European Journal of Agronomy 107 (2019) 43–52

Contents lists available at ScienceDirect

European Journal of Agronomy

journal homepage: www.elsevier.com/locate/eja

Unravelling the relationship between adaptation pattern and yield formation strategies in Mediterranean durum wheat landraces

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ARTICLE INFO

Keywords:
Drought
GE interaction
Water use
Water soluble carbohydrates
Yield components
Grain filling

ABSTRACT

Understanding the environmental and genetic factors behind the adaptation of landraces to different environments may help design breeding strategies and to promote yield improvement. Based on previous results that showed a differential frequency of alleles associated with important agronomic traits in landraces that originated in the east (EM) and the west (WM) of the Mediterranean Basin, this study analysed their patterns of adaptation and the influence this adaptation has on yield formation strategies. Thirteen and thirty-one genotypes selected according to their membership coefficient ($q > 0.900$) from the EM and the WM genetic subpopulations, respectively, were tested during six crop seasons under rainfed Mediterranean conditions. Yearly yields ranged from 3173 to 4917 kg/ha. EM landraces showed more spikes per unit area, while WM ones showed consistently taller plants, larger cycle length to anthesis, a shorter grain filling period, a higher grain filling rate and heavier grains. The contrasting pattern of adaptation of the two subpopulations was based on a differential ability to use the water available before and after anthesis. The yield of EM landraces, originated in the warmest and driest area of the Mediterranean basin, relied mostly on water input before anthesis, which was beneficial for spike production and for the accumulation of water-soluble carbohydrates in the stems prior to anthesis, to be remobilized to grains during grain filling. WM landraces performed better in environments with high water input during grain filling, which was efficiently used to increase grain setting and produce heavy grains. EM landraces could be used in breeding to improve the adaptation of modern varieties to terminal drought.

1. Introduction

Wheat is grown on about 219 million hectares worldwide and provides humans with about 20% of their intake of calories (FAOSTAT, 2016). Durum wheat (*Triticum turgidum* L. var. *durum*) represents about 10% of the global wheat production (Kantety et al., 2005). The Mediterranean Basin is the largest durum-producing region worldwide, as it comprises around 60% of the total growing area. In the region, durum wheat is mainly grown under rainfed conditions and yield is generally constrained by water scarcity, particularly during grain filling, when it is accompanied by high temperatures. Also, the unpredictable seasonal rainfalls cause large yield fluctuations between years (Anderson, 2010; Royo et al., 2010). The expected advent of more adverse weather conditions predicted by future climate change scenarios in the Mediterranean Basin (IPCC, 2014) will require the release of new cultivars adapted to the changing environments. Understanding the environmental and genetic factors behind plant adaptation to drought is critical in order to provide improved varieties with greater and more stable yields under stress environments.

The genotype × environment (GE) interaction complicates selection for broad adaptation as the cultivars perform differently according to climatic variables and soil characteristics during plant growth and development (Blum and Pnuel, 1990; Cooper and Byth, 1996). GE interaction is a challenge for plant breeders as it weakens association between phenotype and genotype and restricts the identification of superior genotypes, hindering genetic improvement in breeding programmes.

Grain growth in wheat is supported by two major sources of carbon: transient photosynthesis during the grain filling period, and the remobilization of water-soluble carbohydrates (WSC) stored in the stem and leaf sheath up to anthesis (Blum, 1998; Gebbing et al., 1999; Xue et al., 2008). As the hot and dry conditions that generally occur during

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Abbreviations: EM, East Mediterranean; WM, est Mediterranean; WSC, zater soluble carbohydrates

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https://doi.org/10.1016/j.eja.2019.04.003
Received 22 February 2019; Received in revised form 11 April 2019; Accepted 15 April 2019

Table 1
Details of the six field experiments conducted at Gimenells (Lleida, north-east Spain, 41°40′ N, 0°20′ E; 200 m a.s.l.).

Year	2007	2008	2009	2013	2014	2015
Soil texture	Clay-loamy	Loamy	Sandy-clay-loamy	Sandy-loamy-clay	Sandy-clay	Sandy-loamy-clay
Sowing date	21-Nov-06	20-Nov-07	20-Nov-08	4-Dec-12	27-Nov-13	21-Nov-14
Harvest date	2-Jul-07	2-Jul-08	15-Jul-09	5-Jul-13	11-Jul-14	6-Jul-15
Environmental conditions from sowing to anthesis						
Tmin (°C)	3.50	3.10	2.50	3.05	2.88	2.98
Tmax (°C)	13.7	14.2	13.2	14.3	13.9	14.0
WI (rainfall + irrigation, mm)	165 + 0	102 + 50	183 + 0	186 + 0	95 + 0	166 + 0
Environmental conditions from anthesis to maturity						
Tmin (°C)	11.4	11.6	12.4	9.02	8.97	10.1
Tmax (°C)	25.7	23.2	27.2	22.6	23.9	25.4
WI (rainfall, mm)	24.3	133	8.60	46.0	8.60	3.60
Average agronomic data						
Days from sowing to anthesis	163a	163a	164a	155b	147c	157b
Days from anthesis to maturity	29.3c	44.2a	26.3e	38.0b	29.8c	27.9d
Yield (kg/ha)	3254c	3818b	3332c	4917a	3173c	4008b
Spikes/m^2	348bc	313d	386a	313d	363ab	324cd
Grains/Spike	20.6d	21.5d	22.6d	35.6a	29.8b	26.7cd
TKW (g)	49.4bc	58.7a	40d	45.1c	37.8d	49.8b

Tmin and Tmax (average minimum and maximum daily temperatures), WI (water input), TKW (thousand kernel weight). Means within rows with different letters are significantly different at $P = 0.05$, following Tukey test.

grain filling in Mediterranean environments limit photosynthesis (Papakosta and Gagianas, 1991; Palta et al., 1994), yield depends greatly on the translocation to the grain of WSC accumulated during pre-anthesis (Blum, 1998; Dreccer et al., 2014). The capacity to synthesize and store WSC in the stems before anthesis is one of the mechanisms used by the plant for drought resistance (Michiels et al., 2004). It has been reported that variation in WSC content is largely genetically determined (Xue et al., 2008). Stem carbohydrate reserves have been estimated to contribute 10%–20% of the final grain yield under relatively non-stressed conditions but more than 40% under severe stress conditions during the grain filling period (Blum, 1998; Gebbing et al., 1999; Ehdaie et al., 2008; Rebetzke et al., 2008). $^{13}C/^{12}C$ carbon isotope discrimination (Δ) measured in mature grains may be used as an indirect indicator of the plant water status and the importance of translocation processes during grain filling (Condon et al., 1992; Araus et al., 2013).

