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ORIGINAL PAPER

Relationships Between Mycorrhizal Attributes and Stable Carbon and Azote Isotopes in a Semi-arid Environment as Influenced by Durum Wheat Cultivars and Salinity Level

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Abstract

The effect of plant species on their root-associated arbuscular mycorrhizal fungi (AMF) under salt stress is well studied, but how cultivars modulate this association remains largely unexplored. To fill in such a gap in knowledge, this study investigates how durum wheat cultivars shape their AMF communities in relation with plant physiological traits. Six durum wheat cultivars were grown in semi-arid areas and irrigated with three salinity levels (6, 12, and 18 dS m^{-1}). The interaction between cultivar and salinity had a considerable impact on AMF status, plant physiological traits, and grain yield (GY). In particular, *Maali* (modern variety) exhibited the highest belowground inputs (mycorrhizal root colonization, spore density, and spore morphotype number) at 6 and 12 dS m^{-1}, while a clear prevalence was obtained for *Agili Glabre* (landrace) at 18 dS m^{-1}. Furthermore, these two cultivars were distinguished by a low yield stress susceptibility index and a high GY. Some AMF genera (e.g., *Glomus*, *Funneliformis*, and *Paraglomus*) seem to interact with most cultivars, while some others including *Acaulospora* and *Septoglomus* preferred to colonize *Agili Glabre* cultivar. This study indicates the contribution of durum wheat cultivar in operating the AMF diversity. Under both conditions (6 and 12 dS m^{-1}), the partial least square structural equation modelling (PLS-SEM) showed that AMF colonization had an indirect effect on GY through C metabolism, expressed mainly by $\delta^{13}C_{\text{flag leaf}}$ and $\delta^{13}C_{\text{grain}}$. These findings highlight that durum wheat cultivar is a determinant factor in AMF symbiosis performance, therefore of salt-tolerance.

Keywords Salinity · Mycorrhizae · Durum wheat · Cultivars · C and N isotope discrimination

1 Introduction

Future agricultural crop productivity is jeopardized by soil salinization and the use of poor quality of water irrigation, particularly in arid and semi-arid climates (Shahid et al. 2018). Durum wheat (*Triticum durum* Desf.), a worldwide grown crop and the main component of pasta industrial chain, is a salt-sensitive glycophyte species (Munns et al. 2006). From 6 dS m − ^{1}, wheat growth and grain yield were reduced by 7.1 percent for every dS m − ^{1} increase in salinity, with a significant yield reduction at 15 dS m − ^{1} (Chinnusamy et al. 2005). To cope with this abiotic stress, there is an increasing trend towards research and development of a viable alternative methods based on several beneficial microorganisms, particularly arbuscular mycorrhizal fungi (AMF, phylum *Glomeromycota*).

The roots of most vascular plants (> 80%) can establish mutualistic symbiotic associations with AMF (Brundrett

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and Tedersoo 2018), helping them to improve plant's resilience to salt stress to consequently prevent their yield losses (Abdel Latef and Miransari 2014; Evelin et al. 2019; Yasmeen et al. 2019). AMF are distributed across a wide range of ecosystems, even in extreme conditions such as saline soils (Becerra et al. 2014). Compared to non-colonized plants, AMF alleviate salt stress-induced damage on colonized plants by modulating nutritional, physiological, and biochemical pathways through (i) improving water and nutrient uptake (Evelin et al. 2019), (ii) decreasing Na^+ concentration to maintain homeostasis (Begum et al. 2019), and (iii) removing reactive oxygen species (ROS) by inducing the activities of antioxidant enzymes (e.g., superoxide dismutase, catalase, glutathione reductase, and peroxidase) or by increasing the accumulation of antioxidant compounds (e.g., ascorbate and glutathione) (Ganugi et al. 2019; Gupta et al. 2021). The soil AMF attributes under salt-affected environments has been the subject of several studies, but the results remained controversial (Barin et al. 2013; Juniper and Abbott 2006). In fact, salinity harmful effects on AMF fitness were observed with considerable evidence on sporulation, root colonization, spore density and richness, and community structure and composition (Melo et al. 2017; Torrecillas et al. 2013). On the other hand, several publications reported either no adverse effect or even boosting effects of salinity on AMF functions (Yano-Melo et al. 2003; Yamatou et al. 2008).

The AMF-induced salt tolerance of crops could significantly differ with AMF species as well as host species and cultivar identity (Estrada et al. 2013; Ganugi et al. 2021; Mao et al. 2014; Zhu et al. 2001). Moreover, a wheat cultivar genetic basis was among the specific linkage to AMF mycorrhization (Hetrick et al. 1992). Only little information is currently available on the AMF diversity within wheat roots under salt stress, and how cultivars control the fungal communities inside their roots. In non-stressed conditions, modern high-yielding wheat cultivars showed a putative loss of susceptibility to AMF in conventional agroecosytems as a result of their ability to uptake mineral nutrients, in particular phosphate, without the aid of their symbionts, compared to landraces (Hetrick et al. 1992; Zhu et al. 2001), whereas recent works revealed that modern plant breeding programs did not lead to the suppression of AMF colonization in wheat (De Vita et al. 2018; Ganugi et al. 2021). In the current study, the effect of durum wheat cultivars on AMF status was assessed through grain yield performance, tolerance index, and physiological features in plants, including the stable isotopes of carbon (^{12}C, ^{13}C) and nitrogen (^{15} N, ^{14} N) in addition to the mycorrhizal attributes. The stable C isotope composition ($\delta^{13}C$) of dry matter reflects C fractionation during photosynthetic carbon dioxide (CO_2) fixation with traces of local environmental conditions (Lawlor and Cornic 2002). The N isotope composition is governed by N^{15} isotope composition ($\delta^{15}N$) of the N source and by various physiological and metabolic processes within the plant (Evans and Poorter 2001). In particular, $\delta^{13}C$ and $\delta^{15}N$ were proposed as a predictive criterion for durum wheat yield under drought and salinity (Yousfi et al. 2012). Nonetheless and probably due to the higher complexity of the N cycle, the $\delta^{15}N$ is more complicated trait, much less understood and more rarely used than $\delta^{13}C$ (Spangenberg et al. 2021). To our knowledge, this is the first study that describes the relationship between mycorrhizal proliferation and $\delta^{13}C$ and $\delta^{15}N$ in durum wheat cultivars under salt stress conditions.

To assess with a high efficiency and to reflect the complex fungal community interaction within durum wheat cultivars under salt stress, open-field tests were conducted in three locations differing by their irrigation water salinity (6, 12, and 18 dS m^{-1}). Thus, six durum wheat cultivars (landraces and modern varieties) and AMF attributes such as root colonization, spore density, and diversity were evaluated after 2 years of saline water application. In addition, the relationship between AMF and durum wheat C and N metabolism was studied. Here, we addressed the following questions:

(1) How the durum wheat cultivars affect the mycorrhizal status within salinity levels?
(2) Does AMF play under the three irrigation conditions the same relevant role to alleviate the salt stress of durum wheat? Does landraces benefit more from AMF colonization than modern varieties that we hypothesized that have lost sensitivity to these symbionts but are even more productive?
(3) Is there a cultivar-specific adaptive symbiosis depending on the degree of salinity?
(4) Is there an effect of mycorrhizal colonization on yield performance following a change in C and N metabolism, as assessed by C and N contents, $\delta^{13}C$, and $\delta^{15}N$ in flag leaves and grains? Does this relationship changes along salinity gradients in the field?

2 Materials and Methods

2.1 Durum Wheat Cultivars

Six (06) durum wheat (*Triticum durum* Desf.) cultivars were used: 3 Tunisian landraces (*Bayadha*, *Souri*, and *Agili Glabre*) chosen based on available information about genetic diversity (Ben Salem et al. 1997) and 3 Tunisian high yielding modern varieties (*Razzek*, *Karim*, and *Maali*) that are the current most cultivated (Table S1). Considering their salt tolerance performance, *Bayadha* and *Razzek* are considered as salt-sensitive cultivars, *Souri* and *Karim* are moderately tolerants, while *Agili Glabre* and *Maali* are recognized as salt-tolerant cultivars (Ben Salem et al. 1997; Boudabbous et al. 2022).

2.2 Experimental Sites

Three (3) experimental sites (St) located in the central area of Tunisia were chosen (Table 1, Fig. 1 and 2). Those regions have a typically Mediterranean semi-arid climate and present very similar weather conditions. Before sowing, the physico-chemical properties of soil (0–20 cm) were analyzed as described by Boudabbous et al. (2020, 2022). Bulk density was determined by the cylinder method (Blake and Hartge 1986).

