

Breeding for salt tolerance in wheat: The contribution of carbon isotopic signatures

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Abstract: Use of low-quality water for supplemental irrigation is expected to become soon a common practice in the Mediterranean area, where durum wheat is the main cultivated cereal. Breeding for salt stress tolerance may contribute to the improvement of wheat resilience to irrigation with brackish water. Various traits can be considered as indicators of salt stress tolerance, which include agronomical and physiological criteria. However, the complexity of salinity tolerance mechanisms, the G × E interaction and the lack of correlation between controlled and open field conditions causes uncertainty in the selection process. The present review highlights the main advantages and limitations of different agronomical and physiological traits used in screening for salt stress tolerance in wheat. Special focus is given to carbon and nitrogen isotope discrimination, that remains a bottleneck in breeding for salt stress tolerance. The use of different statistical tools to analyse data related to salt stress tolerance is also discussed in this review.

Keywords: phenotyping; salinity; screening; stable carbon isotope; statistical approaches; wheat

Water deficit is the major abiotic constraint that limits the durum wheat growth, development and final grain yield in the Mediterranean regions, where this crop is mainly grown under rainfed conditions (Mir et al. 2012; Araus et al. 2013). One efficient strategy to increase the yield and ensure its stability is to apply supplemental irrigation during the key growth stages (De Vita et al. 2007; Chamekh et al. 2017). Although water salinity levels are becoming particularly alarming in the Mediterranean area, poor quality water is currently used for irrigation causing damage to salt-sensitive crops and to soil fertility (Villa-Castorena et al. 2003). Salinity causes,

on the one hand, an increase in the osmotic pressure leading to a reduction in the water uptake and, on the other hand, an increase in the salt concentration in the apoplast or cytoplasm where the vacuoles are unable to accumulate the salt ions (Munns & Tester 2008). As a consequence, the photosynthesis rate declines leading to limited growth and yield (Hay & Porter 2006; Taleisnik et al. 2009).

Durum wheat is the most cultivated cereal in the south and east of the Mediterranean basin and is a major component of the so-called Mediterranean diet (Chahed 2009). Studies revealed that durum wheat is more sensitive to salinity (Maas & Grieve

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1990) when compared with bread wheat and barley (Munns et al. 2006), but high genotypic variability was found for this trait (Munns 2002). As a consequence, a relevant objective of wheat breeding programmes is the selection and development of salt tolerant and yield stable genotypes (Chamekh et al. 2015). This objective is part of the major wheat breeding programme that is leading a global effort to develop and disseminate new genotypes that associate tolerance to biotic and abiotic stresses with high yields and yield stability (Chamekh et al. 2015). Selection for tolerant genotypes rely on the use of several tolerance indicators including yield, agronomic and physiological traits (Araus et al. 2013). However, salt stress tolerance is determined by a set of complex mechanisms (Munns 2002); and breeding programmes for durum wheat salt stress tolerance have had little success due, in part, to a low screening efficiency when individual traits are considered (Munns 2002; Zeng et al. 2002). Moreover, the gene-environment ($G \times E$) interaction, sometimes led to contradictory results and required time that is attributed to the inheritance nature of related traits. Identification of the yield contributing traits and understanding the $G \times E$ interactions and yield stability are essential for breeding new cultivars with improved adaptation to the environmental constraints (Rharrabti et al. 2003).

The use of the stable isotope variation in plant research has grown steadily during the past two decades. This trend will continue as researchers realise that stable isotopes can serve as time integrated indicators of how plants interact with and respond to their abiotic and biotic environments. In that context, analysis of the natural abundances of the stable isotopes of carbon (^{12}C , ^{13}C) and nitrogen (^{14}N , ^{15}N) in plants is of potential interest for studies on salinity resilience. Much of the research presented in this review is still pending confirmation, and it will be stated throughout the text when unconfirmed results were used for deriving the recommendations.

