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Are the agronomic performance and grain quality characteristics of bread wheat Mediterranean landraces related to the climate prevalent in their area of origin?

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ABSTRACT

This study analyses the relationship between the climate of the countries where wheat landraces are specifically adapted, and their agronomic and grain quality characteristics. Regions with similar climate within the Mediterranean Basin were identified based on long-term climatic data of the 23 countries origin of a collection of 153 bread wheat landraces. The panel was genotyped with 13177 SNP markers and was grown on field experiments for two years under rainfed conditions in north-east Spain and 14 agronomic and 11 grain-quality traits were assessed. Great phenotypic variability was found in the collection. The agronomic performance of the landraces varied according to the climate of the four climatic regions identified within the Mediterranean Basin (south-east, south-west, north coast and north-Balkan), which gradually varies from warm and dry to wet and cold. Cycle length, grain-filling rate and yield increased, but grain-filling duration decreased from south-eastern landraces to north Balkan ones. Grain weight accounted for 25% of yield variations and was lowest in landraces from the south-eastern region. Grain quality showed no geographical pattern related to the climatic region. Landraces from Bosnia-Herzegovina, Bulgaria and Romania differed from the rest in their high gluten strength (W), loaf volume (LV), mixing time (MT) and grain hardness, while opposite attributes were found in accessions from Jordan, Lebanon and Cyprus. Landraces from south-western Mediterranean countries had low MT, alveograph-peak, W and LV. Genotypes suitable for use in breeding programmes may be identified. Molecular analyses revealed that genetic structure was mostly influenced by high temperatures before anthesis and rainfall, solar radiation and sunshine after anthesis.

1. Introduction

Bread wheat (*Triticum aestivum* L.) is a major staple food crop, with over 700 million tonnes being harvested annually (FAOSTAT, 2015–2019, http://www.fao.org/faostat/). Wheat grain is a basic ingredient of many foods worldwide, with milled flour being used for a variety of products such as leavened and unleavened breads, noodles, cookies, cakes, pastries and many other foods that provide 18% of the calories and 20% of the protein in the human diet globally (http://www.fao.org/faostat/). The exponential rise of the human population in the last decades predicts a population of more than 9 billion by 2050, which will entail a 60% increase in the global wheat demand that year (Licker et al., 2010). Covering this rising need will be a huge challenge, particularly considering the 6%–25% decrease in wheat productivity projected by climate change models depending on the region. The wheat-growing area represents 27% of the arable land within the Mediterranean Basin (Royo et al., 2017), and global climate change predictions suggest increases in the mean temperature of the region of 4 °C–5 °C in the next few decades, with a decrease in precipitation of 25%–30%, which will probably cause yield reductions of 24% or more (Asseng et al., 2014). Ensuring the food security in the coming decades will require a combination of improved varieties and agronomic practices warranting environmental sustainability.

Wheat was domesticated about 10,000 years BP in the Fertile Crescent (Feldman, 2001) in the southeast of Turkey. From there, wheat was

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Abbreviation list

Tmin	Average minimum daily temperature
Tmax	Average maximum daily temperature
Tmean	Average mean daily temperature
Rad	Average daily solar radiation
Rain	Average daily rainfall
Rh	Average daily relative humidity
ET_0	Accumulated potential evapotranspiration
D_{31}	Days from sowing to the beginning of jointing
D_{45}	Days from sowing to boots swollen
D_{55}	Days from sowing to heading
D_{65}	Days from sowing to anthesis
D_{87}	Days from sowing to physiological maturity
GFD	Grain filling duration
GFR	Grain filling rate
HI	Harvest index
CDW	Crop dry weight
NS	Number of spikes per m^2
NGS	Number of grains per spike
TKW	Thousand kernel weight
PH	Plant height
TW	Test weight
GH	Grain hardness index
FY	Flour yield
GP	Grain protein
FP	Flour protein
FS	Flour sedimentation
MT	Mixing time
W	Strength
P/L	Tenacity/extensibility ratio
LV	Loaf volume
PCoA	Principal coordinates analysis