Table 1 Description of studied sites Echbika (St_1, 6 dS m^{-1}), Barrouta (St_2, 12 dS m^{-1}) and Sidi Bouzid (St_3, 18 dS m^{-1}), and agronomic practices

Experimental site	St_1		St_2		St_3	
Growing season	2010/11	2011/12	2010/11	2011/12	2010/11	2011/12
Geographic and bioclimatic attributes						
Site localization	35°37′N, 9°56′E		35°34′N, 10°02′E		35°02′N, 9°33′E	
Bioclimatic stage	Semi-arid		Semi-arid		Semi-arid	
Soil physico-chemical and biological attributes (0–20 cm)						
Texture	Silt-loam		Silt–clay		Silt–clay	
pH_{water}	8.53		8.86		8.55	
EC (dS m^{-1})	1.21		4.11		5.20	
Bulk density (g cm^{-3})	1.36		1.50		1.50	
SOM (mg g^{-1})	26.39		26.01		25.15	
$CaCO_3$ (mg_g^{-1})	3.18		3.37		3.08	
C (mg_g^{-1})	15.30		15.80		14.07	
Total N(mg-g^{-1})	1.19		1.20		1.30	
C/N	12.85		13.16		10.82	
Available P (mg kg^{-1})	9.40		8.62		8.65	
Available K (mg kg^{-1})	553		466		243	
Na^+ (mg kg^{-1})	246		291		343	
Ca^{2+} (mg kg^{-1})	146		132		243	
Agronomic attributes						
Sowing date	First week of December					
Sowing density (seed m^{-2})	300		300		300	
Number of blocs and plots/site	3 blocs subdivided each into 6 plots (in total 18 plots/site)					
Plot surface/cultivar/replicate (m^2)	2		2		2	
Number and length of row/plot	10 rows of 1 m length with 0.2 m inter-row spacing and 0.5 m inter-plot spacing					
Discharge of each emitter (L h^{-1})	4 at 1.0 bar		4 at 1.0 bar		4 at 1.0 bar	
Interval between emitters of the same line (m)	0.3		0.3		0.3	
Period of irrigation	From sowing to the grain filling stage (Z77)					
Fertilization						
1st N application (kg N ha^{-1})	25, at sowing (Z13)					
2nd N application (kg N ha^{-1})	25, at stem elongation (Z32)					
	Water irrigation chemical attributes					
	$IWS_1 = 6$ dS m^{-1}		$IWS_2 = 12$ dS m^{-1}		$IWS_3 = 18$ dS m^{-1}	
EC (dS m^{-1})	5	6	11	12	18	18
pH	7.65	7.70	8.10	8.18	8.50	8.75
Na^+ (mg kg^{-1})	410	395	570	553	720	785
Ca^{2+}(mg kg^{-1})	62	58	66	69	75	60
K^+(mg kg^{-1})	19	16	16	21	18	19

Given their proximity, the same meteorological data was used for St_1 and St_2. St, site; IWS, irrigation water salinity; EC, electrical conductivity; SOM, soil organic matter; $CaCO_3$, total calcium carbonate; C, carbon; N, nitrogen; P, phosphorus; K, potassium; Na, sodium; Ca, calcium

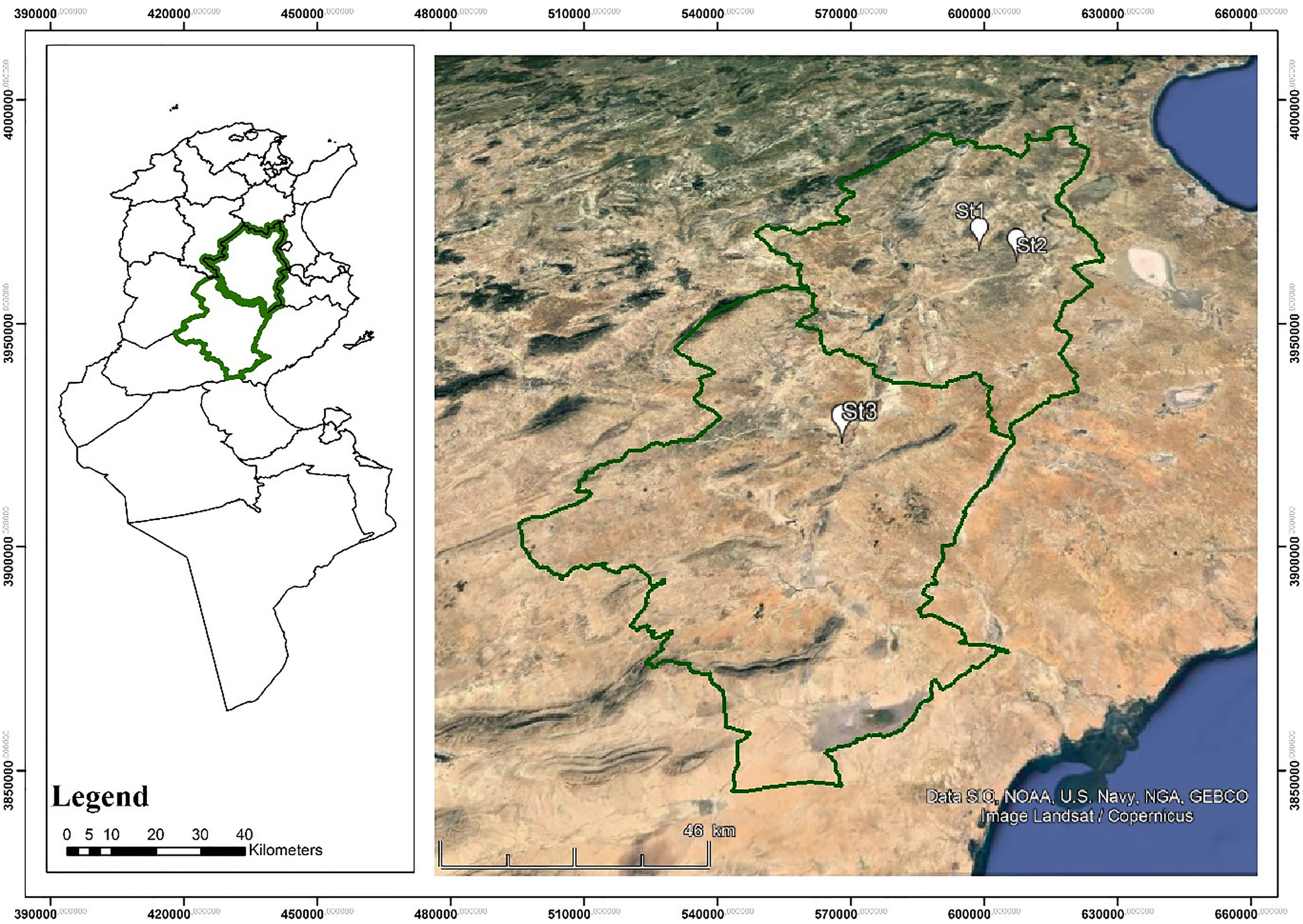
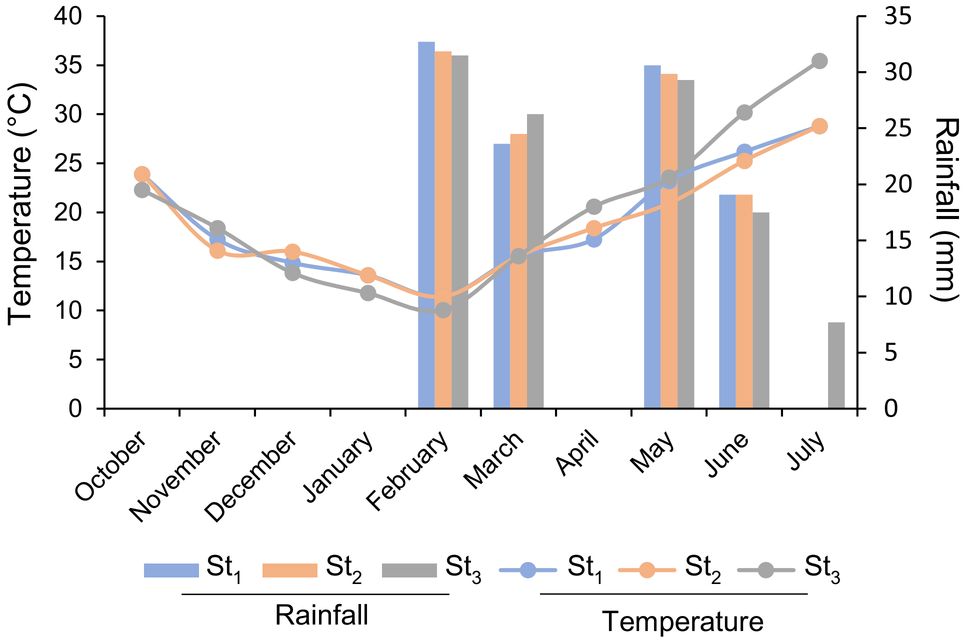


