grain N concentration may be affected not only by physiological traits but also by N supply in the soil. Moreover, Waters et al. (2009) reported that the translocation of Fe, Zn, and N compounds from vegetative tissues to grain in bread wheat shares common mechanisms. Other studies on bread wheat have found parallel patterns of accumulation for N, S, and Fe, but opposite patterns for K accumulation. These results suggest that N accumulation is associated with increased demands for other nutrients, both in terms of total amounts and tissue concentrations (Hamnér et al., 2017). Therefore, further research on the relationship between mineral concentration and nitrogen metabolism could contribute to the phenotyping of durum wheat genotypes growing under arid regions with saline water irrigation and N fertilisation. Hence, improvements to salinity tolerance will require a good knowledge of the physiological mechanisms linked to plant responses to salt stress (Khatabi et al., 2022).

#### 4.6. Durum wheat adaptation to UAE conditions: grain yield and mineral concentration

A significant genotypic difference was found in the GY and TGW in our study, in agreement with previous studies that have found large genotypic effects on biomass (Yousfi et al., 2009, 2010, 2012) and yield (Chamekh et al., 2017; Pastuszak et al., 2022; Royo and Abió, 2003). However, the agronomic performance of these genotypes in our study only matched partially with their classification (Table 1) based on agronomic performance under the stresses (essentially drought) prevailing in the south and east of the Mediterranean basin (Almeselmani et al., 2011, 2012; Ali Saleh, 2017). It is worth mentioning that apart from desert reclamation areas, the growing conditions in the Mediterranean basin are quite different from those of our study. In the Mediterranean basin, durum wheat is a winter-sown crop, usually grown under rainfed conditions and frequently subjected to moderate chemical fertilisation as the only source of external nutrients, and with drought stress and heat episodes followed by salinity as the main abiotic stressors. By contrast, the growing conditions in the UAE only allow wheat cultivation under irrigation with low water quality (i.e. brackish), with crops exposed to high temperatures, and a need for organic amendments. This may explain the differences in behaviour. In this study, “ACSAD 357” and “ACSAD 1289”, which were identified as genotypes susceptible to drought under the growing conditions specific to Syria, were also the two of the most saline susceptible genotypes under UAE growing conditions (Fig. S2). Moreover, Hawrani (a local Syrian variety), characterised as tolerant to drought stress, and “ACSAD 65”, characterised as moderately susceptible to drought stress (Table 1), showed the highest grain yield under saline irrigation conditions at ICBA (Fig. S2). This result confirms the tolerance of these two latter varieties to salinity and their adaptation to the growing conditions of the UAE. Moreover, “ACSAD 1229”, which was characterised as drought stress tolerant under Syrian growing conditions (Table 1), also exhibited better grain yield under salinity than “ACSAD 1105”, “ACSAD 1107”, “SHAM 3” and “SHAM 5” (also described as drought tolerant varieties). In fact, “ACSAD 1107” and “ACSAD 1187”, both considered as drought tolerant cultivars, even performed poorly under the control conditions of our study, indicating their non-adaptation to the growing conditions of the UAE.

Additionally, grain yield was positively correlated with TGW,

indicating that genotypes maintaining better grain filling despite the heat prevalent between mid-February and the end of March, were generally among the best performing in terms of GY. However, it is worth mentioning that “Hawrani”, a landrace with the highest grain yield, exhibited the lowest TGW (Table 3), but in this case the number of grains per spike may be a contributing factor. Indeed, Jaradat, (2006) described “Hawrani” as possessing dense spikes, high numbers of kernels per spike, and round kernel shape, resulting in low TGW values. The high number of grains per spike and the low TGW of wheat lines derived from “Hawrani” is considered a strategy for increasing grain yield under stressed growing conditions (Aberkane et al., 2021). Additionally, our study demonstrated that “ACSAD 65”, which is one of the best genotypes in terms of grain yield, had the lowest Na concentration (Fig. S2), while genotypes with lower grain yield (e.g. “ACSAD 1289” and “ACSAD 357”) exhibited higher Na concentrations. In this context, Saddiq et al. (2021) found that bread wheat genotypes with low Na had higher grain yield. However, the exception in our study was “Hawrani”, which despite possessing a medium Na concentration under control and salinity, had a better grain yield than genotypes with similar or lower Na concentrations such as “ACSAD 1187”. This finding confirms the high tolerance of “Hawrani” to salt stress alongside its tolerance to the major abiotic stress conditions of the Mediterranean. In this regard, Al-Sayaydeh et al. (2023) reported that “Hawrani” is recognised for its excellent drought tolerance and high stability in eastern Mediterranean environments. It is likely that the relatively low TGW of “Hawrani” may be correlated with the high Na concentration of grains. In summary, “Hawrani”, followed by “ACSAD 1229” and “ACSAD 65”, demonstrated superior performance (grain yield) under saline conditions, making them promising candidates as a parental lines for the deserts of the Arabian Peninsula and other desert reclamation areas.