In addition to abiotic stress tolerance and high yield production, genotypes are required to have stable yields over the years. The agronomic concept of genotypic stability is closely related to the conformity between the real yield performance over changing environments and the level of its corresponding prediction or estimation (Messina et al. 2011). Several statistical methods have been developed for the stability analysis with a view of explaining the

information comprised in the $G \times E$ data matrix. Moreover, regression analyses have been extensively used by plant breeders to describe the yield genotypic stability over contrasting environments (Eberhart & Russell 1966).

The main purposes of this review were to (i) evaluate the efficiency of various screening traits for salt tolerance in durum wheat; (ii) explain the advantages of using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ as indirect selection criteria for durum wheat under saline conditions; (iii) present the diverse statistical tools used to analyse the genotypic responses to saline conditions

Screening criteria for salt stress tolerance

One of the aims of cereal breeding is to develop genotypes that can grow and produce high and economic yields under saline conditions. Diverse criteria can be considered in screening programmes in order to assess and distinguish salt tolerant lines from sensitive ones. These criteria are often unrelated to each other and provide different estimates of salt tolerance according to the type of indicator considered. Selection is a major technique in plant breeding. However, the complexity of the plant response to salt stress makes the choice of the selection criteria arguable. In fact, no unique trait is able to confer plant tolerance as the tolerance response is rather a combination of constitutive and induced traits (Okuyama et al. 2005). In addition, the stress severity and duration as well as the moment at which it occurs modulate the traits that are involved in the tolerance response. Numerous selection procedures have been suggested to enhance salinity tolerance in wheat grown in controlled and open field conditions (Royo & Abio 2003; De Vita et al. 2007; Sayer et al. 2008; Chaabane et al. 2011).

Most of these procedures used direct selection for the yield or indirect selection via tolerance indicators. This latter strategy turned out to be more efficient in controlled conditions than the direct selection for the yield in salt affected fields (Shannon 1990; Flowers & Yeo 1995). At the same time, several studies suggested that, due to the complexity of the salt affected soils, the application of the criteria selected under controlled conditions would result in inefficient open-field trials (Sayed 1985; El-Hendawy et al. 2009). These studies concluded a lack of correlation between the obtained performance in greenhouses and open-fields.

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Use of yield and yield components

Improving the grain yield has always been the main objective of wheat breeders. Therefore, the evaluation of the final grain yield and yield components is a crucial aspect in breeding programmes. Several breeding programmes have relied on selection for high yielding wheat cultivars via direct selection for the yield per se. Indices calculated on the basis of the yield under control and stress conditions have frequently been used to evaluate the salt tolerance (Araus et al. 2008). However, the results turned out to be elusive for breeders. In fact, the yield is a complex trait with low heritability and is subject to high $G \times E$ interaction (Cuthbert et al. 2008). Therefore, a great deal of uncertainty accompanies the performance of the cultivar selected in a particular environment when grown in another environment.

Another limitation of direct selection for the grain yield (GY) is that the majority of the selection experiments have been carried out in greenhouses under controlled conditions. These trials, performed on bread or durum wheat, were, in most cases, either not extended to open-field essays or revealed inconsistent results when compared with field assays (Sayed 1985; Munns et al. 2006; El-Hendawy et al. 2009; El-Hendawy et al. 2017). In the study conducted by Chamekh et al. (2015), the GY attained by durum wheat genotypes under control conditions was positively and significantly correlated with the GY of these genotypes at each saline condition (Figure 1).

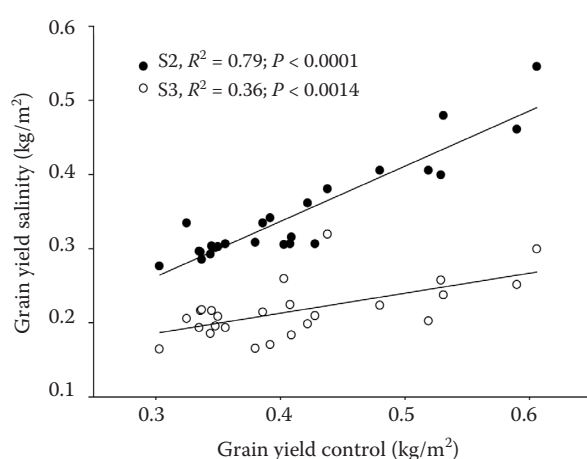


Figure 1. Relationship between the grain yield under control conditions and in the two saline sites S2 and S3 across 25 durum wheat genotypes; each point is the average value of one genotype under the two saline sites across three consecutive years (Chamekh et al. 2015)