Fig. 1 Map of the geographic locations of the study area: St_1 (site 1), irrigated with saline water of 6 dS m^{-1}; St_2 (site 2), irrigated with saline water of 12 dS m^{-1}; St_3 (site 3), irrigated with saline water of 18 dS m.$^{-1}$

Fig. 2 Average monthly rainfall (mm) and temperature (°C) from November 2011 to July 2012 at three sites (St_1, 6 dS m^{-1}; St_2, 12 dS m^{-1}; and St_3, 18 dS m.$^{-1}$)



2.3 Experimental Design and Field Management

The field experiments were irrigated with salty water at three concentration gradients (Table 1): medium irrigation water salinity ($IWS_1 = 6$ dS m^{-1}) in St_1 (Echbika), severe irrigation water salinity ($IWS_2 = 12$ dS m^{-1}) in St_2 (Barrouta), and very severe salinity irrigation water salinity ($IWS_3 = 18$ dS m^{-1}) in St_3 (Sidi Bouzid) (Scianna 2002). The experiments were established in two consecutive cropping seasons (2010/11 and 2011/12). The field trials were conducted in a randomized complete block design with three replicates/treatment ($n = 3$). The treatments were defined by a factorial combination of 6 cultivars and 3 salinity levels. The IWS_1 was considered as control due to the poor quality of water irrigation used in St_2 and St_3. The chemical properties of water and the technical practices are described in Table 1.

2.4 Soil and Root Sampling Procedure

Throughout this investigation, the flowering growth stage (Z65) was chosen for soil and root samplings. In fact, maximum durum wheat root growth occurs at Z65 leading to highest levels of AM colonization (Urbanavičiūtė et al. 2022). Under each rhizosphere's cultivar, five soil cores (20 cm diameter × 30 cm depth) were collected after two cropping seasons of saline water application (i.e., 2011/12 cropping season). Sampling points were located between intra-row durum wheat plants and from the center of inter-row spaces in each plot. Because spores can have an aggregate distribution, the five samples per cultivar and per plot were pooled in a plastic bag to form a composite sample (~1 kg per plot) to assess the AMF spore density (Koske and Halvorson 1981). The roots were collected in Z65 using the same sampling method.

2.5 Assessed Parameters

2.5.1 Root Mycorrhizal Colonization

Freshly fine root fragments were cut into 1 cm pieces, rinsed with distilled water, and cleared in 10% KOH at 90 °C for 30 min. Roots were then rinsed several times with deionized water, acidified with HCl (1%) for 3 min, and stained with Trypan Blue (0.05%, w/v) in lacto-glycerol (1:1:1, lactic acid:glycerol:water) at 90 °C for 1 h (Phillips and Hayman 1970). Before observation under the microscope, the roots were de-stained in lactoglycerol solution for a few minutes to remove the excess stain. The mycorrhizal colonization_ (RC, %), including hyphal, vesicular, and arbuscular abundance, were microscopically (×100 to ×400) examined using the magnified intersection method (McGonigle et al. 1990).

2.5.2 Indigenous AMF Spore Isolation, Quantification, and Morphological Identification

One hundred grams of soil samples per replicate and per cultivar were used for spore isolation by wet-sieving and decanting method followed by sucrose centrifugation (Gerdemann and Nicolson 1963). Spores and debris were collected on 38 µm, 150 µm, and 500 µm sieves with tap water. After centrifugation, the supernatant was poured through a 50-mm mesh and quickly rinsed with tap water and then placed in a 9-cm Petri dish for examination under a binocular stereomicroscope (×40, ×60). Spore density (SD 100 g^{-1} soil) was evaluated by counting the number of spores in 100 g of soil sample.

Morphological identification of AMF was performed based on the genus through stereoscopic microscope (40× magnifications). Isolated spores were counted, transferred to an individual glass slide by wet needle, and then mounted in polyvinyl alcohol-lactic- glycerol (PVLG) either with or without Melzer's reagent (Schenck and Pérez 1990). Spores were identified using morphological criteria and compared to a culture database established by INVAM (http://invam.cag.wvu.edu/). The following parameters were derived based on morphotype identification:

(1) Spore morphotype number (SMN): total number of taxon or morphotype.
(2) Frequency of occurrence (FO): percentage of samples containing a particular taxon or morphotype among all samples, reflecting the distribution status.
(3) Relative spore density (RD): ratio of spore density of a particular taxon or morphotype to the total density of spores, showing comparing sporulation of different morphotypes in a particular soil.
(4) The importance value (IV): evaluation of the dominance of AMF species based on FO and RD, calculated as $IV = (FO + RD)/2$. An $IV \geq 50\%$ indicates that a taxon (genus or species) is dominant; $10\% < IV < 50\%$ applies to common taxa; and $IV \leq 10\%$ indicates that a taxon is rarely recovered (Melo et al. 2019).

2.5.3 Leaf Area and Chlorophyll Content

During 2011/12 cropping season, the flag leaf area (FLA, cm^2) was measured at the flowering growth stage (Z65) from five flag leaves per plot. Measurements were performed using a portable laser leaf area meter (CID Bio-Science, CI-202, USA). The chlorophyll content (SPAD, SPAD value) of the flag leaf was measured in 10 plants per plot using a portable meter (Minolta SPAD 502 m, Plainfield, IL, USA).

2.5.4 Total C and N and Stable C and N Isotope Analyses

The total C (%) and N (%) and the stable C ($\delta^{13}C$, ‰) and N ($\delta^{15}N$, ‰) isotope signatures were analyzed in flag leaves at the flowering stage (Z65) and mature grain samples of St_1 ($IWS_1 = 6$ dS m^{-1}) and St_2 ($IWS_2 = 12$ dS m^{-1}) during 2011/12 cropping season. For each plot, five flag leaves as well as mature grains were dried at 70 °C for 24 h. Powdered leaf and grain samples and reference materials (~1 mg) were weighed into tin capsules and measured with an elemental analyzer (Flash1112EA; Thermo Finnigan, Bremen, Germany) coupled with an isotope ratio mass spectrometer (Delta CIRMS, Thermo Finnigan) operating in continuous flow mode in order to determine the total C and N content and the stable C and N isotopes. Measurements were conducted at the Scientific Facilities of the University of Barcelona. The stable isotope compositions were reported in the delta (δ) notation as variations in the molar ratio (R) of the heavy isotope to light isotope of the element E ($^{h}E/^{l}E$, i.e., $^{13}C/^{12}C$ and $^{15}N/^{14}N$) in the sample relative to an international standard:

$$\delta^{h}E_{sample/standard} = R_{sample/Rstandard} - 1$$

The standard for $\delta^{13}C$ was the Pee Dee Belemnite (PDB) calcium, and that for $\delta^{15}N$ was the molecular nitrogen in air (Air-N_2).

2.5.5 Grain Yield and Yield Stress Susceptibility Index

Plants were harvested one month after the grain has reached physiological maturity at (Z92) around mid-May, 2012. For each experimental unit, an area of 1 m^2 was manually harvested and grain yield (GY, t ha^{-1}) was determined. The yield stress susceptibility percentage index (SSPI) was calculated as reported by Mekliche et al. (2015):

$$SSPI_{GY} = [(GY_{control} - GY_{stress})/GY_{control}] \times 100$$

SPPI combines the relative performance of a genotype under saline stress conditions (IWS_2 and IWS_3) with its GY under control conditions (IWS_1).

2.6 Data Analysis

Physiological, agronomic, and soil variables were compared using analysis of variance (ANOVA) and Tukey post hoc test at 5% significance. Linear regression was used to test the relationships between mycorrhizal RC, GY, and SSPI.

To investigate the relationships between all measured variables among the studied durum wheat cultivars, multivariate analysis was only conducted for IWS_1 and IWS_2 because some physiological variables (C and N contents and the stable C and N isotopes in flag leaves and mature grains) were not determined at IWS_3. The principal component analysis (PCA) was conducted to determine which traits explain most the variation and to determine different groups of cultivars associated with major traits. PCA analysis was assessed using the *Factoextra* package (Kassambara and Mundt 2020). All statistical analyses were performed using the RStudio software version 3.6.0 (R Core Team 2019).

Partial least square structural equation modelling (PLS-SEM) was performed to identify causal relationships between AMF root colonization, physiological parameters, and grain yield of durum wheat cultivars. In this model, AMF root colonization, physiological parameters, and grain yield were defined as latent variables. Each latent variable was composed of a block of indicator variables (Table S2). Multi-collinearity between indicator variables was measured by evaluating the Variance Inflation Factor (VIF) (Hair et al. 2014a). The model was performed in a formative mode with the support of the SmartPLS 3.2.8 Pro software (Ringle et al. 2015). The evaluation criteria for the models included coefficient of determination (R^2), cross-validated redundancy (Q^2), and effect size (f^2) were also assessed to determine the model's predictive accuracy and its relevance (Hair et al. 2011, 2014b).