spread by the human population, reaching Europe via Anatolia and Greece (8000 years BP). In this expansion of the crop, one route went northward through the Balkans to the Danube and another went across Italy, from where two more routes spread wheat to France and Spain (7000 years BP) and to Tunisia, Algeria and Morocco (Feldman, 2001). A southern route dispersed wheat from the Fertile Crescent to Egypt and Libya (6000 years BP). Following the introduction of domesticated wheat, the plants were adapted to the local conditions in the host environments, where selection for adaptive traits took place in a dynamic evolutionary process. Traits that enabled harvesting and that facilitated the colonization of new environments, such as shattering resistance or flowering time fitted to the prevailing environmental conditions of the new territories, were likely initial targets. Many other traits, such as seed size, reduced plant height, lodging resistance, grains per plant, spike weight and grains per spike were probably co-selected by ancient farmers (Eckardt, 2010). During the dispersal of wheat, farmers took their habits wherever they went, not just cropping procedures but also other well-established technologies such as baking and fermenting (Royo et al., 2017). This process of migration and natural and human selection resulted in the establishment of a wide diversity of local landraces specifically adapted to their natural and cultural agricultural environments (Jones et al., 2008). A landrace is defined as 'a mixture of genotypes that evolved, largely by natural selection, under the environmental conditions in which they were grown'. Landraces are considered traditional and regional ecotypes with a high capacity to tolerate biotic and abiotic stresses resulting in an intermediate and stable yield level under low-input agricultural systems (Zeven, 1998).

Wheat landraces were grown for several millennia, evolving and mixing through natural and artificial selection (Zeven, 1998) and thus becoming a source of biodiversity for morphological, phenological, qualitative and quantitative traits (Moragues et al., 2006; Lopes et al., 2015). However, they began to be progressively displaced from cultivation in the early twentieth century with the advent of improved varieties derived from breeding programs. Landraces practically disappeared from commercial fields from the early 1970s due to the massive introduction of the homogeneous and more productive semi-dwarf varieties derived from the Green Revolution. Landrace cultivation is currently restricted to low-input farming conditions or to organic farming because landraces hold some unsuitable agronomic traits, such as tall plants, general lateness, low harvest index, and low yield when grown under intensive agronomic practices. The grains of landraces generally contain more protein, but of lower quality and with poorer rheological properties for modern products than the grains of improved cultivars (Guzman et al., 2019). However, there is a general consensus that landraces are valuable sources of genetic variation for breeding and research programmes, allowing the genetic diversity of modern wheats to be expanded by providing untapped gene pools (Lopes et al., 2015). Increasing crop diversity by exploiting the genetic variability of landraces is a suitable strategy for addressing the new challenges imposed by climate change, the growing human population and the plateau observed in the last decades in the mean yield of wheat (Grassini et al., 2013).

Dealing with the expected effects of climate change on wheat production and grain quality will require a deep understanding of the traits that make wheat fit into a given environment. The genetic variability and the specific adaptation of landraces to the regions where they are endemic make them an excellent plant material for such investigations. Mediterranean landraces are considered to hold great genetic variability for resistance to abiotic and biotic stresses, and for some quality characteristics (Lopes et al., 2015). Studies conducted with durum wheat have demonstrated that the climate prevalent in the zone of adaptation of Mediterranean landraces affected their developmental pattern and yield formation strategies (Royo et al., 2014). Furthermore, germplasm pools with distinct quality profiles have been identified in durum wheat landraces with different geographic origins within the region (Moragues et al., 2006).

The current study was conducted with 153 bread wheat landraces collected in 23 Mediterranean countries, with the aim of determining whether there is a relation between the prevalent climate in the area in which they were collected with their phenotypic expression in terms of agronomic performance and grain quality characteristics, and their genetic structure.