The final yield is determined by the spike number per m^2 , the number of kernels/spike and the thousand kernel weight. These components could be good candidates as selection criteria as they directly contribute to the yield elaboration. However, contradictory results have been reported for the efficiency of these traits as selection criteria for salt stress tolerance; this was mainly related to the selection conditions. Hence, Royo and Abio (2003) found that the spike length, number of spikelets and the number of grains per spike and the harvest index were the most reliable traits. In another study, the spike number per m^2 , the grain weight, the grain number per plant and the number of fertile spikes were found to be poor selection criteria in controlled conditions, but efficient under saline field conditions (El-Hendawy et al. 2009). Moreover, few genotypic differences have been observed with respect to the grain number and grain weight (Zeng & Shannon 2000). Studies have revealed that the salinity rather decreased the spike number and number of kernels per spike resulting in a greater influence on the final grain yield (Araus et al. 1998; Royo & Abio 2003; Ayed-Slama et al. 2018).

Use of agronomic traits

Improving the grain yield under salt stress conditions has been achieved in wheat through the cultivation of tolerant genotypes selected on the basis of agronomic traits that were identified as indicators of salt tolerance in different genetic pools (Tshikunde et al. 2019). These traits include the biomass, plant height, leaf area, leaf number, tiller number, root length and root biomass (Rashid et al. 1999; Meneguzzo et al. 2000; El-Hendawy et al. 2007). Agronomic traits showed high heritability and correlation with the grain yield and have been used as indirect selection criteria in breeding programmes (Chamekh et al. 2015; Tshikunde et al. 2019). However, most of the trials were performed under controlled conditions where the heterogeneity of the soil's chemical and physical properties and rain fluctuations were avoided. For instance, a recent study performed in hydroponics on a collection of Tunisian landrace and improved durum wheat varieties concluded that the shoot length, shoot fresh weight and leaf area could be used as markers for the selection of salt-tolerant wheat genotypes.

The most used selection criterion for salinity tolerance is the biomass production (Kingsbury & Epstein

1984; Javed et al. 2003; Ma et al. 2007). In a screening of 5 000 spring wheat accessions in solution culture salinized with sea salt, Kingsbury and Epstein (1984) identified tolerant genotypes using a progressive selection of genotypes that show high biomass production under several levels of water salinity. In some cases, the assessment relied on the ratio of biomass between the salinity treatment and the control in several studies (Ma et al. 2007; Chaabane et al. 2011; Płazek et al. 2013). It is worth noting that contradictory conclusions resulted from assays that differed in length. Indeed, short-term experiments often revealed similar results for genotypes known to produce a different biomass and yield when grown for longer periods (Munns & James 2003 and references therein). This is to emphasise that conclusions drawn from long-term and short-term experiments might lack consistency.

Under field conditions, the biomass yield was suggested as a good criterion to identify salt tolerant genotypes that are tolerant to salt stress that are able to maintain the production of high dry matter under stress conditions (Munns & James 2003; Oyiga et al. 2016; Tshikunde et al. 2019). Several studies considered the leaf or root elongation rate to identify genetic differences in response to moderate salinity, but these traits turned out to be inefficient under field conditions. Root growth was found to be less sensitive to salt stress (Oyiga et al. 2016). For instance, Tshikunde et al. (2019) reported that there is a negative relationship between root-related traits, such as the root to shoot ratio, and agronomic traits, such as the plant height, number of tillers, shoot biomass, thousand grain weight, and grain yield. The leaf area was also found to be related to a high grain yield potential (El-Hendawy et al. 2009).

El-Hendawy et al. (2009) found that, in spring wheat, the area of the upper two leaves of the main stem were effective as screening criteria for salt stress tolerance under field conditions. Measurements performed on the lower two leaves and on the leaves' dry weight showed that these traits are poorly associated with stress tolerance.