3 Results

3.1 Effect of Salinity on AMF Traits and Diversity

In the present study, the roots of all durum wheat cultivars from the three locations were colonized by AMF with colonization rates ranging from 8.23% to 54.93% (Table S3). Salinization of irrigation water affected significantly (all $p < 0.001$) the root colonization (RC), the spore density (SD), and the number of spore morphotypes (SMN). Compared to the control (IWS_1), RC and SD reached their maximum at IWS_2 with an increase rate of 42.74 and 63.95%, respectively. At IWS_3, RC maintained the same tendency as in control conditions, while the SD was decreased by 14.56%. The average number of morphotypes was 2.00 using IWS_1, increased to 2.83 with IWS_2, and then slightly declined with IWS_3 to achieve 2.44 (Table S3).

Altogether, 6 genera of AMF were identified (Table 2). *Paraglomus* (frequency of occurrence (FO) of 66.66 and 83.33%, respectively) and *Funneliformis* (FO of 66.66 and 83.33%, respectively) were the most often detected genera at IWS_1 and IWS_3, whereas at IWS_2, *Glomus* had the highest FO of 100%, followed by *Septoglomus* and *Rhizophagus* (66.66% each). Considering the AMF sporulation, the highest RD was recorded for *Glomus* at both IWS_2 (46.63%) and IWS_3 (61.79%). Nonetheless, *Funneliformis* showed the best value at IWS_1 (30.94%). According to the IV, dominant

Table 2 Distribution of arbuscular mycorrhizal fungi (AMF) genus among salinities and cultivars. Frequency of occurrence (FO), relative spore density (RD), and importance value (IV) were calculated

AMF morphotypes	Cultivar	FO (%)			RD (%)			IV (%)		
		IWS_1	IWS_2	IWS_3	IWS_1	IWS_2	IWS_3	IWS_1	IWS_2	IWS_3
Paraglomus	*Bayadha*	16.66	0	16.66	20.83	0	36.36	18.74	0	26.51
	Souri	0	0	16.66	0	0	8.33	0	0	12.49
	Agili Glabre	16.66	16.66	16.66	37.31	18.18	27.81	26.98	17.42	22.23
	Razzek	0	0	16.66	0	0	34.42	0	0	25.54
	Karim	16.66	16.66	16.66	34.29	34.09	100	25.47	25.37	58.33
	Maali	16.66	16.66	0	3.53	7.098	0	10.09	3.54	0
	Total	66.66	50	83.33	16.24	12.64	48.02	41.45	22.98	65.67
Acaulospora	*Bayadha*	16.66	0	0	29.16	0	0	22.91	0	0
	Souri	0	0	0	0	0	0	0	0	0
	Agili Glabre	16.66	16.66	16.66	62.68	9.09	11.47	39.67	12.87	14.06
	Razzek	0	0	0	0	0	0	0	0	0
	Karim	0	16.66	0	0	9.09	0	0	12.87	0
	Maali	0	16.66	0	0	39.93	0	0	28.29	0
	Total	33.33	50	16.66	16.73	19.72	6.22	25.03	34.86	11.44
Glomus	*Bayadha*	0	16.66	16.66	0	18.03	27.27	0	17.34	21.96
	Souri	0	16.66	16.66	0	62.90	61.11	0	39.78	38.88
	Agili Glabre	0	16.66	16.66	0	36.72	44.15	0	26.69	30.40
	Razzek	16.66	16.66	16.66	12.62	29.03	0	14.64	22.84	8.33
	Karim	0	16.66	0	0	45.45	0	0	31.05	0
	Maali	16.66	16.66	16.66	38.58	27.15	55.24	27.62	21.90	30.95
	Total	33.33	100	83.33	9.35	46.63	61.79	21.34	73.34	64.22
Septoglomus	*Bayadha*	0	0	0	0	0	0	0	0	0
	Souri	16.66	0	0	28.32	0	0	22.49	0	0
	Agili Glabre	0	0	16.66	0	0	7.72	0	0	12.19
	Razzek	0	16.66	0	0	3.22	0	0	9.94	0
	Karim	0	16.66	0	0	11.36	0	0	14.01	0
	Maali	0	16.66	0	0	0.95	0	0	13.78	0
	Total	16.66	50	16.66	5.83	5.86	4.19	11.24	44.59	2.09
Funneliformis	*Bayadha*	16.66	16.66	16.66	50	27.32	36.36	33.33	21.99	21.51
	Souri	16.66	0	16.66	71.67	0	30.55	44.13	0	23.60
	Agili Glabre	0	16.66	16.66	0	9.09	8.83	0	12.87	12.74
	Razzek	16.66	0	0	29.12	0	49.18	22.89	0	0
	Karim	16.66	0	0	38.64	0	0	8.33	0	0
	Maali	0	0	16.66	0	0	44.75	0	0	30.70
	Total	66.66	33.33	66.66	30.94	5.05	35.92	48.8	19.19	59.62
Rhizophagus	*Bayadha*	0	16.66	0	0	54.64	0	0	27.18	0
	Souri	0	16.66	0	0	37.70	0	0	22.18	0
	Agili Glabre	0	0	0	0	0	0	0	0	0
	Razzek	16.66	16.66	16.66	12.62	67.74	16.39	14.64	42.20	16.52
	Karim	16.66	0	0	31.40	0	0	24.03	0	0
	Maali	16.66	16.66	0	57.87	23.93	0	37.26	20.29	0
	Total	50	66.66	16.66	17.22	24.02	1.19	25.27	45.34	8.92

AMF genera were principally found at IWS_3 for *Paraglomus* (65.67%), *Glomus* (64.22%), and *Funneliformis* (59.62%), while *Glomus* (71.31%) was the only dominant genus at IWS_2. All other genera were common under the three salinity levels, except the two genera *Septoglomus* and *Rhizophagus* which remained seldom at IWS_3.

3.2 Interactive Effect of Cultivar and Irrigation Water Salinity on AMF Traits and Diversity

The mycorrhizal RC and SD varied significantly according to cultivars and showed also a significant interaction with irrigation water salinity (all $p < 0.001$) (Table S3). Under medium (IWS_1) and severe (IWS_2) salinity conditions, *Maali* followed by *Agili Glabre* recorded constantly the best rate of RC and SD. Nonetheless, under extreme saline conditions (IWS_3), *Agili Glabre* was noticeably the most mycorrhized cultivar showing the greatest spore abundance in its rhizosphere. At IWS_1, the number of morphotypes was similar for almost all cultivars (~ 2 morphotypes), except *Souri* and *Agili Glabre* who showed the lowest SMN. However, at IWS_2, *Maali* showed the highest SMN (~ 5 morphotypes) followed by *Agili Glabre*. At IWS_3, the maximum AMF morphotype number was recorded under the rhizosphere of *Agili Glabre* (Table S3).

Under severe salinity (IWS_2), roots of high yielding modern varieties (*Maali*, *Karim*, and *Razzek*) were more colonized by AMF and revealed higher SD and SMN compared to landraces (*Agili Glabre*, *Souri*, and *Bayadha*) (Table S3). However, under extreme salinity (IWS_3), landraces performed well compared to modern varieties. Intriguingly, *Maali* underwent the most important reduction of RC and SMN.

The AMF diversity (FO, RA, and IV) varied according to cultivars as well as the interaction between cultivars and irrigation water salinity (Table 2). At IWS_1, results showed that *Paraglomus* and *Funneliformis* genera were identified under the rhizosphere of the most of cultivars, while *Acaulospora* was found for two landraces and *Glomus* for two modern varieties. In contrast, *Septoglomus* was rarely detected and identified only for *Souri*. At IWS_2, *Glomus* and *Rhizophagus* were registered for the most cultivars, whereas at IWS_3, the most common cultivars had *Glomus* and *Paraglomus* under their rhizosphere. Interestingly, *Acaulospora* and *Septoglomus* were only identified for *Agili Glabre* and *Rhizophagus* for *Razzek*.

Furthermore, the highest RD was noted for *Paraglomus* and *Acaulospora* for *Agili Glabre*, *Glomus* and *Rhizophagus* for Maali, and *Septoglomus* and *Funneliformis* for Souri at IWS_1 (Table 2). Nonetheless, at IWS_2 and IWS_3, a great heterogeneity was registered according to cultivars.