2. Materials and methods

2.1. Plant material

With the aim of sampling a portion of the unexplored genetic diversity of ancient wheats from the Mediterranean Basin, a panel of 153 bread wheat (*Triticum aestivum* L.) landraces from 23 coastal Mediterranean countries were used in the current study (Table S1). Landrace populations were provided by public gene banks from Germany (IPK, Gatersleben), Italy (ISC, S. Angelo Lodigiano), Romania (Suceava GenBank, Suceava), Russia (VIR, St. Petersburg), Spain (CRF-INIA, Madrid), the Netherlands (CGN-WUR, Wageningen) and the USA (NSGC-USDA, Aberdeen, ID). Accessions were bulk-purified during two cropping cycles to select the dominant type, and seed was increased on plots in the same field the year preceding each experiment to ensure a common origin for all lines.

2.2. Experimental set up

Field experiments were conducted under rainfed conditions in Gimenells, Lleida, north-east Spain in the 2016 and 2017 harvesting seasons (Table S2). The experiments consisted of a non-replicated augmented design with two replicated checks, the modern cultivars 'Anza' and 'Soissons' at a ratio of 1:5 between checks and tested genotypes. Plots consisted on eight rows of 3 m length spaced 0.15 m apart. Sowing density was adjusted to 250 germinable seeds m^{-2}. Minimum and maximum temperatures and rainfall were recorded daily from a weather station located close to the experimental fields.

At each plot the development of plants was monitored on a twice-weekly basis to record the following growth stages: GS31 (beginning of jointing), GS45 (boots swollen), GS55 (heading), GS65 (anthesis) and GS87 (physiological maturity). A plot was considered to have reached a given developmental stage when approximately 50% of the plants exhibited the stage-specific phenotypic characteristics. Plant height (PH, cm) was measured at GS87 in three main stems per plot from the tillering node to the top of the spike, excluding the awns. Before harvesting, samples of the plants in a 1-m-long stretch were pulled up in a central row of each plot. Samples were weighed after oven-drying them at 70 °C for 24 h, and harvest index (HI), crop dry weight (CDW, g m^{-2}), number of spikes per m^2 (NS) and number of grains per spike (NGS) were recorded. Grain yield (t ha^{-1}) was determined by mechanically harvesting the plots at ripening and is expressed at a 12% moisture level. Thousand kernel weight (TKW, g) was determined by counting the grains in 10 g drawn randomly from harvested grains of each plot. Grain filling duration was calculated as the number of days from anthesis to physiological maturity (GFD, days). The mean rate of grain filling (GFR, mg day^{-1}) was calculated for each plot as the ratio between grain weight and GFD.

Grain quality analyses were conducted at the Quality Laboratory of the International Maize and Wheat Improvement Centre (CIMMYT, Mexico). Test weight (TW, kg hL^{-1}) analysis was performed according to the AACC method 55-10 (https://www.cerealsgrains.org/resources/methods). The single kernel characterization system (SKCS) 4100 equipment (Perten Instruments, Sweden) was used to estimate grain hardness index (GH). Grain protein content (GP, % at 12.5% moisture basis) was determined using an NIR Systems 6500 machine (Foss, Denmark) with a calibration validated using the Kjeldahl method AACC 46–11A (AACC 2010) and the Dumas method (Leco equipment FP828, Leco Instruments, USA). Before milling, the grain samples were tempered with water according to their hardness and to the official AACC method 26–95 (AACC, 2010). The samples were milled into refined flour using a Brabender Quadrumat Senior mill (C.W. Brabender OHG, Germany). Flour yield (FY, %) was recorded. In the flour samples, protein (FP, % at 14% moisture basis) was determined by a DA7200 NIR machine (Perten Instruments, Sweden). Overall gluten quality was determined with the SDS-sedimentation test (FS, mL) performed according to Pena et al. (1990). Dough rheological properties were tested in the mixograph (National Mfg. Co.) to obtain optimum dough mixing time (MT, min) and torque (Peak, %Torque × min) according to the AACC method 54-40A (AACC, 2010). Additionally, 60 g flour samples were used in the alveograph (Chopin, France) to measure the tenacity/extensibility ratio (P/L) and elasticity or strength (W, J x 10^{-4}) according to the manufacturer's instructions and the AACC method 54-30A (AACC, 2010). Finally, bread-making quality was assessed using a direct dough method with 100 g of flour (AACC method 10-09). Bread loaf volume (LV, mL) was measured by rapeseed displacement using a volume meter. The dough water absorption levels used to run the mixograph, alveograph and baking tests were calculated according to Guzman et al. (2015).