Archaeological evidence dates the earliest domesticated wheats from the Fertile Crescent to approximately 10,000 years BP. They subsequently spread across the Mediterranean Basin, reaching the Iberian Peninsula around 7000 years BP (Feldman, 2001; Mac Key, 2005). After arriving in a given territory, they adapted progressively to the varying conditions of the new area and gradually established new strategies for phenology fitting and yield formation, which likely conferred adaptive advantages under the new environmental conditions (Moragues et al., 2006). The evolution of wheat during this migration and the role of human selection after the advent of agriculture resulted in the establishment of local landraces that are generally considered to be endemic to a particular region to which they are well adapted. Landraces possess a useful source of stress-adaptive traits and a wide genetic diversity for adaptation to different conditions according to their place of origin (Lopes et al., 2015).

A previous study conducted with a collection of 172 durum wheat landraces and modern cultivars from 21 Mediterranean countries revealed that landraces collected in the warmest and driest zone of the Mediterranean Basin had a shorter cycle length to anthesis, more spikes and grains m^{-2}, lighter grains, and lower yields than those originated in colder and wetter zones (Royo et al., 2014). A subsequent study using the same set of germplasm, clustered landraces from the east and the west of the Mediterranean Basin (hereafter EM and WM landraces, respectively) into different genetic subpopulations (Soriano et al., 2016). A more recent study demonstrated that the contrasting agronomic performance of EM and WM landraces was due to a differential frequency of alleles associated with important agronomic traits (Soriano et al., 2018). EM landraces had higher frequencies of alleles associated with increased grain filling duration, spikes and grains per unit area, and others reducing cycle length and kernel weight (Soriano et al., 2018). Based on these previous results that suggest a different pattern of adaptation of EM and WM landraces, the current study aimed to: i) analyse and compare the yield formation strategies of eastern and western Mediterranean landraces, ii) evaluate the GE interaction for yield and the influence of meteorological variables before and after anthesis on the pattern of adaptation, and iii) identify putative main drivers for the evolutionary divergence of the two subpopulations in terms of adaptation.

2. Material and methods

2.1. Plant material

The current study was conducted with 44 genotypes selected from a panel of 172 durum wheat landraces and modern varieties from 21 Mediterranean countries developed by Royo et al. (2014) and structured into five genetic subpopulations (SP) by Soriano et al. (2016). Considering the differential frequency of alleles affecting agronomic performance in landraces from the east (EM) and the west (WM) regions of the Mediterranean Basin (Soriano et al., 2018), we used a membership coefficient of $q > 0.900$ to select 13 and 31 genotypes from the EM and WM landrace-subpopulations, respectively (supplementary Table 1).

2.2. Field experiments

The experiments were carried out during six crop seasons (harvesting years 2007, 2008, 2009, 2013, 2014 and 2015) in Lleida, north-east Spain (Table 1). The experiments were arranged following a non-replicated modified augmented design with replicated checks (cultivars ‘Claudio’, ‘Simeto’ and ‘Vitron’) and plots of 6 m^2 for the first three years and checks ‘Avispa’ and ‘Euroduro’ and plots of 3.6 m^2 for the last three. Sowing density was adjusted to 250 viable seeds/m^2 on experimental plots, with eight rows spaced 0.15 m apart. Average minimum and maximum daily temperatures (Tmin and Tmax, °C) and water input (WI, mm) were recorded from a weather station placed in the same field, and means were calculated for the periods from sowing to anthesis and from anthesis to physiological maturity. Soil moisture was monitored in one of the repeated checks from the seedling stage by means of soil probes (model EC-20, ECH2O Dielectric Aquameter,