Regarding IV values, no AMF genus were dominant in any of the six durum wheat cultivars, except *Paraglomus* under the rhizosphere of *Karim* (Table 2).

3.3 Salinity and the Interactive Cultivars and Salinity Effects on Measured Physiological Traits

Significant variations ($p < 0.01$) among the irrigation water salinity were obtained for all tested physiological traits, except $C_{\text{flag leaf}}$, $\delta^{13}C_{\text{flag leaf}}$, and $\delta^{13}C_{\text{grain}}$ (Table S4). The use of brackish water negatively affected FLA, leaf chlorophyll content, $C_{\text{flag leaf}}$, $N_{\text{flag leaf}}$, $\delta^{13}C_{\text{flag leaf}}$, $\delta^{15}N_{\text{flag leaf}}$, C_{grain}, N_{grain}, and $\delta^{15}N_{\text{grain}}$, but increased the $\delta^{13}C_{\text{grain}}$ even though there is no significant difference between salinity levels. FLA, chlorophyll content, $\delta^{13}C_{\text{flag leaf}}$, N_{grain}, $\delta^{15}N_{\text{grain}}$, and $\delta^{13}C_{\text{grain}}$ significantly ($p < 0.05$) varied according to durum wheat cultivars (Table S4). Nonetheless, significant variations ($p < 0.05$) were only obtained for FLA, chlorophyll content, $N_{\text{flag leaf}}$, $\delta^{15}N_{\text{flag leaf}}$, and $\delta^{15}N_{\text{grain}}$. Overall, *Souri* followed by *Bayadha* showed the highest value of FLA under the three saline levels, while *Maali* exhibited the best SPAD value. Otherwise, the general trend revealed that the four cultivars, *Souri*, *Maali*, *Bayadha*, and *Agili Glabre*, showed the highest values for C and N content and C and N isotopic composition in both flag leaves and grain. Results showed clearly that landraces had higher FLA, C and N contents, and stable C and N isotope in flag leaves and grains compared to modern varieties.

3.4 Effect of Salinity and Cultivar on Grain Yield and Yield Stress Susceptibility Index

The present investigation showed a considerable variation ($p < 0.001$) of GY and SSPI according to salinity treatment (Table S4). The use of brackish water negatively affected the GY by 9.25 and 28.79% for IWS_2 and IWS_3, respectively. Otherwise, the increase in salinity increased the SSPI by 212.65%.

A significant genotypic variation ($p < 0.05$) was also observed for grain yield and yield stress susceptibility index (Table S4). At IWS_1 and IWS_2, modern varieties out-yielded the landraces, with *Maali* being the best performing cultivar. However, at IWS_3, *Maali* (modern variety) followed by *Agili Glabre* (landrace) showed the highest best yield. Considering SSPI, *Agili Glabre*, *Bayadha*, and *Maali* could be considered as salt-tolerant cultivars at IWS_2. The most performant cultivars at IWS_3 were *Agili Glabre*, *Souri*, and *Maali*.

3.5 Relationship between AMF Root Colonization, Grain Yield, and Yield Stress Susceptibility Index

Significant positive relationships were found between GY and RC for all salinity levels of water irrigation ($r = 0.53$, $p = 0.023$; $r = 0.55$, $p = 0.020$; $r = 0.54$, $p = 0.020$) at IWS1, IWS2, and IWS3, respectively (Fig. 3). However, only at IWS3 ($r = -0.50$, $p = 0.033$) was the correlation between SSPI and RC significantly negative.

3.6 Association between AMF, Physiological and Grain Yield Traits

Two principal component analyses (PCAs) were generated to study the relationships between AMF, physiological, and grain yield traits of the six durum wheat cultivars. Eigenvalues of the studied traits are reported for each irrigation water salinity (Table S5). Under irrigation water

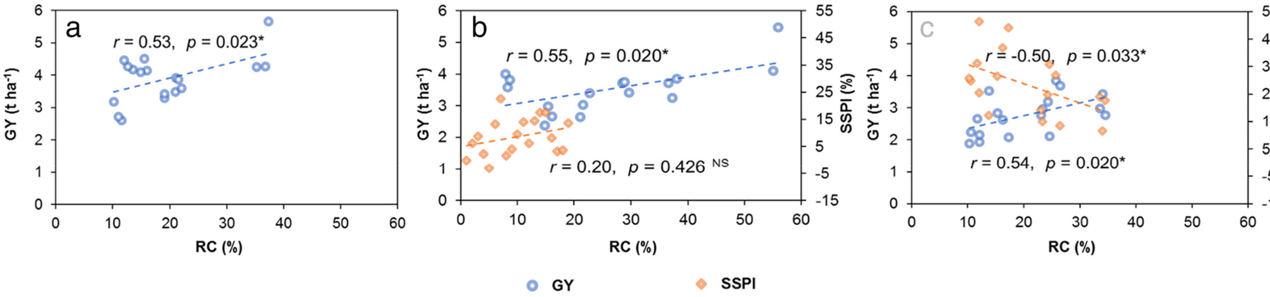


Fig. 3 Linear regression between arbuscular mycorrhizal fungi root colonization (RC), grain yield (GY), and stress susceptibility percentage index (SSPI) of durum wheat cultivars at three levels of irrigation water salinity: IWS$_1$ = 6 dS m^{-1} (**a**), IWS$_2$ = 12 dS m^{-1} (**b**), and IWS$_3$ = 18 dS m^{-1} (**c**)