2.3. Climate data

Long-term climatic data of the 23 countries origin of landraces was taken from the CLIMWAT 2.0 FAO database, using the CROPWAT software (http://www.fao.org/land-water/databases-and-software/cropwat). Following the methodology of Royo et al. (2014), a minimum of 15 years of data from 3 to 7 climatic stations located in the main wheat-growing areas of each country were used to determine the average daily values for minimum, maximum and mean temperatures (Tmin, Tmax and Tmean, °C), sunshine (h), solar radiation (Rad, MJ m^{-2} day^{-1}), relative air humidity (Rh, %), potential evapotranspiration (ET_0, mm, calculated by the Penman-Monteith method) and rainfall (Rain, mm). Climatic data were averaged for each country for the periods November 20–March 31 and April 1–June 30, assuming that they are almost coincident with the two main growing periods of wheat in the Mediterranean Basin, namely from sowing to anthesis (S-A) and from anthesis to physiological maturity (A-M) (Royo et al., 2014).

2.4. Genotyping

The 153 Mediterranean landraces were genotyped with 13177 SNP markers using the Illumina Infinium 15K Wheat SNP Array at Trait Genetics GmbH (Gatersleben, Germany). Markers were analysed for the presence of duplicated patterns and missing values. After excluding those markers with more than 25% missing values and a minor allele frequency (MAF) lower than 5%, a total of 10090 SNPs remained.

2.5. Statistical analyses

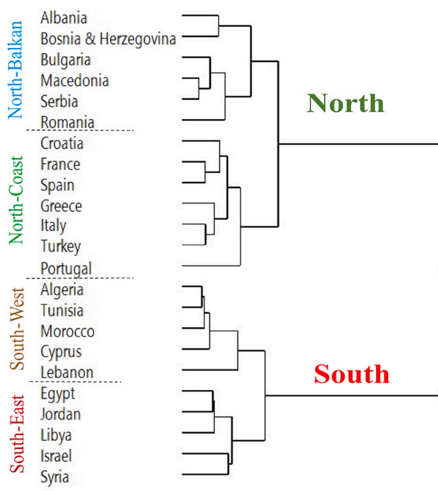
A hierarchical cluster analysis was performed with the average long-term values of Tmin, Tmax, Tmean, sunshine, Rad, Rh, ET_0 and Rain of the 23 countries of origin of the landraces for the periods S-A and A-M using the Ward method of the JMP V.14 software (SAS Institute Inc.) As the cluster clearly separated four geographic regions (Fig. 1A), differences between them for each long-term climatic trait and growing period were tested through ANOVAs in which country within region was used as error term. Raw data for agronomic and grain quality traits were fitted to a linear mixed model in which the check cultivars were considered as fixed effects and the row number, column number and landrace as random effects. Restricted maximum likelihood (REML) was used to estimate the variance components and to produce the best linear unbiased predictors (BLUPs) for the agronomic and grain quality data of each accession each year. The MIXED procedure of the SAS-STAT statistical package (SAS Institute Inc, Cary, NC, USA) was used with year, genotype and region as factors with the Kenward-Roger correction due to the unbalanced number of genotypes within each region. To compare the mean values between climatic regions of the agronomic and grain quality traits analysed, genotype within region was used as error term. Means were compared with the Tukey-Kramer correction at $P = 0.05$. Principal component analyses were performed separately for the 14 agronomic and the 11 grain quality traits using the correlation matrices obtained from the mean values of each of the 23 countries origin of the landraces. Pearson correlation coefficients were calculated between traits with the mean data of each genotype across years.

Genetic dissimilarities between countries were calculated according to Nei's genetic distance (Nei, 1972) using the with the GenAlEx software version 6.502 Peakall and Smouse (2012) and cluster analysis. The un-rooted neighbor joining tree and a principal coordinate analysis (PCoA) were performed using DARWin software version 6.0.11(https://darwin.cirad.fr/).