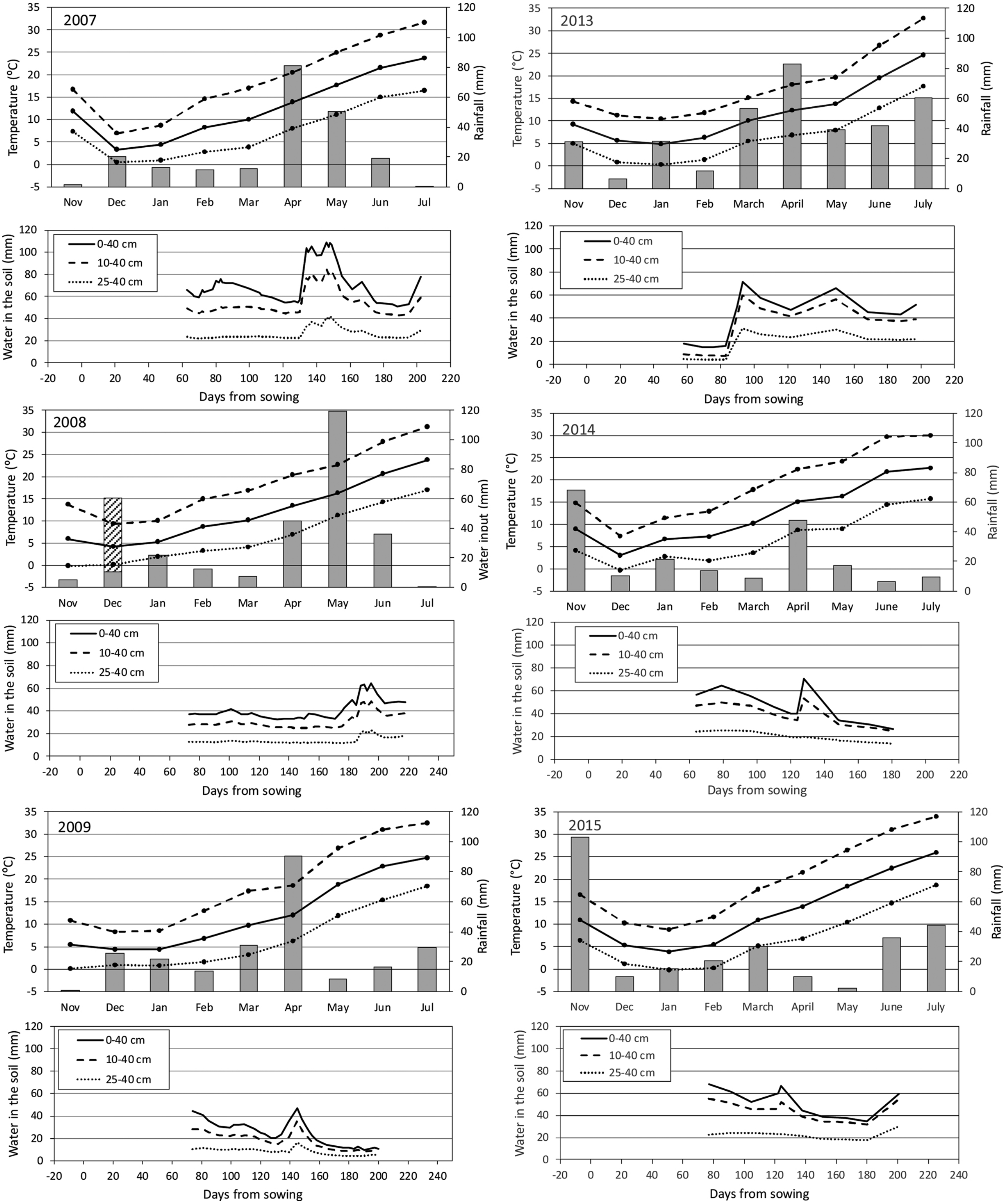

Fig. 1. Monthly water input and maximum (dashed line), mean (solid line) and minimum (dotted line) temperatures during the growth cycle of each crop season. The lowest figures indicate the water soil content at three depths (0–40, 10–40 and 25–40 cm) for each year.

Decagon Devices, Inc.) located at three depths (0–10, 10–25 and 25–40 cm). Weeds and diseases were controlled following standard practices.

Zadoks et al. (1974) growth stages (GS) 65 (anthesis) and 87 (physiological maturity) were determined on each plot. At ripening, samples of the plants in a 0.5-m-long row were pulled up in a central row of each plot to determine the number of spikes per m^2 and the number of grains per spike. Thousand kernel weight (TKW, g) was assessed in three samples of 100 g of the mechanically harvested grain per plot. Plant height (cm) was measured at GS87 in three main stems per plot from the tillering node to the top of the spike, excluding the awns. Grain yield (kg/ha) was expressed on a 12% moisture basis after combine harvesting.

In the experiments conducted in 2007, 2008 and 2009 the main

Table 2
Percentage of the sum of squares of the ANOVA model for yield, yield components, remobilization of water-soluble carbohydrates and carbon isotope discrimination measured on a collection of 44 durum wheat landraces structured on East Mediterranean (EM) and West Mediterranean (WM) genetic subpopulations (SP).

Source of variation	df	Yield (kg/ha)	Spikes/ m^2	Grains/ spike	TKW	Plant height	$Days_{SA}$	$Days_{AM}$	df	WSC_A	WSC_M	DMT	DMTe	df	Δ
Year	5	65.6 ***	23.6 ***	64.6 ***	61.9 ***	15.2 ***	77.6 ***	94.1 ***	2	44.2 ***	29.0 ***	48.2 ***	45.7 ***	1	90.3 ***
Between SP	1	2.57 ***	9.08 ***	0.54	8.63 ***	48.5 ***	14.9 ***	1.79 ***	1	14.7 ***	0.01	0.01	12.5 ***	1	1.23 ***
Within SP	42	8.42 ***	17.5 ***	8.55 **	11.3 ***	18.1 ***	4.27 ***	1.05 ***	18	9.8	24.3	11.0	7.70	42	3.04
Year x Between SP	5	5.05 ***	8.70 ***	3.55 ***	2.56 ***	1.77 ***	0.70 ***	0.65 ***	2	13.4 ***	10.8 *	20.8 ***	18.4 ***	1	1.66 ***
Year x Within SP	210	18.3 NT	41.1 NT	22.7 NT	15.6 NT	16.4 NT	2.55 NT	2.39 NT	35	17.9 NT	35.9 NT	20.0 NT	15.7 NT	41	3.37 NT
Total	263								58					86	

TKW (thousand kernel weight); $Days_{SA}$ and $Days_{AM}$ (average number of days from sowing to anthesis and from anthesis to maturity, respectively); WSC_A and WSC_M (water-soluble carbohydrates at anthesis and physiological maturity, respectively); DMT (dry matter translocation); DMTe (DMT efficiency); Δ (carbon isotope discrimination in mature kernels). $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. NT: not testable.

stems (including leaf sheaths and blades) of 10 plants per plot chosen at random were taken in 20 cultivars (5 EM and 15WM), at GS65 and GS87 to determine water-soluble carbohydrates (WSC). The samples were oven-dried at 70 °C for 48 h, weighed, ground to pass through a 1-mm sieve, and scanned by the Scientific-Technical Services of the University of Lleida using a near-infrared reflectance spectroscopy (NIR) unit previously calibrated using the anthrone method (Ruuska et al., 2006; Yemm and Willis, 1954). WSC concentration was expressed as a percentage. Dry matter translocation (DMT) was calculated per main stem as the difference in WSC (g/stem) at anthesis and maturity. Dry matter translocation efficiency (DMTe, %) was computed as 100 x DMT/dry weight per stem at anthesis. In the experiments conducted in 2007 and 2008, carbon isotope discrimination (Δ) was determined on a sample of about 2 g of mature grains from each plot. The $^{13}C/^{12}C$ ratio was determined by mass spectrometry at the Stable Isotope Laboratory (COIL) of Cornell University following the methodology described in Farquhar et al. (1989) and Royo et al. (2008).

2.3. Statistical analyses

Raw data were fitted to a linear mixed model with the check cultivars as fixed effects and the row number, column number and genotype as random effects (Little et al., 1997). Restricted maximum likelihood (REML) was used to estimate the variance components and to produce the best linear unbiased predictors (BLUPs) for the agronomic data of each accession in each environment using the SAS statistical package (SAS Institute Inc, Cary, NC, USA). Combined analyses of variance were performed for all variables with the SAS statistical package with the Kenward-Roger correction due to the unbalanced number of genotypes within subpopulations. The sum of squares of the cultivar and the cultivar × year interaction were partitioned into differences between genetic subpopulations and differences within them. Means were compared using the Tukey test (Tukey, 1949) with the JMP v13 statistical package (SAS Institute Inc, Cary, NC, USA).