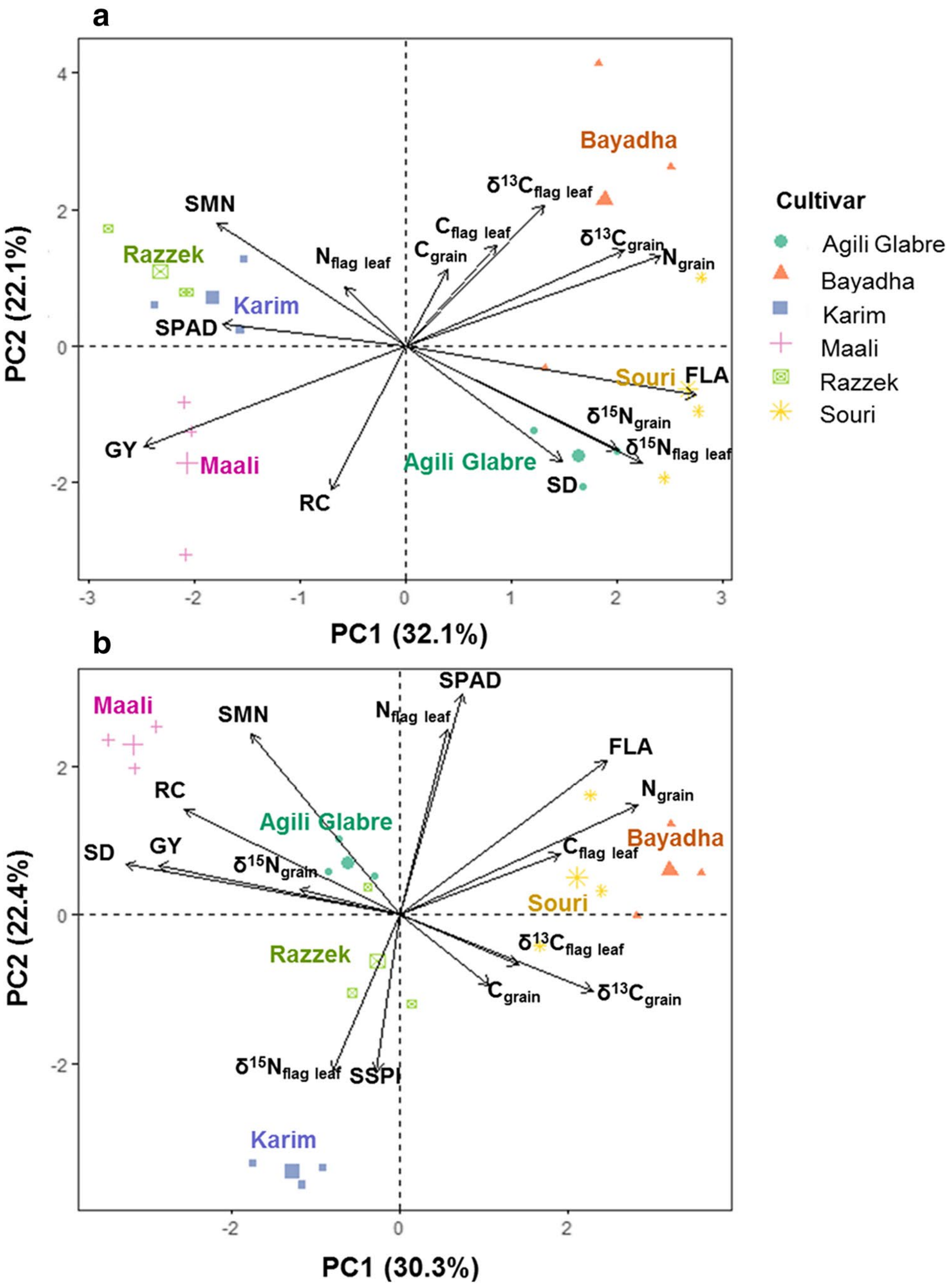


Fig. 4 Principal component analysis (PCA) of six durum wheat cultivars submitted to two levels of irrigation water salinity: IWS$_1$ = 6 dS m^{-1} (**a**) and IWS$_2$ = 12 dS m^{-1} (**b**). Symbols indicate the different wheat cultivars and arrows represent the variables: *RC*, root colonization; *SD*, spore density; *SMN*, spore morphotype number; *FLA*, flag leaf area; *SPAD*, leaf chlorophyll content; $C_{\text{flag leaf}}$, carbon content of flag leaves; $N_{\text{flag leaf}}$, nitrogen content of flag leaves; $\delta^{13}C_{\text{flag leaf}}$, stable carbon isotope composition of flag leaves; $\delta^{15}N_{\text{flag leaf}}$, stable nitrogen isotope composition of flag leaves; C_{grain}, carbon content of mature grains; N_{grain}, nitrogen content of mature grains; $\delta^{13}C_{\text{grain}}$, stable carbon isotope composition of mature grains; $\delta^{15}N_{\text{grain}}$, stable nitrogen isotope composition of mature grains; *GY*, grain yield; *SSPI*, stress susceptibility percentage index

stress of 6 dS m^{-1}, the first two PCA explained 54.2% of the total variability (Fig. 4a, Table S5). The PC1 was mainly and positively associated with FLA, $\delta^{15}N_{\text{flag leaf}}$, $\delta^{13}C_{\text{grain}}$, and $\delta^{15}N_{\text{grain}}$ and negatively with GY. PC2 was highly and positively associated with $\delta^{13}C_{\text{flag leaf}}$ and SMN and negatively with RC. The results revealed clear differences among cultivars. In fact, *Maali*, *Karim*, and *Razzek* showed the highest GY, SPAD, and SMN. However, *Souri* and *Agili Glabre* were characterized by high *FLA*, $\delta^{15}N_{\text{flag leaf,}}$ $\delta^{15}N_{\text{grain}}$ and *SD* values and low GY. Otherwise, *Bayadha* had higher $C_{\text{flag leaf}}$, N_{grain}, and C isotopic compositions in flag leaves and grains which were negatively correlated with GY and RC. Under IWS_2, the first two axes of the PCA explained 52.7% of the total variation (Fig. 4b, Table S5). The PC1 exhibited a negative association with SD, GY, and RC and positive association with N_{grain}, *FLA*, and $\delta^{13}C_{\text{grain}}$. However, PC2 displayed a positive association with SPAD and $N_{\text{flag leaf}}$, and a negative association with SSPI. The PCA results showed that cultivars, *Agili Glabre* and *Maali* had the highest GY and AMF traits (RC, SD, and SMN). *Karim* and *Razzek* had higher SSPI and $\delta^{15}N_{\text{flag leaf}}$, while *Bayadha* and *Souri* had higher N_{grain}, FLA, SPAD, and $C_{\text{flag leaf}}$. In contrast to *Agili Glabre* and *Maali*, these cultivars had low GY and AMF traits.

3.7 Grain Yield as Affected by AMF Root Colonization and Physiological Parameters under Water Salinity

PLS-SEM analysis was performed to examine significant effects between AMF root colonization and physiological parameters as explanatory variables of wheat grain yield across different genotypes. The priori model included SD and SMN as measured variables of AMF root colonization, but these variables had high VIF (variance inflation factor) values and were therefore removed. All retained variables had low VIF (<5). Figure 5 illustrates the final PLS model. The significance of the path coefficients and the loading of the variables are shown in Tables S6 and S7, respectively. At IWS_1, the results showed that wheat yield is largely explained ($R^2 = 0.80$) by its latent variables with a predictive relevance ($Q^2 = 0.45$) (Fig. 5a). There was a direct positive effect of AMF root colonization (+0.34, $p < 0.01$) on flag leaf nitrogen which was stronger than the indirect effects mediated through flag leaf carbon and grain carbon ($-0.48 \times +0.56 \times -0.49 = +0.14$, $p < 0.1$). On the other hand, AMF root colonization had significant positive effect on leaf flag nitrogen (+0.34, $p < 0.1$) which affect positively grain nitrogen (+0.54, $p < 0.05$), whereas this later had not significant effect on wheat yield (Table S6). At IWS_2, AMF root colonization as well as physiological parameters explained a large variance ($R^2 = 0.75$) of the wheat yield with a predictive relevance ($Q^2 = 0.62$) (Fig. 5b). In this second PLS-SEM, AMF root colonization had only significant direct positive effect on wheat yield (+0.27, $p < 0.1$), while its indirect effects were not significant. Both grain carbon and grain nitrogen directly influenced wheat yield (−0.52, $p < 0.01$ and −0.37, $p < 0.05$) (Table S6).

4 Discussion

In our investigation, a salinity effects on below- and aboveground traits of durum wheat were obtained. Several studies showed discrepant results among salinity effects on mycorrhizal status (i.e., root colonization, spore density and morphotypes) as negative (Klinsukon et al. 2021) or positive (Bencherif et al. 2015; Silva-Flores et al. 2019) effects. Our results showed that mycorrhizal set up was observed at IWS_2 of 12 dS m^{-1} with a better mycorrhizal RC, SD, and SMN. AMF sporulation could be an efficient reproductive strategy to survive under stress conditions by developing dormant structures (Cao et al. 2020). Otherwise, the present study revealed that IWS_3 (18 dS m^{-1}) was a critical salinity to AMF species in the studied areas. In fact, as compared to IWS_2, RC and SMN were altered, although they are still greater than those under IWS_1 (6 dS m^{-1}) except for SD which was more affected. This decline could either be an outcome of (i) direct effects of salinity on spore germination, hyphal growth in soil, and hyphal spreading after initiating the infection (Alrajhei et al. 2022) and (ii) indirect effects of salinity on durum wheat root development which could be severely affected since 15 dS m^{-1} (Chinnusamy et al. 2005) leading to reduced root and hyphal contact in soil (Juniper and Abbott 2006), and/or an increase in the H_2O_2 accumulation in the mycorrhized roots which might ultimately lead to arbuscular degradation (Fester and Hause 2005).

Based on reviewed literature (Pal et al. 2017; Parihar et al. 2019) and our results, we suggested that irrigation water salinity affects the mycorrhizal abundance and diversity. Salinity might regulate the diversity of soil fungal communities due to changes in soil properties (e.g., total carbon and nitrogen, and bulk density) induced by soil salinization (Adenan et al. 2021). Our results revealed that *Glomus* and *Paraglomus* were the most abundant genera respectively in severe (IWS_2) and extreme salinity (IWS_3), showing that they might be particularly adaptable to this semi-arid ecosystem characterized by harmful environmental circumstances including salinity (Sitieneia et al. 2015; Zhang et al. 2019). The same results were reported by Mosbah et al. (2018) who showed that the genus *Glomus* was dominant in semi-arid and arid climates due to its resilience to elevated temperature. The predominance of AMF species belonging to the order *Glomerales* was