Use of physiological traits

Ion accumulation. Plant tolerance to salt stress relies on several complex mechanisms that remain, so far, insufficiently investigated; these include ion exclusion, osmotic tolerance and tissue tolerance. Under saline conditions, Na^+ tends to accumulate in the plant reaching toxic levels. Most enzymes require

K^+ as a cofactor; an increase in Na^+ and the Na^+/K^+ ratio inhibits their activities resulting in alterations in the plant's metabolism (Munns et al. 2006). It is, therefore, not surprising that the ability to maintain ion homeostasis has been suggested as a salt tolerance trait in plants. In cereals and other crops, the high ability for Na^+ exclusion was associated with salinity tolerance (Garcia et al. 1995; Munns & James 2003; Borrelli et al. 2011; Negrão et al. 2017). Other studies suggested that the K^+/Na^+ discrimination was a better indicator (Munns et al. 2000; Borrelli 2011; Borrelli et al. 2018; Hussain et al. 2021). At the same time, excessive K^+ accumulation in response to salinity stress is also toxic and can be accompanied by decreased growth and, hence, does not represent an adaptive trait to salt stress (Meneguzzo et al. 2000). Other studies have suggested that maintaining low Na^+ and Cl^- levels in actively growing tissues, such as young flag leaves and sheaths, could be responsible for the enhanced salt tolerance observed in some genotypes (Hasegawa et al. 2000; Zeng 2005).

Osmotic adjustment. The salinity increases the soil osmotic pressure reducing the ability of plants to acquire water. The ability of genotypes to maintain an adequate hydration level and limit dehydration is related to their ability to tolerate salt stress. The relative water content (RWC) gives an estimate of the plant's water status with respect to the full saturation conditions (Tanentzap et al. 2015). This parameter was found to be negatively affected by salt stress conditions (Azizpour et al. 2010; Annunziata et al. 2017; Borrelli et al. 2018) and was reported to be, with the dry weight, the best index of plant sensitivity to salinity (Płazek et al. 2013).

A high RWC under stress conditions was found to be a good indicator of salt stress tolerance (Borrelli et al. 2018; Płazek et al. 2013). RWC was found to be highly correlated with the yield-related parameters (Borrelli 2011). This highlights the key role played by the osmotic adjustment in overcoming the effects of salinity and, hence, achieving high yields under stress conditions (Płazek et al. 2013).

Use of the isotopic signatures to predict selection

Stable isotope: Concept and nomenclature. Carbon (C) and nitrogen (N) isotopes are the most commonly used stable isotopes in physiological and agronomical studies (Araus et al. 1998). The use of the stable isotopes of carbon, nitrogen, oxygen, and hydrogen to study physiological processes has

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increased in the past three decades. Since that time, ecologists have identified clear isotopic signatures based not only on different photosynthetic pathways, but also on eco-physiological differences, such as the photosynthetic water-use efficiency (WUE) and sources of water and nitrogen use efficiency (NUE). The stable isotope ratios (δ) are determined by means of an elemental analyser coupled with an Isotope Ratio Mass Spectrometer and expressed in δ notation (Coplen 2008). The stable isotope composition is calculated according to the following formula:

$$\delta (\text{‰}) = ([R \text{ sample}/R \text{ reference} - 1] \times 1\,000)$$

(Farquhar et al. 1989)

The natural abundance of C and N isotopes in higher plants can be used to compare their physiology and environmental effects (Serret et al. 2008). Probably due to the higher complexity of the N cycle, the natural abundance of N isotopes ($^{15}\text{N}/^{14}\text{N}$ ratio) has been used less intensively than that of C isotopes ($^{13}\text{C}/^{12}\text{C}$ ratio) in plant physiology and ecology studies (Farquhar et al. 1989; Höglberg 1997).

Carbon isotope signature. Investigations of carbon isotope composition ($\delta^{13}\text{C}$) in plants have provided insights on the effects of environmental stresses on the transpiration, water use and photosynthesis. The carbon isotope composition ($\delta^{13}\text{C}$) was, therefore, proposed as a predictive criterion for wheat yield under drought (Araus 2004) and salinity and was successfully used as a subsidiary selection trait to improve salt tolerance in durum wheat (Yousfi et al. 2013).