The GE interaction was partitioned for yield and yield components according to the AMMI model (Gauch and Zobel, 1997) and the percentage of the sum of squares explained by each interaction principal component axis (IPCA) was calculated. Factorial regression analysis was performed in order to identify the meteorological covariates (Tmin, Tmax and WI from sowing to anthesis and from anthesis to physiological maturity) that best explained the GE interaction for yield and yield components. Following a sequential analysis of variance to establish their relative importance, covariates were introduced progressively in the factorial regression model, and finally those showing mean square values higher than the deviations were selected (Voltas et al., 2005). As the half-normal plot of the residuals of the GE interaction showed no obvious patterns, the deviations mean squares of the factorial regression were chosen as an estimate error for this analysis, which was carried out using GenStat v18 (VSN International Ltd, Hemel Hempstead, UK) software. As WI from anthesis to maturity was the only covariate entered in the model that best explained the GE interaction for yield, vectors representing WI from sowing to anthesis and from anthesis to physiological maturity were depicted in the AMMI biplots for yield and yield components.

3. Results

3.1. Environmental

The experimental site has a typical Mediterranean climate characterized by low temperatures in winter that increase rapidly during the spring, accompanied by an irregular pattern of yearly rainfall distribution (Fig. 1). The highest WI during the growth cycle was recorded in 2008 (285 mm) and 2013 (232 mm), and in the latter the maximum average yield (4917 kg/ha) was achieved (Table 1). The minimum yield (3173 kg/ha) was recorded in 2014, when the crop received only

104 mm of rainfall during the growth cycle and suffered severe water scarcity during grain filling. Water stress also occurred during grain filling in 2009 and 2015 (Table 1 and Fig. 1).

3.2. Yield formation

The results of the ANOVA showed that the year effect was significant for all the analysed traits (Table 2). It accounted for most of the total variation for phenology, yield and yield components (except number of spikes per m^2), DMT and Δ, but had a lower effect on plant height. Differences between the subpopulations were significant for all traits except number of grains per spike, WSC at maturity and DMT, and explained 1.23% (for Δ) to 48.5% (for plant height) of the total variation of the model. Differences within subpopulations were significant for yield and yield components, and accounted for a larger percentage of the sum of squares of the model than differences between them. Within-subpopulations differences were still significant for plant height and length of developmental periods, but they accounted for a lower percentage of variation than the between-subpopulations differences. Variability within subpopulations was not significant for WSC accumulation at anthesis and maturity, DMT, DMT$_e$ and Δ. The year × between genetic subpopulation interaction was significant for all traits (Table 2).

The comparison of mean values of the two subpopulations showed that the WM landraces outyielded the EM ones on average across years and in all experiments except the ones conducted in 2009 and 2015, when the differences were not statistically significant (Table 3). The number of spikes per m^2 was higher in EM landraces in all the experiments. The WM subpopulation showed consistently heavier grains, taller plants, a longer cycle length to anthesis and a shorter grain filling period. The number of grains per spike was significantly higher in the EM subpopulation in all experiments except in 2015, when the result was the opposite. This contrasting behaviour resulted in a similar number of grains per spike on average across years (Table 3).

The results of the experiments conducted in 2007, 2008 and 2009 showed that the percentage of WSC accumulated at anthesis on main stems was significantly higher in EM landraces, but similar values were obtained for the WSC accumulated at physiological maturity (Table 3). On average, DMT per stem was similar in the two subpopulations, although in 2007 and 2008 it was higher in the WM subpopulation (Table 3). For DMT$_e$, differences between subpopulations were statistically significant only in 2009 and across years, but the tendency for EM landraces to have higher values was the same in all three experiments. Finally, results of the Δ data recorded in 2007 and 2008 showed significant differences between subpopulations in 2007 and across years, with EM landraces reaching the highest values for this variable (Table 3).

3.3. GE interaction for yield

The first two IPCAs of the AMMI model explained 77.4% of the GE interaction for yield (Table 4a). The biplot of the first two IPCAs of the AMMI model showed that IPCA1, which accounted for 45.6% of the GE variation, separated the genotypes into two partially overlapping clusters corresponding to EM and WM subpopulations (Fig. 2). Variability among WM landraces appeared to be greater than that among EM ones. Points located on Fig. 2 close to and far from the origin of the axes can be seen for both subpopulations, suggesting the presence of landraces with small and large yield variations between years, respectively.

The position of the environments within the biplot of the AMMI analysis (Fig. 2) showed that the years 2008 and 2015 were separated from the remaining ones, as they were the only ones located on the negative side of the IPCA2 axis. However, a large distance separated them for IPCA1, as 2008 was located in the negative direction of this axis and 2015 in the positive direction.

The most explanatory model obtained by factorial regression

Table 3
Mean values of yield, yield components, remobilization of water-soluble carbohydrates and carbon isotope discrimination for each year and across years of durum wheat landraces structured on East Mediterranean (EM) and West Mediterranean (WM) genetic subpopulations.