Additionally, our findings showed significant genotypic differences in  $\delta^{13}\text{C}$ , with more productive genotypes displaying lower  $\delta^{13}\text{C}$  values (Fig. 4). In this sense, a negative correlation was found between GY and  $\delta^{13}\text{C}$  under control and 10 dSm<sup>-1</sup>. Furthermore, “Hawrani” exhibited a lower increase in  $\delta^{13}\text{C}$  in response to salinity than the other genotypes (Fig. S2D). These results highlight the adaptation of this variety to salinity, possibly through the maintenance of stomatal conductance under saline conditions. Moreover, the landrace variety “Hawrani” displayed not only the highest yield but also had among the highest N values, while “ACSAD 357”, which was the most saline-susceptible genotype in this study, had the lowest yield and the lowest nitrogen concentration.

Our study showed a high genotypic difference in all minerals studied, except for Ti and Si. Genotypes with poor productivity (“ACSAD 1289” and “ACSAD 1105”) showed high concentrations of essential nutrients (Figs. S2 and S3). Conversely, genotypes with high yield (“ACSAD 1229” and “ACSAD 65”) had the lowest concentrations of most essential nutrients, indicating their lower grain quality. Indeed, Caldelas et al. (2023) reported that none of the highest-yielding wheat varieties stood out as having highly nutritious grains, while wheat varieties with the lowest yields had the highest mineral concentrations. Thus, susceptible genotypes in terms of production were better in terms of quality. The PCA analysis confirmed these results, as genotypes that clustered into high yield and poor production were not the same genotypes when we used mineral concentration as a criterion (Fig. 5A and B). However, an interesting result of this study was the behaviour of the “Hawrani” landrace. “Hawrani” is considered a valuable genetic source when breeding for the conditions of the Middle East (Jaradat, 1991; Pecetti et al., 1992). It showed a higher yield under both control and salinity and also exhibited huge concentrations of most of the essential nutrients under control and saline conditions, including the highest K concentration. Certainly, the selective uptake of K over Na is considered one of the key physiological mechanisms contributing to salt tolerance in many plant species (Gorham et al., 1987; Ashraf and Khanum, 1997; Noble and Rogers, 1992). In addition, “ACSAD 1105” (with poor productivity) showed the highest level of Zn and Fe under salinity, with these two

minerals being considered as a marker of human nutritional quality (De Santis et al., 2021). Notably, “Hawrani” exhibited high levels of Al (Table 9), but the nutrient uptake of this genotype was not affected by salinity. It has been reported that Al can be beneficial to plants by stimulating growth and mitigating biotic and abiotic stresses (Ofae et al., 2022). Nevertheless, Al is also recognised as a significant limiting factor that restricts plant growth and productivity in acidic soils (Ofae et al., 2022), although this is probably not the case for the sandy, moderately alkaline soils of ICBA (Gill et al., 2020). Therefore, this study emphasised the high genetic potential of “Hawrani” in terms of yield and grain quality under arid areas subjected to saline irrigation. In addition, we underscored that the high accumulation of Na by some genotypes (“ACSAD 1289”, “ACSAD 1105”) was accompanied by a low yield, even though the capacity of essential nutrient uptake was not affected.

## 5. Conclusions

Saline irrigation significantly decreased grain yield in durum wheat, mainly due to reduced grain weight and, to a lesser extent, fewer spikes per plant. Salinity also impacted the grain concentrations of nitrogen and most minerals, although these changes were mostly unrelated to grain weight. For the majority of minerals, the concentration changes followed a dual pattern, initially increasing then decreasing as salinity rose. Exceptions included Na, which increased significantly, and Rb, which decreased with rising salinity. Seasonal effects were significant for grain yield, grain weight, nitrogen, and the accumulation of certain minerals, which was likely due to heat stress during grain filling. Genotypic effects were highly significant for yield, agronomic components, nitrogen, and mineral concentrations. However, some genotypes performed differently under saline irrigation in the UAE compared to their classification as tolerant or susceptible in the Mediterranean. Nevertheless, the genotypic performance determined in this study aligned with the physiological mechanisms typically associated with salinity tolerance. The best-performing genotypes maintained better water status and greater stomatal conductance (as inferred by a lower  $\delta^{13}\text{C}$ ), and lower Na accumulation in grains, thus reducing leaf senescence. In terms of grain quality, the highest-yielding genotypes generally had lower grain nitrogen and mineral concentrations, except for “Hawrani,” which had high yield and mineral content despite modest grain weight. This study offers insights for improving durum wheat cultivation in the arid conditions of the Arabian Peninsula. Future research should explore the impact of saline irrigation on additional grain quality traits and their interactions with yield. The long-term objective of this work is to establish agronomic practices and breeding strategies that optimize both durum wheat yield and grain quality in regions with saline irrigation conditions.