The carbon isotope composition of plant leaves is related to the photosynthetic gas exchange, because $\delta^{13}\text{C}$ is, in part, determined by C_i/C_a , (ratio of the internal leaf CO_2 concentration and the ambient CO_2 concentration). A variation in $\delta^{13}\text{C}$ may result from changes in the photosynthetic capacity, stomatal conductance or both. The C_i/C_a ratio differs among varieties because of the variation in the stomatal opening and the chloroplast demand for CO_2 .

The natural ^{13}C abundance in plant matter provides time integrated information on the stress effects on the photosynthetic carbon assimilation of C_3 species (Tcherkez et al. 2011). Salt stress inducing the stomatal closure restricts the CO_2 supply carboxylation sites, which then increase the carbon isotope composition of plant matter (Rivelli et al. 2002; Yousfi et al. 2010). Therefore, the carbon isotope composition measured from the dry matter provides information on the long-term water use efficiency

of C_3 plants (Farquhar et al. 1989). Chamekh et al. (2016) reported that the most productive genotypes are those with lower $\delta^{13}\text{C}$ in grains, which suggests they exhibit higher stomatal conductance (due to a better water status) and lower intrinsic water use efficiency than susceptible genotypes. However, more productive genotypes also exhibited the highest $\text{WUE}_{\text{yield}}$ (Figure 2).

However, $\delta^{13}\text{C}$ may indirectly reflect the available water use by the plant. Thus, a lower $\delta^{13}\text{C}$, as a result of an increased water use, would explain the commonly reported negative relationships between $\delta^{13}\text{C}$ and the yield in C_3 cereals when plants growing under different saline condition are compared (Araus et al. 1998). $\delta^{13}\text{C}$ was found to positively correlate with the transpiration efficiency (TE), a trait that plays a prominent physiological role in the adaptation, productivity and salt stress tolerance which is strongly sought by breeders (Farquhar et al. 1989; Condon et al. 2004). This finding encouraged the breeder to integrate, the use of $\delta^{13}\text{C}$ in breeding programmes in various species and conditions.

Nitrogen isotope signatures. The natural variation in the plant N isotope composition ($\delta^{15}\text{N}$) was proposed as a useful trait for screening under drought or salinity because it is linked to the plant N metabolism, even though there is no precise knowledge of the underlying mechanisms or function (Coque et al. 2006; Yousfi et al. 2012). Reduced stomatal conductance caused by salinity leads to a decrease

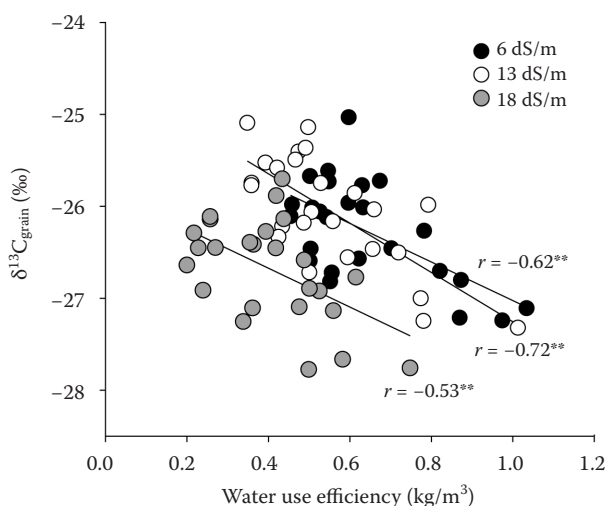


Figure 2. Relationship between the carbon isotope composition ($\delta^{13}\text{C}$) of the mature kernels and crop water use efficiency ($\text{WUE}_{\text{yield}}$) under the three different growing conditions assayed: (6, 13 and 18 dS/m) (Chamekh et al. 2016)