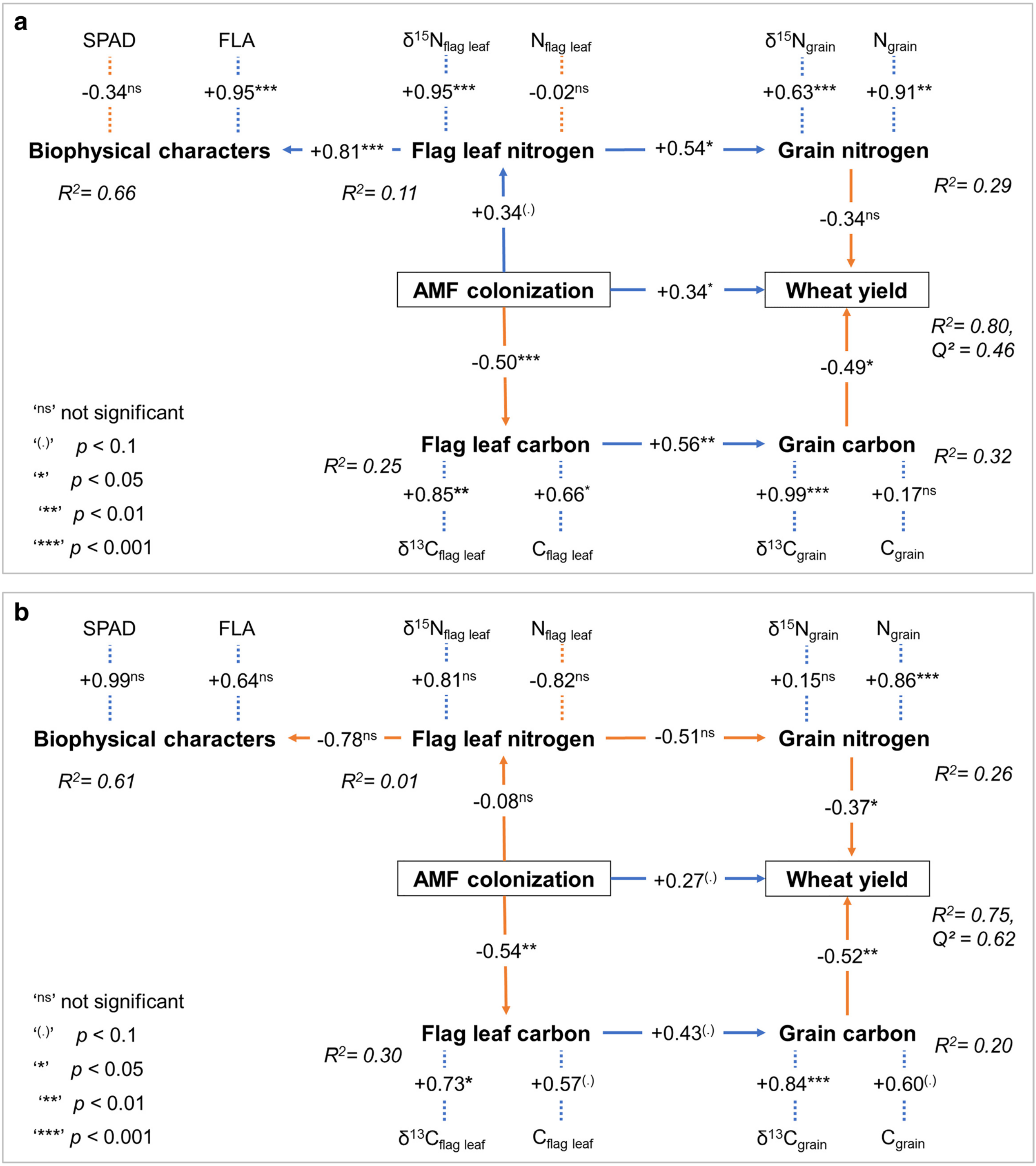


Fig. 5 Partial least square structural equation modeling (PLS-SEM) for the effects of arbuscular mycorrhizal fungi (AMF) root colonization and physiological parameters on durum wheat grain yield under two levels of irrigation water salinity: $IWS_1 = 6$ dS m^{-1} (**a**) and $IWS_2 = 12$ dS m^{-1} (**b**). The number on the solid arrows between latent variables indicate the path coefficients, while the number on the dashed arrows between each latent variable and indicator variables represent the loadings. Positive and negative effects are shown by blue and orange lines, respectively. FLA, flag leaf area; SPAD, leaf chlorophyll content; $C_{\text{flag leaf}}$, carbon content of flag leaves; $N_{\text{flag leaf}}$, nitrogen content of flag leaves; $\delta^{13}C_{\text{flag leaf}}$, stable carbon isotope composition of flag leaves; $\delta^{15}N_{\text{flag leaf}}$, stable nitrogen isotope composition of flag leaves; C_{grain}, carbon content of mature grains; N_{grain}, nitrogen content of mature grains; $\delta^{13}C_{\text{grain}}$, stable carbon isotope composition of mature grains; $\delta^{15}N_{\text{grain}}$, stable nitrogen isotope composition of mature grains

also documented in salt-affected soils in China (Krishnamoorthy et al. 2020), in particular the *Glomus* genus (Lumini et al. 2020; Malik et al. 2022; Zhong et al. 2022). Contrarily to our findings, a set of studies reported that *Funneliformis* was the less abundant taxa in saline soils (Becerra et al. 2014; Floc'h et al. 2022). According to Yang and Sun (2020), the abundance of mycorrhizae species might be explained by the fact that some species develop endospores and could therefore survive in severe salinity environments.

Glomus was the most abundant specie with the highest relative spore density under high salinity at IWS_2 and IWS_3. Those observations could be explained in part by the highest sporulation rate of this genus leading to a faster recovery and thus a better adaptability to severe conditions (Zhang et al. 2019). *Paraglomus* was the most abundant at IWS_1. This funding is in line with those of Guana et al. (2020) who found that AMF species from *Paraglomus* were more dominant under fresh water compared to seawater. In contrast, according to Symanczik et al. (2015), *Paraglomus* may prefer undisturbed environments (e.g., salinity or water stress).

The abundance and diversity of root-associated biota, as well as the plant's physiological traits, were all altered by irrigation water salinity. Expectedly, durum wheat FLA and chlorophyll content substantially decreased in response to salinity. According to Soni et al. (2021), the decrease in chlorophyll content might be due to reduced activity of the aminolevulinic acid synthase enzyme responsible for the chlorophyll synthesis or increased activity of the chlorophyll-degrading enzyme, chlorophyllase. It is well documented that salinity alters the photosynthetic machinery and transpiration, thereby restricting plant biomass (Centritto et al. 2003).

Salt stress decreased the C and N contents as well as their stable isotopic compositions in both flag leaves and mature grains, except $\delta^{13}C_{\mathrm{grain}}$. During photosynthetic C fixation, C3 plants usually discriminate against ^{13}C in favor of lighter ^{12}C, leading to a lower δ^{13}C. Although the difference was not significant between the two salinity levels, the harmful conditions increased $\delta^{13}C_{\mathrm{grain}}$, as usually reported elsewhere (Araus et al. 2003; Sanchez-Bragado et al. 2020; Yousfi et al. 2012). As suggested by Ben-Jabeur et al. (2022), the increase in δ^{13}C under saline or water scarcity conditions might be ascribed to (i) a restriction in CO_2 diffusion to carboxylation sites due to decreased stomatal and mesophyll conductance and/or a likely alteration of Rubisco activity causing decreases in CO_2 fixation, which leads to increases in grain ^{13}C, and (ii) an inability of the photosynthetic machinery to use internal CO_2, implying a greater sensitivity of the photosynthetic apparatus. However, in the current study, $\delta^{13}C_{\mathrm{flag\ leaf}}$ decreased slightly under severe saline conditions, but the difference was not significant. This result suggests that symbiosis with AMF could enhance carbon metabolism during the flowering stage to increase the carbohydrate content in leaves and to improve their remobilization to grains which might explain the non-significant difference in $C_{\mathrm{flag\ leaf}}$ at IWS_1 and IWS_2. This result corroborates with those of Eroğlu et al. (2020) who demonstrated that AMF increased wheat grain yield under salt stress through modulating carbon use efficiency.

Regarding nitrogen metabolism, the heavier stable isotope ^{15}N is discriminated against ^{14}N, leading to a lower ^{15}N/^{14}N ratio, and thus, a higher δ^{15}N (Sanchez-Bragado et al. 2017). Salt stress affects nitrogen metabolism by decreasing N uptake, assimilation, and fractionation, resulting in δ^{15}N and N content decrease (Sanchez-Bragado et al. 2017), while others reported an increase in δ^{15}N which suggests that salt affects plant δ^{15}N in a different way (Handley et al. 1997; Lopes and Araus 2006). Alteration of C and N metabolism as well as the photosynthetic activity contributed subsequently to the decrease in final GY.

In addition to the specific effect of salinity, genotypic variation among the below-ground and aboveground traits of durum wheat with respect to salinity levels was recorded. The wheat effects on the establishment of mycorrhizal symbiosis are widely examined in optimal conditions (Dupont 2018; Garcıa de Leon et al. 2020). The present study adds a new perspective on host effects on durum wheat cultivar salt stress tolerance. This finding corroborates with previous studies (Mao et al. 2014). Besides, others studies indicated that mycorrhizal traits (e.g., AM colonization, arbuscular colonization, extraradical hyphal density, spore abundance, or AMF diversity) inside roots and in soils did not significantly vary across cultivars with a differential agronomic performance (Hildermann et al. 2010; Mao et al. 2014).