## CRedit authorship contribution statement

**Rukhsar Ayesha:** Writing – original draft, Methodology, Data curation. **Kanbar Osama:** Visualization, Validation, Supervision, Methodology, Investigation, Conceptualization. **Mahmoudi Henda:** Visualization, Validation, Supervision, Methodology, Investigation, Conceptualization. **Yousfi Salima:** Writing – review & editing, Writing – original draft, Visualization, Software, Investigation, Data curation. **Araus José Luis:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Serret Maria Dolores:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Data curation, Conceptualization.

## Declaration of Competing Interest

As a person for correspondence, I declare in behalf of all the co-authors that there is not Conflict of Interest related with the results used

and the manuscript submitted to European Journal of Agronomy journal.

## Acknowledgements

This study was funded in part through the Project PID2022-138307OB-C21 (HolisticWheat), from Ministerio de Ciencia, Innovación y Universidades, Spain.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.eja.2025.127585](https://doi.org/10.1016/j.eja.2025.127585).

## Data Availability

Data will be made available on request.

## References

- Abbas, G., Saqib, M., Rafique, Q., Rahman, A.U., Akhtar, J., Haq, M.A.U., Nasim, M., 2013. Effect of salinity on grain yield and grain quality of wheat (*Triticum aestivum* L.). *Pak. J. Bot.* 50, 185–189.
- Abdehpour, Z., Ehsanzadeh, P., 2019. Concurrence of ionic homeostasis alteration and dry mass sustainment in emmer wheats exposed to saline water: implications for tackling irrigation water salinity. *Plant. Soil.* 440 (1–2), 427–441.
- Abdehpour, Z., Ehsanzadeh, P., 2024. Foliar-applied zinc is beneficial to growth, grain yield, and quality of standard and ancient wheats grown under saline and non-saline conditions. *Inter. J. Plant Prod.* 1–14.
- Aberkane, H., Amri, A., Belkadi, B., Filali-Maltouf, A., Kehel, Z., Tahir, I.S., Meheesi, S., Tsvelikas, A., 2021. Evaluation of durum wheat lines derived from interspecific crosses under drought and heat stress. *Crop. Sci.* 61, 119–136.
- Ahanger, M.A., Qin, C., Begum, N., Maodong, Q., Dong, X.X., El-Esawi, M., El-Sheikh, M. A., Alatar, A.A., Zhang, L., 2019. Nitrogen availability prevents oxidative effects of salinity on wheat growth and photosynthesis by up-regulating the antioxidants and osmolytes metabolism, and secondary metabolite accumulation. *Plant. Biol.* 19, 479.
- Akram, M., Hussain, M., Akhtar, S., Rasul, E., 2002. Impact of NaCl salinity on yield components of some wheat accessions/varieties. *Int. J. Agric. Biol.* 4 (1), 156–158.
- Ali Saleh, R., 2017. The Annual Technical Report 2017- The Arab Center for the Studies of Arid Zones and Dry Lands (ACSAD). [Library/ACSAD.ORG. \(https://acsad.org/en/library/\)](https://acsad.org/en/library/).
- Almeselmani, M., Abdullah, F., Hareri, F., Naaesan, M., Adel Ammar, M., Zuher Kanbar, O., Alrzak Saud, A., 2011. Effect of drought on different physiological characters and yield component in different varieties. *Syr. Durum Wheat. J. Agric. Sci.* 3 (3), 127–133.
- Almeselmani, M., Alrzak Saud, A., Hareiri, F., Al-Nasan, M., Adel Ammar, M., Zuher Kanbar, O., Al-Naseef, H., 2012. Physiological traits associated with drought tolerance of Syrian durum wheat varieties under rainfed condition. *Indian J. Plant Physiol.* 17 (2), 166–169.
- Al-Sayaydeh, R., Shtaya, M.J., Qubjab, T., Al-Rifae, M.K., Alabdallah, M.A., Migdadi, O., Gammoh, I.A., Al-Abdallat, A.M., 2023. Performance and stability analysis of selected durum wheat genotypes differing in their kernel characteristics. *Plants* 12, 2664.
- Araus, J.L., Cairns, J.E., 2014. Field high-throughput phenotyping: the new crop breeding frontier. *Plant. Sci.* 19 (1), 52–61.
- Araus, J.L., Tapia, L., 1987. Photosynthetic gas exchange characteristics of wheat flag leaf blades and sheaths during grain filling: the case of a spring crop grown under Mediterranean climate conditions. *Plant Physiol.* 85 (3), 667–673.
- 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.
- Araus, J.L., Cabrera-Bosquet, L., Serret, M.D., Bort, J., Nieto-Taladriz, M.T., 2013. Comparative performance of  $^{13}\text{C}$ ,  $^{18}\text{O}$  and  $^{15}\text{N}$  for phenotyping durum wheat adaptation to a dry land environment. *Funct. Plant. Biol.* 40, 595–608.
- Araus, J.L., Kefauver, S.C., Vergara Díaz, O., Gracia-Romero, A., Rezzouk, F.Z., Segarra, J., Buchailot, M.L., Chang-Espino, M., Vatter, T., Sanchez-Bragado, R., Fernandez-Gallego, J.A., Serret, M.D., Bort, J., 2022. Crop phenotyping in a context of global change: what to measure and how to do it. *J. Integr. Plant. Biol.* 64, 592–618.
- Arbuckle, J.L., 1997. *Amos Users' Guide*, v. 3. Small Waters Corporation, Chicago, IL, p. 6.
- Arshad, M.J., Khan, M.I., Ali, M.H., Farooq, Q., Hussain, M.I., Seleiman, M.F., Asghar, M. A., 2024. Enhanced wheat productivity in saline soil through the combined application of poultry manure and beneficial microbes. *Plant. Biol.* 24, 423.
- Ashraf, A., Khanum, A., 1997. Relationship between ion accumulation and growth in two-spring wheat lines differing in salt tolerance at different growth stages. *J. Agron. Crop Sci.* 178, 39–51.