in the loss of ammonia and nitrous oxide, which, in turn, results in a reduced $\delta^{15}\text{N}$ (Smart & Bloom 2001). Thus, the N leaves' concentration decreases with the increased salinity, leading to a decrease in the plant enzymatic activity. Salt stress was shown to cause a much stronger reduction in the nitrate reductase (NR) and glutamate synthetase (GS) activity. These two enzymes have apparently similar discrimination factors (Yoneyama et al. 1993), and their activity is reduced by the salinity in wheat (Carillo et al. 2005). Alternatively, they may arise from differences in the N demand for active growth, which would discriminate against ^{15}N , thus increasing the $\delta^{15}\text{N}$ in plants (Pritchard & Guy 2005). Probably due to the higher complexity of the N cycle, the natural abundance of N isotopes ($^{15}\text{N}/^{14}\text{N}$ ratio) has been used less intensively than that of C isotopes ($^{13}\text{C}/^{12}\text{C}$ ratio) in plant physiology and ecology studies (Farquhar et al. 1989; Höglberg 1997). Robinson et al. (2000) proposed that measuring the natural abundance of $\delta^{15}\text{N}$ may give an indication of response to stress. Yousfi et al. (2009) reported a nearly 0.2‰ decrease in the shoot $\delta^{15}\text{N}$ per increase of soil electrical conductivity (ECs). A high external N concentration relative to a modest demand would also lead to the salinity-induced depletion in ^{15}N (Mariotti et al. 1982). A positive relationship under different salinity treatments between $\delta^{15}\text{N}$ and the biomass has already been reported in durum wheat (Yousfi et al. 2009).

Implication for breeding. Isotope signatures, such as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, were found to be effective screening criteria to identify salt stress tolerant

phenotypes (Yousfi et al. 2012, 2013). Yousfi et al. (2012) suggested that screening for high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the shoot may be the most effective way of selecting genotypes that will grow better under saline conditions. $\delta^{13}\text{C}$ provides an integrative assessment of the leaf transpiration efficiency in cereals such as durum wheat. The high transpiration efficiency measured by $\delta^{13}\text{C}$ and the water use efficiency were successfully used as selection criteria in breeding programmes to optimise productivity under stress conditions (Richards 2006), where commercial varieties were released. Genotypic variability has been reported for this trait in small grain cereals in the leaves as well as in the grain. Therefore, selecting genotypes with higher $\delta^{13}\text{C}$ may help to improve the productivity by increasing the water use efficiency under salt stress conditions. The selection of high $\delta^{13}\text{C}$ genotypes arises as a positive choice in any of the saline conditions assayed; a high $\delta^{15}\text{N}$ may represent a sensible trait to assist identifying genotypes adapted to saline growing conditions (Yousfi et al. 2012). It has been suggested that a positive relationship exists between $\delta^{13}\text{C}$ and the grain yield (Araus 2004). A high genetic correlation of $\delta^{13}\text{C}$ with the grain yield was reported in durum wheat under deficit irrigation (Araus et al. 2013), with the biomass and plant height (Figure 3) under saline irrigation (Xu et al. 2007; Chamekh et al. 2016). In this context, deficit irrigation – as a strategy consisting in limiting water applications to crucial growth stages (Geerts & Raes 2009) – turned out to be an efficient method to optimise water use and stabilise yields in wheat