Year	SP	Yield (kg/ha)	Spikes/m^2	Grains/spike	TKW (g)	Plant height (cm)	Days$_{SA}$	Days$_{AM}$	WSC$_A$ (%)	WSC$_M$ (%)	DMT (g/stem)	DMTe (%)	Δ (‰)
2007	EM	3205 b	371 a	19.6 b	42.7 b	91.0 b	157 b	30.7 a	28.0 a	7.59 a	0.25 b	19.7 a	16.4 a
	WM	3274 a	338 b	21.0 a	52.2 a	115 a	165 a	28.8 b	27.7 a	7.56 a	0.39 a	19.6 a	16.0 b
2008	EM	3133 b	324 a	19.1 b	51.5 b	88.6 b	159 b	45.8 a	40.9 a	10.1 a	0.54 b	31.4 a	17.6 a
	WM	4106 a	309 a	22.4 a	61.7 a	110 a	165 a	43.5 b	36.0 b	7.49 b	0.72 a	29.5 a	17.6 a
2009	EM	3398 a	467 a	19.7 b	37.8 b	107 b	162 b	26.7 a	36.6 a	8.93 a	0.58 a	30.2 a	
	WM	3304 a	351 b	23.8 a	40.9 a	125 a	165 a	26.1 b	19.5 b	11.5 a	0.25 b	10.6 b	
2013	EM	4783 b	336 a	34.6 b	42.9 a	88.1 b	151 b	40.4 a					
	WM	4974 a	291 b	35.9 a	46.0 a	117 a	157 a	37.1 b					
2014	EM	2840 b	375 a	29.3 b	35.7 b	91.1 b	143 b	30.0 a					
	WM	3312 a	358 b	30.0 a	38.6 a	108 a	148 a	29.8 a					
2015	EM	4035 a	340 a	29.8 a	46.2 b	95.2 b	153 b	30.2 a					
	WM	3996 a	317 b	25.4 b	51.4 a	115 a	158 a	27.0 b					
Average EM		3566 b	367 a	25.4 a	42.8 b	93.5 b	154 b	34.0 a	35.2 a	8.88 a	0.46 a	27.1 a	17.0 a
Average WM		3828 a	330 b	26.4 a	48.5 a	115 a	160 a	32.0 b	27.6 b	8.89 a	0.45 a	19.6 b	16.8 b

TKW (thousand kernel weight); Days$_{SA}$ and Days$_{AM}$ (average number of days from sowing to anthesis and from anthesis to maturity, respectively); WSC$_A$ and WSC$_M$ (water-soluble carbohydrates at anthesis and physiological maturity, respectively); DMT (dry matter translocation); DMTe (DMT efficiency); Δ (carbon isotope discrimination in mature kernels). EM and WM means within each year and across years with different letters are significantly different at $P = 0.05$, following a Tukey test.

Table 4
Percentage of the sum of squares (SS) in the AMMI and factorial regression models for the partitioning of the GE interaction for yield and yield components of 44 durum wheat landraces representative of Mediterranean eastern and western genetic subpopulations and tested in six field experiments.

Source of variation	df	SS (%)	*p*-Value
a) Yield			
AMMI			
Year x Cultivar	215	23.4	
IPCA 1	47	45.6	< 0.001
IPCA 2	45	31.8	< 0.001
Residuals	123	22.6	
Factorial Regression			
Year x Cultivar	215	23.4	
WI_AM x Cultivar	43	38.1	< 0.001
Deviations	172	61.9	
b) Number of spikes/m^2			
AMMI			
Year x Cultivar	215	49.8	
IPCA 1	47	50.6	< 0.001
IPCA 2	45	34.3	< 0.001
Residuals	123	15.1	
Factorial Regression			
Year x Cultivar	215	49.8	
Tmax_SA x Cultivar	43	37.9	< 0.001
WI_AM x Cultivar	43	35.3	< 0.001
Deviations	129	26.8	
c) Number of grains/spike			
AMMI			
Year x Cultivar	215	26.3	
IPCA 1	47	51.8	< 0.001
IPCA 2	45	23.4	< 0.001
Residuals	123	24.9	
Factorial Regression			
Year x Cultivar	215	26.3	
WI_AM x Cultivar	43	29.8	0.0095
Deviations	172	70.2	
c) Thousand kernel weight			
AMMI			
Year x Cultivar	215	18.1	
IPCA 1	47	58.2	< 0.001
IPCA 2	45	19.1	< 0.001
Residuals	123	22.7	
Factorial Regression			
Year x Cultivar	215	18.1	
Tmin_AM x Cultivar	43	30.9	0.0047
Deviations	172	69.1	

WI_AM (water input from anthesis to physiological maturity, mm); Tmax_SA (average maximum daily temperature from sowing to anthesis, °C); Tmin_AM (average minimum daily temperature from anthesis to physiological maturity, °C).

analysis accounted for 38.1% of the SS of the GE interaction, with 20% of its degrees of freedom, and only included as a meteorological covariate the WI from anthesis to maturity (Table 4a). The vector of this covariable, depicted in the AMMI biplot shown in Fig. 2, is located on the side of the WM landraces and close to the year 2008, suggesting that WM landraces performed better than EM ones in terms of yield in environments with high WI during grain filling, which was the case in 2008. On the other hand, the vector representing WI from sowing to anthesis was located on the opposite side of the biplot and closer to the points representing EM landraces, indicating their better performance in environments with high WI before anthesis.

3.4. GE interaction for yield components

The first two IPCAs of the AMMI model explained 84.9% of the SS of the GE interaction for number of spikes per m^2 (Fig. 3a). The model obtained by factorial regression analysis accounted for 73.2% of the SS of the GE interaction with WI from anthesis to maturity explaining 35.3% of it (Table 4b). As in the case of yield, vectors representing WI before and after anthesis had opposite senses in the biplot. The years 2007 and 2013–2015 were close, and near to the vector representing WI before anthesis, suggesting that water availability during the early stages of crop development contributed considerably to the formation of spikes in these years. The years 2009 and 2008 were separated from the rest and situated on opposite sides of IPCA2. The points representing landraces were distributed along the two axes without a clear subpopulation structure for this trait. Nevertheless, most points representing EM landraces were in the positive sense of IPCA2, some of them showing the greatest values for this axis, while the most negative ones were recorded in two WM landraces. The closeness of some points to particular years suggest that they were beneficial for the formation of spikes.

For number of grains per spike, the biplot of the first two axes of the AMMI model explained 75.2% of the SS of the GE interaction (Fig. 3b). The factorial regression analysis included only WI from anthesis to maturity as covariate (Table 4c). The wide distribution of points representing WM landraces along the whole plot suggests that some WM landraces had a large GE interaction for number of grains per spike. The majority of points representing EM landraces were in the negative sense of IPCA1, on the opposite side of the vector representing WI from anthesis to maturity, suggesting that WI during grain filling had a low effect on the final number of grains per spike for the genotypes included in the EM subpopulation. On the other hand, the majority of points representing WM landraces were in the positive direction of IPCA1 and close to the same vector, indicating that WM landraces took advantage of the water available during grain filling to increase the number of grains per spike. The small length of the vector representing WI from sowing to anthesis suggests that the amount of water available before anthesis was irrelevant for grain setting. The experiments conducted in 2008 and 2015 were separated from the rest in the biplot (Fig. 3b).