- Ashraf, M., 2014. Stress-induced changes in wheat grain composition and quality. *Crit. Rev. Food Sci. Nutr.* 54 (12), 1576–1583.
- Awaad, H.A., Mansour, E., Akrami, M., Fath, H.E.S., Javadi, A.A., Negm, A., 2020. Availability and feasibility of water desalination as a non-conventional resource for agricultural irrigation in the MENA region. *Sustainability* 12 (18).
- Ayers, R.S., Westcott, D.W., 1989. Water quality for agriculture. In: *FAO Irrigation and Drainage Paper*, 29. FAO, Rome.
- Barnabás, B., Jäger, K., Fehér, A., 2008. The effect of drought and heat stress on reproductive processes in cereals. *Plant. Cell. Environ.* 31 (1), 11–38.
- Boggini, G., Namoune, H., Abecassis, J., Cuq, B., 2012. *Other Traditional Durum-Derived Products. : Durum Wheat (Second Ed. ) Book Chem. Technol. Am. Assoc. Cereal Chem. Int.* 177–199.
- Borzouei, A., Mousavi Shalmani, M.A., Eskandari, A., 2020. Effects of salt and nitrogen on physiological indices and carbon isotope discrimination of wheat cultivars in the northeast of Iran. *J. Integr. Agric.* 19 (3), 656–667.
- Bouras, E., Jarlan, L., Khabba, S., Er-Raki, S., Dezetter, A., Sghir, F., Trambly, Y., 2019. Assessing the impact of global climate changes on irrigated wheat yields and water requirements in a semi-arid environment of Morocco. *Sci. Rep.* 9, 19142.
- Bouras, H., Mamassi, A., Devkota, K.P., Choukr-Allah, R., Bouazzama, B., 2023. Integrated effect of saline water irrigation and phosphorus fertilization practices on wheat (*Triticum aestivum*) growth, productivity, nutrient content and soil properties under dryland farming. *Plant. Stress.* 10, 100295.
- Cabrera-Bosquet, L., Albrizio, R., Nogués, S., Araus, J.L., 2011. Dual  $\Delta^{13}\text{C}/\delta^{18}\text{O}$  response to water and nitrogen availability and its relationship with yield in field-grown durum wheat. *Plant. Cell. Environ.* 34, 418–433.
- Caldelas, C., Rezzouk, F.Z., Aparicio Gutiérrez, N., Díez-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.
- 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,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of landraces and improved durum wheat varieties. *Plant Sci.* 251, 44–53.
- Chamekh, Z., Karmous, C., Ayadi, S., Sahli, A., Belhaj Fraj, M., Yousfi, S., Rezgui, S., Ben Aissa, N., Serret, M.D., McCann, I., Trifa, Y., Amara, H., Araus, J.L., 2017. Comparative performance of  $\delta^{13}\text{C}$ , ion accumulation and agronomic parameters for phenotyping durum wheat genotypes under various irrigation water salinities. *Ann. Appl. Biol.* 170, 229–239.
- Chaves, M.M., Flexas, J.J., Pinheiro, C., 2009. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. *Ann. Bot.* 103, 551–560.
- 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.
- Condon, A.G., Richards, R.A., Rebetzke, G.T., Farquhar, G.D., 2002. Improving intrinsic water use efficiency and crop yield. *Crop. Sci.* 42, 128–133.
- 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.
- El Sabagh, A., Islam, M.S., Skalicky, M., Ali Raza, M., Singh, K., Anwar Hossain, M., Hossain, A., Mahboob, W., Iqbal, M.A., Ratnasekera, D., et al., 2021. Salinity stress in wheat (*Triticum aestivum* L.) in the changing climate: adaptation and management strategies. *Front. Agron.* 3, 661932.
- Elazab, A., Bort, J., Zhou, B., Serret, M.D., Nieto-Taladriz, M.T., Araus, J.L., 2015. The combined use of vegetation indices and stable isotopes to predict durum wheat grain yield under contrasting water conditions. *Agric. Water Manag.* 158, 196–208.
- 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 (7), 840–850.
- El-Sheikh, A.M., Ulrich, A., Broyer, T.C., 1967. Sodium and rubidium as possible nutrients for sugar beet plants. *Plant. Physiol.* 42, 1202–1208.
- Farquhar, G.D., Richards, R.A., 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Aust. J. Plant. Physiol.* 11, 539–552.
- Farquhar, G.D., Firth, P.M., Wetselaar, R., Weir, B., 1980. On the gaseous exchange of ammonia between leaves and the environment: measurements of the ammonia compensation point. *Plant. Physiol.* 66, 710–714.
- 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 (9), 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 wheat1. *Agron. J.* 78 (6), 1053–1058.
- Frank, A.B., Bauer, A., Black, A.I., 1987. Effects of air temperature and water stress on apex development in spring wheat. *Crop Sci.* 27, 113–116.
- Gill, S., Alshankiti, A., Shahid, S.A., Rodriguez, J.P., 2020. Amending soil health to improve productivity of alternate crops in marginal sandy soils of the UAE. *Emerging Research in Alternative Crops*. Publisher: Springer Nature, Switzerland AG, pp. 93–123.
- Gorham, J., Hardy, C., Wyn Jones, R.G., Joppa, L.R., Law, C.N., 1987. Chromosome location of a  $\text{K}^+/\text{Na}^+$  discrimination character in the D genome of wheat. *Theor. Appl. Genet.* 74, 584–588.
- Guzmán, C., Atrique, J.E., Mondal, S., Singh, R.P., Govindan, V., Morales-dorantes, A., Posadas-Romano, G., Crossa, J., Ammar, K., Peña, R.J., 2016. Response to drought and heat stress on wheat quality, with special emphasis on bread-making quality, in durum wheat. *Field Crop. Res.* 2016 (186), 157–165.