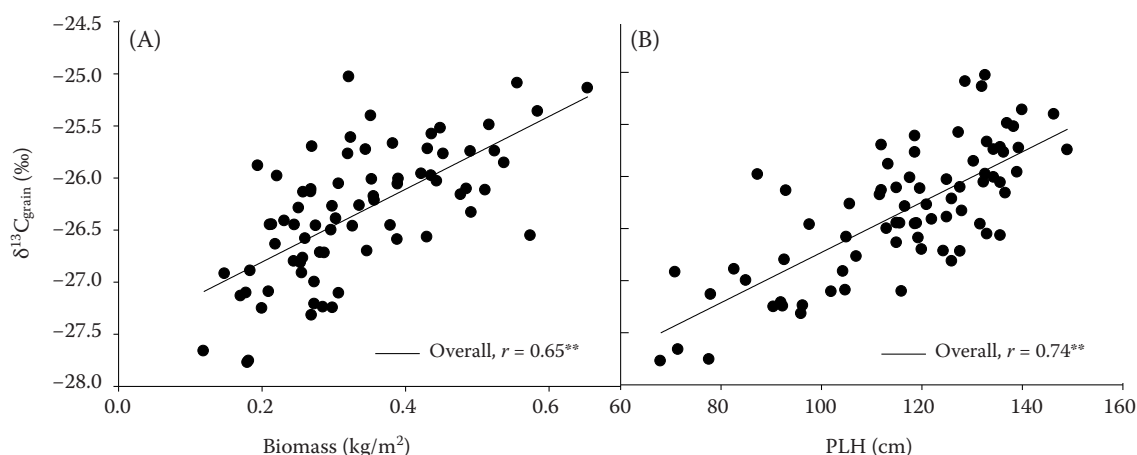


Figure 3. Relationships between the carbon isotope composition of the mature kernels ($\delta^{13}\text{C}_{\text{grain}}$) with the biomass (A) and plant height (PLH) (B) for all three sites; for each growing condition, the genotypes are plotted together. Each point represents the mean value for the three replicates per genotype (Chamekh et al. 2017)

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in arid environments (Zhang et al. 2005; Zhou 2020; Memon et al. 2021)

Although the $\delta^{13}\text{C}$ of the kernels was associated with moderate and severe stress, it was noted that the constitutive value of $\delta^{13}\text{C}$ as a selection trait was valid. In addition, the heritability for $\delta^{13}\text{C}$ was reported for durum wheat as being comparable to or higher than the heritability of the grain yield (Araus et al. 1998). In addition, $\delta^{13}\text{C}$ measured in mature kernels showed a negative relationship with the grain yield and it was proposed as an integrator of genetic difference based on the stomatal conductance and a predictor of grain yield. The difference in $\delta^{15}\text{N}$ may also be involved in the genotypic performance under saline conditions (Zheng et al. 2006), suggesting that ^{15}N may accumulate more in tolerant genotypes attributed to a higher enzymatic activity, such as NR and GS, under salinity. Yousfi et al. (2010) suggest that $\delta^{15}\text{N}$ correlated significantly with the biomass under control conditions, but also with biomass under moderate stress and a nearly significant manner with the biomass under severe stress. Yousfi et al. (2009) noted that under all growing conditions, the $\delta^{15}\text{N}$ was altered by the salinity stress except for the most severe stress. Moderate salinity was the most suitable growing condition in which to evaluate the genotypic performance under salinity.

Statistical analysis for genotypic screening under saline conditions

The wheat grain yield results from the integration of many variables that affect the plant growth and development throughout the growing period (Leilah & Al-Khateeb 2005). The grain yield is a complex quantitative characteristic presumably controlled by many genes and influenced by various factors, such as the environment, genotype and their potential interactions. Several statistical methods have been developed to explain the $G \times E$ interaction and were used for a stability and adaptability analysis by the data matrix method (Crossa et al. 1990; Romagosa & Fox 1993). Durum wheat yield modelling was based on the use of various statistical methods, namely multivariate analysis, simple correlations (Khan et al. 2011), path analysis (Mollasadeghi et al. 2011), linear regression (Eberhart & Russell 1966) and stepwise regression (Leilah and Al-Khateeb 2005). The use of a correlation analysis for breeding salt tolerant crops is extensively reviewed elsewhere. A correlation analysis is a crucial statistical method to evaluate breeding programmes

for high yield. It is based on the understanding of the direct and indirect contribution of the best trait related to the genotypic performance (Mohamed 1999). Dissecting the coefficient of correlation into direct and indirect effects can be performed using path analysis techniques (Dewey & Lu 1959). A path analysis was used by a number of researchers in wheat. In regard to this, the path coefficient analysis could be used as an important procedure in order to understand the appropriate cause and effect relationship between the yield and its various related traits.