The biplot of the first two axes of the AMMI model for TKW explained 77.3% of the SS of the GE interaction (Fig. 3c). The points corresponding to WM landraces were located in the upper right part of the figure, while the ones representing EM were in the lower left part, with very few overlapping between them. The only variable included in the factorial regression model was the minimum temperature from anthesis to maturity that accounted for 38.1% of the SS of the GE interaction (Table 4d). WI from anthesis to maturity was not included in the model though it accounted for 11.5% of its SS. The location of the points representing WM landraces close to the vector corresponding to WI after anthesis suggests that this subpopulation took advantage of it to increase its grain weight. By contrast, the points representing EM landraces were closer to the vector corresponding to WI before anthesis. IPCA2 was mostly associated with WI after anthesis and, accordingly, the years 2007, 2008 and 2013 were in the positive sense of this axis, while the remaining years were in the negative sense.

4. Discussion

The current study explains, in terms of adaptation, previous results showing differences in yield and yield components between landraces collected in the east and the west of the Mediterranean Basin that conform two different genetic subpopulations (Soriano et al., 2016, 2018). Experiments were conducted during six years on a site located in the west of the Mediterranean Basin that showed the meteorological variability characteristic of the climate in the region.

Variation in weather conditions resulted in yields ranging from 3173 kg/ha in 2014, the year with the lowest rainfall, to 4917 kg/ha in 2013, a year in which rainfall was not the highest but was the most evenly distributed. The high yield recorded in 2014 considering the low water input that year could be attributed to the high soil fertility (about 3% of organic matter) and the superficial sub-soil water layer at this site (Moragues et al., 2006). The year effect explained 66% of yield variability and 24% to 65% of the variance observed for yield components, values slightly lower than those reported in previous studies conducted on durum wheat (Subira et al., 2015). However, the year effect only

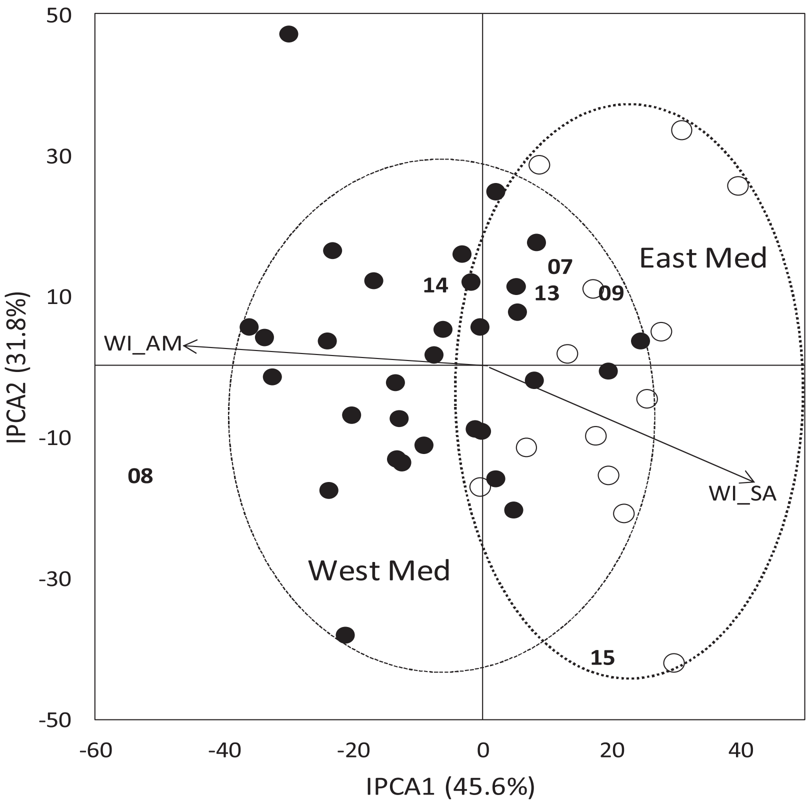

Fig. 2. Biplot of the first two axes of the AMMI model summarizing the relationships between water input and yield. Years are represented in bold with their last two digits. Cultivars are identified as follows for each genetic subpopulation: ○ (East Mediterranean) and ● (West Mediterranean). WI_SA and WI_AM (water input from sowing to anthesis and from anthesis to physiological maturity, respectively).

accounted for a small proportion of the variability for plant height, which was consistently higher in WM landraces.

On average, WM landraces outyielded EM ones by 7.3%. This result was expected, given that the experimental site is located in the west of the Mediterranean Basin. Yield differences between the two subpopulations were statistically significant in four of the six experiments. In the biplot of the first two axis of the AMMI model that analysed the GE interaction for yield, years 2009 and 2015, when both subpopulations achieved a similar yield, were located close to the vector representing WI from sowing to anthesis. The points corresponding to the years 2007 and 2013, in which yield differences between subpopulations were significant but very low (2% and 4%, respectively), were also located on the positive side of the first IPCA axis. These results suggest that EM landraces had the best yield performance in environments with high water input before anthesis. On the other hand, the largest yield divergence between subpopulations was observed in 2008, when the WM subpopulation outyielded the EM one by 31%. The greatest rainfall received in 2008 after anthesis is in accordance with the location in the biplot of the point corresponding to this year close to the vector symbolizing water input during grain filling. The positioning of most points representing WM landraces in the same direction of this vector suggests that they had the best yield performance in the environment with the highest water input after anthesis. The WM subpopulation was more variable than the EM one with regard to the effect of the distribution of the water available to explain the GE interaction for yield, likely partially due to the larger number of genotypes included in this subpopulation. The points close to the origin of the first axis denoted yield stability across years in terms of the distribution of the water available during crop cycle.

These results suggest that EM landraces showed good adaptation to environments with high water input before anthesis, but low water input during grain filling, denoting a high efficiency in the use of the water available for the crop before anthesis to generate yield. In contrast, the positioning of most points of the WM subpopulation on the left part of axis 2 reflects a better efficiency than the EM subpopulation in the use of the water available during grain filling to increase yield. To understand these results, the influence of the distribution of the water available in the two growing periods was analysed for each yield component.