- 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.
- Handley, L.L., Raven, J.A., 1992. The use of natural abundance of nitrogen isotopes in plant physiology and ecology. *Plant. Cell. Environ.* 15 (9), 965–985.
- Hnilickova, H., Kraus, K., Vachova, P., Hnilicka, F., 2021. Salinity stress affects photosynthesis, malondialdehyde formation, and proline content in *Portulaca oleracea* L. *Plants* 10 (5).
- Horrliche, F.J., Benabdallah, S., 2020. Assessing aquifer water level and salinity for a managed artificial recharge site using reclaimed water. *Water* 12 (2), 341.
- Hu, B., Chu, C., 2020. Nitrogen–phosphorus interplay: old story with molecular tale. *New Phytol.* 225, 1455–1460.
- Hu, Y., Schmidhalter, U., 2005. Drought and salinity: a comparison of their effects on mineral nutrition of plants. *J. Plant. Nutr. Soil. Sci.* 168 (4), 541–549.
- Huang, F., Zhang, Y., Zhang, D., Chen, X., 2019. Environmental groundwater depth for groundwater-dependent terrestrial ecosystems in arid/semiarid regions. *Int. J. Environ. Res. Public Health* 16 (5), 763.
- Husain, S., Munns, R., Condon, A.G., 2003. Effect of sodium exclusion trait on chlorophyll retention and growth of durum wheat in saline soil. *Aust. J. Agric. Res.* 54, 589–597.
- Iqbal, M.N., Rasheed, R., Ashraf, M.Y., Ashraf, M.A., Hussain, I., 2018. Exogenously applied zinc and copper mitigate salinity effect in maize (*Zea mays* L.) by improving key physiological and biochemical attributes. *Environ. Sci. Pollut. Res.* 25, 23883–23896.
- Isla, R., Aragües, R., Royo, A., 1998. Validity of various physiological traits as screening criteria for salt tolerance in barley. *Field Crops Res.* 58, 97–107.
- Jaradat, A.A., 1991. Phenotypic divergence for morphological and yield-related traits among landrace genotypes of durum wheat in Jordan. *Euphytica* 52, 155–164.
- Jaradat, A.A., 2006. Phenotypic divergence in the meta-population of the Hourani durum wheat landrace. *J. Food Agric. Environ.* 4, 186–191.
- Javaid, T., Farooq, M.A., Akhtar, J., Saqib, Z.A., Anwar-ul-Haq, M., 2019. Silicon nutrition improves growth of salt-stressed wheat by modulating flows and partitioning of Na<sup>+</sup>, Cl<sup>-</sup> and mineral ions. *Plant. Physiol. Biochem.* 141, 291–299.
- Javed, I.U.H., Akhtar, S., Akram, M., Arfan, M., Shazia, Y., 2003. Differential yield responses of barley genotypes to NaCl salinity. *Int. J. Agric. Biol.* 5, 233–235.
- Kamkar, B., Kaf, M., Nassiri Mahallati, M., 2004. Determination of the most sensitive development period of wheat (*Triticum aestivum*) to salt stress to optimize saline water utilization. Proceedings of the International Crop Science Congress. 4th International Crop Science Congress September 2004 Brisbane, Australia.
- Karaköy, T., Erdem, H., Baloch, F.S., Toklu, F., Eker, S., Kilian, B., Özkan, H., 2012. Diversity of macro- and micronutrients in the seeds of lentil landraces. *Sci. World J.* 710412.
- 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 (2), 85–91.
- Khattabi, D., Sakar, E.H., Louahlia, S., 2022. Flag leaf tolerance study in Moroccan barley (*Hordeum vulgare* L.) varieties submitted to a severe salt stress. *Biointerface Res. Appl. Chem.* 12 (3), 2787–2799.
- Li, C.C., 1975. Path Analysis. A primer. The Boxwood Press, Pacific Grove, CA, USA.
- Lopez-Bellido, R., Shepherd, C., Barraclough, P., 2004. Predicting post-anthesis N requirements of bread wheat with a Minolta SPAD meter. *Eur. J. Agron.* 20, 313–320.
- Iqbal, N., Ashraf, H.Y., Javed, F., Iqbal, Z., Shah, G.H., 1998. Effect of salinity on germination and seedling growth of wheat (*Triticum aestivum* L.). *Pak. J. Biol. Sci.* 1 (3), 226–227.