Multiple linear regression, or stepwise regression, proved to be more efficient than the full model regression to determine the predictive equation for the yield (Naser & Leilah 1993; Mohamed 1999). In addition, stepwise regression is a method that is used to estimate the value of each quantitative independent variable regarding its relationship to one or some other quantitative dependent variables. Stepwise regression is the sequence of multiple linear regressions in a step-by-step procedure. One trait is added to the regression model at each step to reduce the error sum of squares (Leilah & Al-Khateeb 2005; Soleymanifard et al. 2012). Draper and Smith (1966) used this procedure to determine the variable that explain the majority of the total yield variability. Chamekh et al. (2017) used stepwise regression to evaluate the potential of different traits to explain the genotypic variation in GY. In a few cases dealing with salinity, drought and heat stress effects, stepwise regression explaining the yield variation across genotypes as a function of many variables related to photosynthesis, water use efficiency and $\delta^{13}\text{C}_{\text{grain}}$ was performed independently for each treatment. N_{grain} was chosen by the model as the first explanatory variable in the control condition, while at moderate and severe stress, $\delta^{13}\text{C}_{\text{grain}}$ was the first variable. Overall, > 60% of the yield variability was explained by the combination of one to three independent traits in three of the models, whereas 40 % of the total variability was explained by just one variable ($\delta^{13}\text{C}_{\text{grain}}$) under moderate and severe stress. At the same, the time stepwise regression did not show any association between GY and its Na^+ or K^+ content. The contribution of Na^+ and K^+ towards explaining the genotypic variability in GY was minor (Table 1).

Though the concept of stability is largely unclear in plant breeding literature, partly due to the myriad of definitions that were used to represent this concept (Basford & Cooper 1998), it is a powerful tool to partition the $G \times E$ into mean squares responsible

Table 1. Multiple linear regression (stepwise) explaining the grain yield (GY) variation across genotypes within each of the three growing irrigation water salinity sites as a dependent variable, and the nitrogen concentration of grains (N_{grain}), ion accumulation, stable isotope composition of grains ($\delta^{13}C_{\text{grain}}$) as independent variables

Treatment	Variable chosen	R^2	Significance
GY _{S1}	N_{grain}	0.32	**
	$N_{\text{grain}}, \delta^{13}C_{\text{grain}}$	0.58	**
GY _{S2}	$\delta^{13}C_{\text{grain}}$	0.42	**
	$\delta^{13}C_{\text{grain}}, N_{\text{grain}}, Na^+$	0.76	**
GY _{S3}	$\delta^{13}C_{\text{grain}}$	0.47	**
	$\delta^{13}C_{\text{grain}}, N_{\text{grain}}$	0.60	**

** $P < 0.01$

for its occurrence. High yield stability usually refers to a genotype's ability to perform consistently, whether at high or low yield levels, across a wide range of environments (Annicchiarico 2002). The ultimate reason for the differential stability among the genotypes and for differential results from various test environments is non-repeatable $G \times E$ (Yan & Hunt 2002). A large number of univariate and multivariate, parametric and non-parametric stability models have been suggested to assess the causes of $G \times E$ interaction. One model that is used by breeders is based on linear regression to describe the dynamic yield stability which uses the regression coefficient (b_i) (Finlay & Wilkinson 1963) and (S_d^2) deviation from the regression (Eberhart & Russell 1966). The other models used include a regression line intercept and (R^2) a coefficient of determination (Akçura et al. 2005). The stability of cultivars was defined by the high mean yield and regression coefficient ($b_i > 1$) and a low deviation from the regression line (S_{di}^2) (Berzsenyi et al. 2000; Akçura et al. 2005). The ideal situation would be characterised by a highly stable improved genotype with a high yield potential (Tollenaar & Lee 2002; Duvick et al. 2004) compared to landraces in contrasting environments. It is nearly impossible to identify and recommend a single variety that is the “best” across multiple environments due to the infinite possibilities of the genotype environment interaction.

Future issues

Significant breakthroughs have been made on the gene expression and the physiological mechanisms of salinity tolerance. Nevertheless, the link between the

gene expression and the physiological mechanisms should be further explored in order to fill gaps in breeding for salinity tolerance.

Molecular processes that control the Na^+ management have received much attention, but other essential processes in the Na^+ and Cl^- tissue tolerance and osmotic adjustment remain relatively unknown.

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