In all experiments EM landraces produced a significantly higher number of spikes per unit area than the WM ones, on average 11.2% more. Hütsch et al. (2019) observed that under heat stress, wheat plants tend to increase the number of ear-bearing tillers as an adaptation strategy. The greater frequency of alleles increasing the number of spikes per unit area in EM than in WM landraces found previously in the collection used in the current study (Soriano et al., 2018) was likely a result of the adaptation of EM landraces to warm environments. However, differences between subpopulations ranged from 4.7% (in 2014) to 33% (in 2009). In the biplot, vectors representing water input before and after anthesis were in opposite sense, and only 2008 was located in the direction of WI after anthesis, in agreement with the fact that rainfall was highest during grain filling in this year. The position in the biplot of the points corresponding to 2008 and 2009 on opposite sides of IPCA2 concords with the lowest number of spikes per m^2 recorded in 2008 and the highest recorded in 2009. Furthermore, the position of the vector representing water input before anthesis is on the same side of IPCA2 as the points of all years except 2008, in agreement with the well-documented positive effect of water during early growth stages on the production and survival of tillers (Begg and Turner, 1976; Turner and Begg, 1978). The distance in the biplot between the point corresponding to 2009 and the vector symbolizing water input before anthesis denotes that other factors may have contributed to the large spike number that year. The low temperatures recorded before anthesis in 2009 could have also stimulated the production of tillers and the subsequent spikes, as low temperatures in the early stages of growth promote tiller formation in wheat and other cereals (Chaturvedi et al., 1981). The dispersion of points representing genotypes along both sides of the two axes denotes high variability within subpopulations regarding the strategy of water use for spike formation. However, a small number of points representing landraces from the two subpopulations

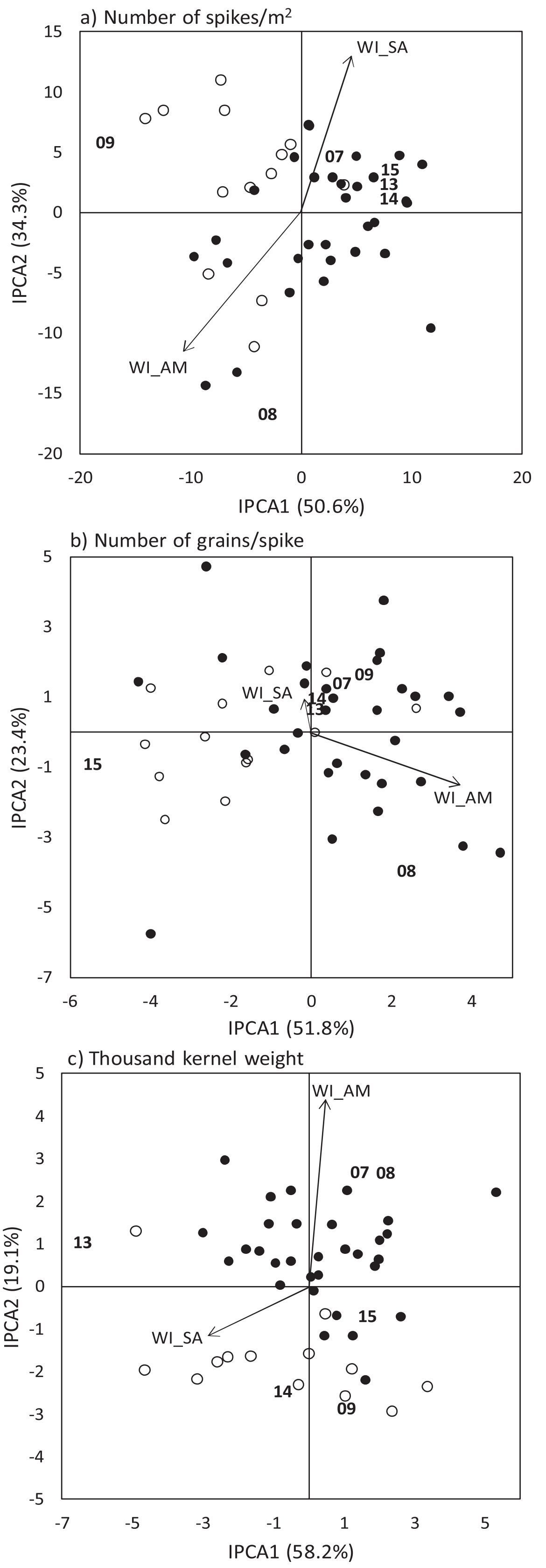

Fig. 3. Biplot of the first two axes of the AMMI model summarizing the relationships between water input and: a) Number of spikes/m^2, b) Number of grains/spike and c) Thousand kernel weight (TKW). Years are represented in bold with their last two digits. Cultivars are identified as follows for each genetic subpopulation: ○ (East Mediterranean) and ● (West Mediterranean). WI_SA and WI_AM (water input from sowing to anthesis and from anthesis to physiological maturity, respectively).

were located in the biplot close to the vector representing water input after anthesis, which may indicate that in these genotypes late rainfall could benefit the survival of spikes or the emergence of new spikes in late-formed tillers.

Though the average number of grains per spike across years was similar for both subpopulations, WM landraces produced significantly more grains per spike than EM ones in five of the six experiments, and only in 2015 was the opposite observed. The biplot of the first two axes of the AMMI model helped to interpret this result. The position and length of the vectors in the biplot clearly showed that water input before anthesis had a negligible effect on the number of grains per spike when compared with the main effect of water input during grain filling. The only year positioned in the negative sense of IPCA1, on the opposite side of the vector representing water input after anthesis, was 2015, in agreement with the fact that the rainfall was lowest during grain filling in this year. The location of the remaining years and the majority of points representing the WM subpopulation in the same direction of this vector is in line with the largest number of grains per spike recorded in WM landraces in all years except in 2015. The placement of points representing EM landraces close to this year and in the opposite direction of the vector symbolizing water input after anthesis indicates a good adaptation of this subpopulation to water scarcity during grain filling. This finding can be at least partially explained by early anthesis in the EM landraces to escape terminal drought and exposure to slightly lower temperatures during grain filling, in agreement with results obtained by Lopes et al. (2018) in Turkey and Iran, where severe terminal drought and heat causes this type of response. The relative position of points of both subpopulations in the biplot also suggests that the WI after anthesis had a much lower effect on grain setting in EM landraces than in WM ones. Our results also indicate that water stress after anthesis in 2015 was more detrimental for grain setting in WM landraces than in EM ones. In consequence, the larger number of grains per spike of EM landraces in that year resulted in a similar yield in both subpopulations, though the grains were heavier in the WM landraces. Although the genotype effect only explained 9% of the total variation for number of grains per spike, high variability was found within the WM subpopulation for this trait, as revealed by the dispersion in the biplot of the points representing genotypes. The larger number of grains per unit area reported previously for EM landraces (Soriano et al., 2018) was due to a consistently higher number of spikes per unit area, as the number of grains per spike tended to be higher in the WM subpopulation.