- Majeed, A., Muhammad, Z., 2019. Salinity: a major agricultural problem-causes, impacts on crop productivity and management strategies. In: Hasanuzzaman, M., Hakeem, K., Nahar, K., Alharby, H. (Eds.), *Plant Abiotic Stress Tolerance*. Springer, Cham.
- Martínez-Moreno, F., Ammar, K., Solís, I., 2022. Global changes in cultivated area and breeding activities of durum wheat from 1800 to date: a historical review. *Agronomy* 12 (5), 1135. <https://doi.org/10.3390/agronomy12051135>.
- Martre, P., Porter, J.R., Jamieson, P.D., Tribou, E., 2003. Modeling grain nitrogen accumulation and protein composition to understand the sink/source regulations of nitrogen remobilization for wheat. *Plant. Physiol.* 133 (4), 1959–1967.
- Masoni, A., Ercoli, L., Mariotti, M., Arduini, L., 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.
- Mazhar, Z., Akhtar, J., Alhodaib, A., Naz, T., Zafar, M.I., Iqbal, M.M., Fatima, H., Naz, I., 2023. Efficacy of ZnO nanoparticles in Zn fortification and partitioning of wheat and rice grains under salt stress. *Sci. Rep.* 13.
- Moustafa, E.S.A., El-Sobky, E.S.E.A., Farag, H.I.A., Yasin, M.A.T., Attia, A., Rady, M.O.A., Awad, M.F., Mansour, E., 2021. Sowing date and genotype influence on yield and quality of dual-purpose barley in a salt-affected arid region. *Agronomy* 11, 717.
- Munns, R., James, R.A., 2003. Screening methods for salinity tolerance: a case study with tetraploid wheat. *Plant. Soil.* 253, 201–218.
- Munns, R., Tester, M., 2008. Mechanisms of salinity tolerance. *Annu. Rev. Plant Biol.* 59, 651–681.
- Munns, R., James, R.A., Lauchli, A., 2006. Approaches to increasing the salt tolerance of wheat and other cereals. *J. Exp. Bot.* 57, 1025–1043.
- Munns, R., James, R.A., Sirault, X.R.R., Furbank, R.T., Jones, H.G., 2010. New phenotyping methods for screening wheat and barley for beneficial responses to water deficit. *J. Exp. Bot.* 61, 3499–3507.
- Nadeem, H., Sohail, Y., Shakeel, N., Javed, M., Bano, H., Gul, H.D., Ullah Zafar, Z., Zaky Hassan, I.F., Ghaffar, A., Athar, H.R., Ajaj, R., 2022. Role of mineral nutrients, antioxidants, osmotic adjustment and PSII stability in salt tolerance of contrasting wheat genotypes. *Sci. Rep.* 12, 12677.
- Nadeem, M., Tariq, M.N., Amjad, M., Sajjad, M., Akram, M., Imran, M., Shariati, M.A., Gondal, T.A., Kenjiz, Kulikov, D., 2020. Salinity-induced changes in the nutritional quality of bread wheat (*Triticum aestivum* L.) genotypes. *Agrivita J. Agric. Sci.* 42, 1–12.
- Nakayama, R., Safi, M.T., Ahmadzai, W., Sato, K., Kawaura, K., 2022. Comparative transcriptome analysis of synthetic and common wheat in response to salt stress. *Sci. Rep.* 12 (1).
- Noble, C.L., Rogers, M.E., 1992. Arguments for the use of physiological criteria for improving the salt tolerance in crops. *Plant. Physiol.* 146, 99–107.
- Ofoe, R., Gunupuru, L.R., Wang-Pruski, G., Fofana, B., Thomas, R.H., Abbey, L., 2022. Seed priming with pyroligneous acid mitigates aluminium stress, and promotes tomato seed germination and seedling growth. *Plant. Stress.* 4, 100083.
- Page, M.J., Di Cera, E., 2006. Role of Na and in enzyme function. *Physiol. Rev.* 86, 1049–1092.
- Pastuszak, J., Dziurka, M., Hornyák, M., Szczerba, A., Kopéc, P., Plázek, A., 2022. Physiological and biochemical parameters of salinity resistance of three durum wheat genotypes. *Int. J. Mol. Sci.* 23, 8397.
- Pecetti, L., Damania, A.B., Kashour, G., 1992. Geographic variation for spike and grain characteristics in durum wheat germplasm adapted to dryland conditions. *Genet. Resour. Crop. Evol.* 39, 97–105.
- 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.
- Rivelli, A.R., James, R.A., Munns, R., Condon, A.G., 2002. Effects of salinity on water relations and growth of wheat genotypes with contrasting sodium uptake. *Funct. Plant. Biol.* 29, 1065–1074.