Under severe to very severe salinity conditions, *Maali* and *Agli Glabre* exhibited the greatest number of morphotypes under their rhizosphere, respectively. These two cultivars seem to favor the proliferation of a maximum number of AMF genera. Notably, *Acaulospora* and *Septoglomus* were detected under the rhizosphere of *Agili Glabre* at IWS_3. These AMF genera seem to act in coordination to improve durum wheat's resilience to salinity stress. Similarly, Mao et al. (2014) reported that 3 out of 16 AMF phylotypes interacted with most wheat cultivars, while some phylotypes preferred to colonize specific cultivars. Our findings respond to the addressed question and clearly highlight the contribution of durum wheat cultivar in structuring AMF communities inside roots, after the irrigation with severe to extreme saline water (> 12 dS m^{-1}). Genotypic differences among durum wheat were among the interactions with specific AM species (Stefani et al. 2020). The variation in AMF community structure was attributed to cultivar genetic component that might be related to (i) genes of host plant affecting the structure of roots (Van Geel et al. 2021), (ii) receptivity to fungal colonization, and (iii) physiological function of the

AMF associations, particularly the degree to which the fungal symbionts act as a carbon storage and nutrient source for their host plants (Walder et al. 2012; Watts-Williams et al. 2019).

Taken as a whole, the mycorrhizal association under durum wheat rhizosphere of modern varieties was higher compared to that of landraces at severe salinity level (IWS_2). Under higher salt stress conditions (IWS_3), it appeared that landraces respond better than modern varieties in AMF symbiosis, especially *Agili Glabre*. Previous studies, conducted in non-stress conditions, speculated a positive relationship between mycorrhizal attributes and the introduction of semi-dwarfing genes *Rht* during breeding programs (De Vita et al. 2018). Nonetheless, our controversial results highlight revealed the enigmatic relationship suggesting that the cultivar-AMF interaction is strongly dependent on salt stress level. This resulting beneficial symbiosis could be related to the genetic markers in linkage with chromosome regions involved in AM root colonization (De Vita et al. 2018).

With our set of cultivars, distinct genotypic performances were obtained in terms of GY and salt-tolerance (SSPI). Interestingly, under very severe saline conditions (IWS_3), *Maali* (modern variety) followed by *Agili Glabre* (landrace) were the best performing cultivars in terms of GY and conversely for salt tolerance. The specific salt stress tolerance of landraces was well documented. These genotypes contain genes that confer adaptability to adverse situations, making them a valuable source of genetic variety for modern plant breeding to improve abiotic or biotic stress adaption, yield performance, and quality attributes in restricted environments (Marone et al. 2022). In addition, it is well established that improved varieties are more tolerant and adapted to salinity than modern varieties (Chamekh et al. 2016). In fact, highly stable improved genotypes with a high yield potential are most salt stress tolerant compared to landraces (Chamekh et al. 2022).

A genetic variation was also obtained under salinity for FLA, chlorophyll content, $\delta^{13}C_{\text{flag leaf}}$, N_{grain}, $\delta^{15}N_{\text{grain}}$, and $\delta^{13}C_{\text{grain}}$, as noted in previous studies (Araus et al. 2013; Omrani et al. 2022; Yousfi et al. 2012). The more productive cultivars (i.e., modern varieties) are those with lower $\delta^{13}C$ in flag leaves and mature grains, which suggests that they exhibit higher stomatal conductance and photosynthetic activity. Otherwise, these cultivars showed a lower N content and $\delta^{15}N$ in grains compared to landraces. It is well known that landraces are characterized by higher quality than modern varieties due to higher protein content (Ben Krima et al. 2021; Frankin et al. 2021). The natural variation of the stable nitrogen isotopes $^{15}N/^{14}N$ assessed through the nitrogen isotope composition ($\delta^{15}N$) is linked to nitrogen sources used by the plant (NH_4^+ uptake will induce ^{15}N enrichment compared to NO_3^-), to the activity of enzymes involved in the assimilation of ammonium (glutamine synthetase, GS) or nitrate (nitrate reductase, NR), and to the nature of compounds resulting from nitrogen fractionation.

Our study also stated a link between AMF, physiological characteristics, and grain yield. Under control (IWS_1) and severe water irrigation salinity (IWS_2), AMF root colonization showed a direct positive effect on wheat yield, especially for *Maali* with the highest RC and SD. A positive indirect effect of AMF on wheat yield was mediated through carbon in flag leaves and grains. The relationship between AMF root colonization and flag leaf carbon was negative. As previously stated, plants have a substantial impact on C allocation to mycorrhizal fungi (Thirkell et al. 2019). To improve mineral nutrients (e.g., P and N) transport to host plants, higher AMF proliferation should result in greater C demand and reduced plant storage carbon (Thirkell et al. 2019). In fact, Wang et al. (2021) showed that AMF colonization rate is negatively related to the rate of plant's rhizodeposit decomposition, implying an exchange in carbon allocation between rhizodeposit and mycorrhizal symbiosis.

Otherwise, the negative relationship between AMF colonization and C suggests that AMF enhance the stomatal conductance to improve plant C content and salt tolerance. In fact, the salt-tolerant cultivars (e.g., *Agili Glabre* and *Maali*) with a greater AMF root colonization had a low $\delta^{13}C_{\text{flag leaf}}$. AMF symbiosis changes stomatal morphology by reducing stomatal density and increasing the size of the guard cells and stomatal pores, thereby improving the stomatal conductance and water relations of wheat leaves under salinity stress (Zhu et al. 2018). Then, cultivars characterized by high level of C in flag leaves should maintain a good level of C in grains. C_{grain} content is the result of the combined C values of assimilates produced by different photosynthetic organs (flag leaf and ear) contributing to grain filling (Sanchez-Bragado et al. 2014). Otherwise, carbon in grain, which is largely described by ^{13}Cgrain, has a negative impact on wheat yield. In fact, the most productive cultivars (*Maali*, *Karim*, and *Razzek*) displayed lower $\delta^{13}C_{\text{grain}}$, suggesting higher stomatal conductance and water use efficiency (Araus et al. 1998). However, at IWS_2, only *Razzek* and *Maali* exhibited a low $\delta^{13}C_{\text{grain}}$. In contrast to previous studies using $\delta^{13}C$ (Araus et al. 2003; Yousfi et al. 2010), tolerant cultivars (e.g., *Agili Glabre*, *Bayadha*, and *Maali*) did not necessarily express lower $\delta^{13}C$ than susceptible ones with respect to salinity tolerance.

At IWS_1, AMF root colonization positively affected flag leaf nitrogen, explained mostly by $\delta^{15}N_{\text{flag leaf}}$ and positively related to biophysical traits and grain nitrogen. Several studies have reported that AMF colonization helps increase N uptake under salt stress conditions (Evelin et al. 2019). This might be due directly to (i) maintaining membrane stability, up-regulating of nitrate (*NRT1.1*, *NAR2.2*) and ammonium (*AMT1.1* and *AMT1.2*) transporters and increasing NR activity (Felicia et al. 2017; Talaat and Shawky 2014) and/or indirectly to (ii) stimulating soil bacteria involved in the mineralization processes of soil organic matter (Saia et al. 2014). Nonetheless, at IWS_2, this relationship between these latent variables was not significant probably due to the higher complexity of the N cycle which might explain the less intensively use of N isotopes ($^{15}N/^{14}N$ ratio) compared to C isotopes ($^{13}C/^{12}C$ ratio) in plant physiology and ecology studies (Farquhar et al. 1989; Högberg 1997). Under the same conditions (IWS_2), grain nitrogen negatively affected the wheat yield. Landraces with low GY performance clearly have more N content in grain than modern varieties, with the superiority of *Bayadha*.

In contrast to IWS_1, the PCA revealed that salt-tolerant cultivars (e.g., *Agili Glabre* and *Maali*) with better AMF proliferation showed a greater diversity after irrigation with IWS_2 which explains the positive correlation between the mycorrhizal traits (i.e., RC, SD, and SMN).

5 Conclusions

This is the first report of a field-based comparison of arbuscular mycorrhizal fungi (AMF) association across durum wheat cultivars and salinity stress using stable isotopic traits. The current research showed that under extreme salinity conditions, durum wheat landrace *Agili Glabre* benefit more from AMF colonization than modern varieties. In fact, its rhizosphere was harbored by the maximum of AMF genera where some gather specific association with cultivar that seems to act in coordination to improve durum wheat's resilience to salinity stress. Besides, we showed that the effect of mycorrhizal colonization on yield performance follows a change in carbon and nitrogen metabolism. More interestingly, at 6 and 12 dS m^{-1}, AMF colonization had an indirect effect on grain yield through carbon metabolism, explained largely by stable carbon isotope composition of flag leaves and mature grains. Establishing a firm relationship between mycorrhizal partners and isotopic signatures appears to be difficult, but a better understanding of the mechanisms underlying specific cultivar–AMF receptivity under stress conditions remains important in the future-breeding program.

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Declarations

Conflict of Interest The authors declare no competing interests.

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