Kernel weight of WM landraces was consistently higher than that of EM ones. The difference was 13.3% across years, but this percentage ranged from 8% to 22% depending on the year. The first and second axis of the AMMI biplot that analysed the GE interaction for kernel weight were related to water input before and after anthesis, respectively. Accordingly, the points corresponding to the years 2007, 2008 and 2013 were located on the positive part of IPCA2 close to the vector representing water input after anthesis, and the remaining years were placed on the negative part of the same axis.

The position in the TKW biplot of the majority of points representing WM landraces in the positive sense of IPCA2 indicates that they made the most of the water input after anthesis to fill their grains. In contrast, the location of points corresponding to EM landraces on the negative part of IPCA2 and closer to the vector symbolizing water input before anthesis suggests that they relied mostly on the water available before anthesis to fill their grains. The results obtained when comparing the concentration of WSC on main stems at anthesis support this conclusion, as EM landraces had consistently higher average values than WM ones in the three years in which this analysis was carried out. These results suggest that the EM landraces used the water available for the crop before anthesis efficiently to accumulate carbohydrates on their stems, probably as a mechanism of adaptation to drought, as it has been reported that WSC content is enhanced in drought-resistant wheats (Hou et al., 2018).

The WM landraces flowered on average 6 days later than the EM ones (3 to 8 days depending on the year), suggesting that they filled their grains under hotter and drier conditions, which was probably the reason for their shorter grain-filling period. Thus, the heavier grains of WM landraces were a consequence of a higher grain filling rate (1.52 mg/day in WM and 1.25 mg/day in EM, derived from Table 3), in agreement with their greater ability to use water after anthesis to the benefit of kernel weight.

The similar WSC concentration on main stems at physiological maturity, in view of the fact that it was much higher in the EM landraces at anthesis, denotes a greater relative contribution of WSC to grain filling in this subpopulation than in the WM one. This indicates that the plant canopy of WM landraces had a greater capacity to photosynthesize after anthesis, as transient photosynthesis and translocation of stored reserves accumulated prior to anthesis are the two sources of carbon for grain growth (Blum, 1998; Royo et al., 2018). This is in agreement with the higher yields of WM landraces. However, in absolute values (g/stem), the remobilization to the filling grains of WSC accumulated prior to anthesis in main stems was higher in the WM landraces in 2007 and 2008, which concords with their taller plants. The only year in which DMT was greater in the EM subpopulation was 2009, coinciding with the crop season that received the lowest precipitation after anthesis. Drought during grain filling in this year likely promoted the remobilization of WSC to the filling grains of the EM landraces, which resulted in a DMT efficiency 19.6% superior in them than in the WM ones. Our results indicate that drought stress after anthesis decreased the deposition of dry matter on the filling grains of the WM landraces, as shown by the low differences in grain weight between the two subpopulations in 2009 ($< 8\%$), which finally resulted in similar yields.

The large environmental effect on WSC reported in the literature (Blum, 1998; Ehdaie et al., 2006; Shearman et al., 2005) was confirmed by the current study, because in 2008 (the year of the three analysed that received the lowest water input before anthesis, particularly in April just before flowering) the concentration of WSC at anthesis and DMT in grams per stem were the highest for the two subpopulations. This may reflect the positive effect of water deficit before flowering in the accumulation of WSC in stems, in agreement with Ruuska et al. (2006) and Yang et al. (2000, 2001).

Results of carbon isotope discrimination measured in mature grains in 2007 and 2008 showed similar values in 2008 in both subpopulations, probably as a consequence of the relatively high water input after anthesis in this year. It has been reported that Δ is reduced by drought (Sayre et al., 1995), in agreement with the lower Δ values recorded in 2007, which received less water after anthesis than 2008. In addition, the higher values of EM landraces in 2007 are in agreement with the greater importance of translocation processes during grain filling in this subpopulation, and could indicate that water stress developed more rapidly and deeply during grain filling in WM landraces.

5. Conclusions

The results of the current study demonstrate that the dispersal of durum wheat landraces from the east to the west of the Mediterranean Basin caused important changes in their pattern of adaptation and yield formation strategies. When durum wheat migrated from the eastern zone, whose climate is characterized by high temperatures and low rainfall, particularly after anthesis (Royo et al., 2014), to the western one, the populations established new strategies for yield formation, which conferred adaptive advantages according to the new environmental conditions. The results of the current study showed that landraces from the eastern Mediterranean Basin had the best yield performance in environments with high water input before anthesis, which they used efficiently to produce spikes and to accumulate water soluble carbohydrates in the main stem prior to anthesis to be remobilized to the grains to support drought stress during grain filling. In contrast, landraces collected in the western Mediterranean countries, characterized by lower temperatures and more rain either before or after anthesis (Royo et al., 2014), were better adapted to environments with more water availability during grain filling, which they used to the benefit of a large grain setting and the production of heavier grains. Our results suggest that eastern Mediterranean landraces are more adapted to terminal drought than western ones. In addition to this general pattern suggesting a differential efficiency for water use before and after anthesis in the two subpopulations, the dispersion of points representing landraces in all biplots indicated that variability within each subpopulation was high in terms of adaptation to Mediterranean environments.

Acknowledgements

This research was funded by projects AGL 2015-65351-R, AGL-2006-09226-C02-01 and AGL-2012-37217 from the Spanish Ministry of Economy and Competitiveness, project RTA2015-00072-C03 from the Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA), and the CERCA Programme/Generalitat de Catalunya. MR was a recipient of a PhD grant from INIA. JMS was hired by the INIA-496 CCAA programme funded by INIA and the Generalitat de Catalunya. Thanks are given to Dr. Jaume Puy from the University of Lleida and to Dr. Mark E. Sorrells from Cornell University to facilitate chemical analyses. The skilled technical assistance of the staff of the Sustainable Field Crops programme of IRTA is gratefully acknowledged.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.eja.2019.04.003.

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