- Rose, T.J., Raymond, C.A., Bloomfield, C., King, G.J., 2015. Perturbation of nutrient source-sink relationships by post-anthesis stresses results in differential accumulation of nutrients in wheat grain. *J. Plant. Nutr. Soil. Sci.* 178 (1), 89–98.
- Royo, A., Abió, D., 2003. Salt tolerance in durum wheat cultivars. *Span. J. Agric. Res.* 1 (3), 27–35.
- Saddiq, M.S., Afzal, I., Iqbal, S., Hafeez, M.B., Raza, A., 2021. Low leaf sodium content improves the grain yield and physiological performance of wheat genotypes in saline-sodic soil. *Trop. Agric. Res.* 51 (18), e67663.
- Saini, P., Kaur, H., Tyagi, V., Saini, P., Ahmed, N., Dhaliwal, H.S., Sheikh, I., 2022. Nutritional value and end-use quality of durum wheat. *Cereal. Res. Commun.* 51, 283–294.
- Scherer, H.W., 2008. Impact of sulfur on N<sub>2</sub> fixation of legumes. *Sulfur Assimilation and Abiotic Stress in Plants*. Springer, Berlin/Heidelberg, Germany, pp. 43–54.
- Serret, M.D., Ortiz-Monasterio, I., Pardo, A., Araus, J.L., 2008. The effects of urea fertilisation and genotype on yield, nitrogen use efficiency,  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  in wheat. *Ann. Appl. Biol.* 153, 243–257.
- 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 (1), 190–198.
- Shahid, M., Shukla, A.K., Bhattacharyya, P., et al., 2016. Micronutrients (Fe, Mn, Zn and Cu) balance under long-term application of fertilizer and manure in a tropical rice-rice system. *J. Soils Sediment.* 16, 737–747.
- Shahid, S.A., Zaman, M., Heng, L., 2018. Introduction to soil salinity, sodicity and diagnostics techniques. In: Zaman, M., Shahid, S.A., Heng, L. (Eds.), *Guideline for Salinity Assessment, Mitigation and Adaptation Using Nuclear and Related Techniques*. Springer, Cham, pp. 1–42.
- Shin, J.M., Chung, K., Sakamoto, S., Kojima, S., Yeh, C.M., Ikeda, M., Mitsuda, N., Ohme-Takagi, M., 2017. The chimeric repressor for the GATA4 transcription factor improves tolerance to nitrogen deficiency in Arabidopsis. *Plant. Biotechnol.* 34, 151–158.
- Smart, D.R., Bloom, A.J., 2001. Wheat leaves emit nitrous oxide during nitrate assimilation. *Proc. Natl. Acad. Sci. USA* 98, 7875–7878.
- Soni, S., Kumar, A., Sehrawat, N., Kumar, A., Kumar, N., Lata, C., Mann, A., 2021. Effect of saline irrigation on plant water traits, photosynthesis and ionic balance in durum wheat genotypes. *Saudi. J. Biol. Sci.* 28 (4), 2510–2517.
- Sorour, S.G., Aiad, M.A., Ahmed, A.A., Henash, M.I.A., Metwally, E.M., Alharby, H., Bamagoos, A., Hossain, A., Barutcular, C., Saneoka, S., El Sabagh, A., 2019. Yield of wheat is increased through improving the chemical properties, nutrient availability and water productivity of salt affected soils in the north delta of Egypt. *Appl. Ecol. Environ. Res.* 17, 8291–8306.
- Tareq, M.Z., Hossain, M.A., Mojakkir, M.A., Ahmed, R., Fakir, M.S.A., 2011. Effect of salinity on reproductive growth of wheat. *Bangladesh J. Seed. Sci. Technol.* 15, 111–116.
- Turki, N., Shehzad, T., Harrabi, M., Okuno, K., 2023. Mapping novel QTLs for tolerance to salt stress at the late vegetative stage in durum wheat (*Triticum durum* L.). *J. King Saud. Uni. Sci.* 35, 102506.
- 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.
- Ullah, A., Nadeem, F., Nawaz, A., Siddique, K.H., Farooq, M., 2022. Heat stress effects on the reproductive physiology and yield of wheat. *J. Agro. Crop. Sci.* 208 (1), 1–17.
- Wang, X., Liu, F., 2021. Effects of elevated CO<sub>2</sub> and heat on wheat grain quality. *Plants* 10 (5), 1027.
- Wardlaw, I.F., Blumenthal, C., Larroque, O., Wrigley, C.W., 2002. Contrasting effects of chronic heat stress and heat shock on kernel weight and flour quality in wheat. *Funct. Plant. Biol.* 29 (1), 25–34.

- Waters, B.M., Uauy, C., Dubcovsky, J., Grusak, M.A., 2009. Wheat (*Triticum aestivum*) NAM proteins regulate the translocation of iron, zinc, and nitrogen compounds from vegetative tissues to grain. *J. Exp. Bot.* 60 (15), 4263–4274.
- Xynias, I.N., Mylonas, I., Korpetis, E.G., Ninou, E., Tsaballa, A., Avdikos, I.D., Mavromatis, A.G., 2020. Durum wheat breeding in the Mediterranean region: current status and future prospects. *Agronomy* 10 (3), 432.
- 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 (3), 276–282.
- Yousfi, S., Serret, M.D., Araus, J.L., 2009. Shoot  $\delta^{15}\text{N}$  gives a better indication than ion concentration or  $\Delta^{13}\text{C}$  of genotypic differences in the response of durum wheat to salinity. *Funct. Plant. Biol.* 36 (2), 144–155.
- Yousfi, S., Serret, M.D., Voltas, J., Araus, J.L., 2010. Effect of salinity and water stress during the reproductive stage on growth, ion concentrations,  $\Delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$  of durum wheat and related amphiploids. *J. Exp. Bot.* 61 (13), 3529–3542.
- Yousfi, S., Serret, M.D., Márquez, A.J., Voltas, J., Araus, J.L., 2012. Combined use of  $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$  and  $\delta^{15}\text{N}$  tracks nitrogen metabolism and genotypic adaptation of durum wheat to salinity and water deficit. *New. Phytol.* 194 (1), 230–244.
- Yousfi, S., Serret, M.D., Araus, J.L., 2013. Comparative response of  $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$  and  $\delta^{15}\text{N}$  in durum wheat exposed to salinity at the vegetative and reproductive stages. *Plant, Cell. Environ.* 36, 1214–1227.
- 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 (1).