Multiple linear regression was performed for the 23 Mediterranean countries among the climatic data and the two first principal components from the PCoA using JMP V.14 software (SAS Institute Inc.).

3. Results

The current study reports on the relationship between environmental conditions in the zone of adaptation and phenotypic diversity for agronomic and grain quality traits relevant for breeding and commercial purposes of a panel of 153 bread wheat Mediterranean landraces grown a)



b)

Climatic zone	Tmin (°C)	Tmax (°C)	Tmean (°C)	Sunshine (h)	Rad (MJ $m^{-2}d^{-1}$)	Rain (mm)	Rh (%)	ET_0 (mm)
Sowing-anthesis								
South-East	7.8^{a}	19.0^{a}	13.4^{a}	6.2^{a}	12.7^{a}	188^{a}	67.1^{c}	299.2^{a}
South-West	7.7^{a}	17.8^{a}	12.7^{a}	5.4^{a}	11.1^{a}	316^{a}	70.9^{bc}	242.5^{a}
North-Coast	4.5^{b}	12.5^{b}	8.5^{b}	3.5^{b}	7.8^{b}	357^{a}	74.8^{ab}	171.1^{b}
North-Balkan	0.4^{c}	8.4^{c}	4.4^{c}	2.4^{b}	6.4^{b}	340^{a}	80.5^{a}	53.6^{c}
Anthesis-maturity								
South-East	15.1^{a}	29.3^{a}	22.2^{a}	9.6^{a}	23.7^{a}	20.0^{b}	51.0^{b}	531.1^{a}
South-West	13.8^{ab}	25.7^{b}	19.7^{b}	8.7^{a}	22.3^{a}	62.8^{b}	63.2^{a}	391.9^{b}
North-Coast	11.6^{bc}	22.3^{c}	16.9^{c}	7.3^{b}	19.4^{b}	152.1^{a}	63.8^{a}	333.6^{b}
North-Balkan	10.4^{c}	21.8^{c}	16.1^{c}	6.6^{b}	18.5^{b}	195.5^{a}	67.4^{a}	149.4^{c}

c)

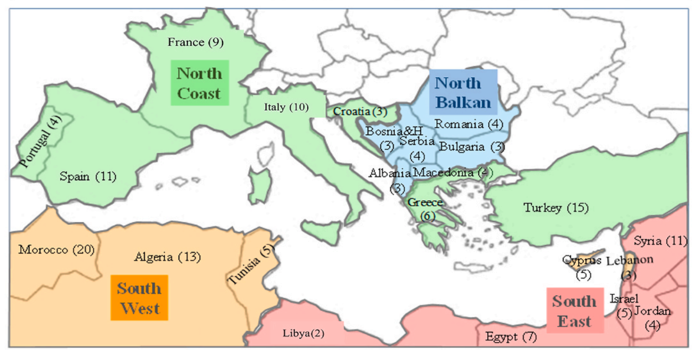


Fig. 1. Climatic regions identified in the Mediterranean Basin according to the long-term climatic data of the 23 countries where landraces were collected. a) Cluster showing the relationships between the long-term climatic data of the countries origin of the landraces, b) Average long-term climatic data of the four climatic regions arisen from the cluster, c) Map showing the number of landraces collected on each country. Colours indicate the four climatic regions arisen from the cluster. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

during two years in a random Mediterranean environment.

3.1. Climatic regions

Similarities in climatic conditions between the 23 countries were identified through a cluster analysis conducted with the long-term climatic data of each country for the periods sowing-anthesis and anthesis-maturity (Fig. 1A). The cluster included two main branches that further divided into another two. The two upper branches shown in Fig. 1A include northern Mediterranean countries: one includes countries of the north Balkan Peninsula (Albania, Bosnia & Herzegovina, Bulgaria, Macedonia, Serbia and Romania) and the other countries neighbouring the northern Mediterranean coast (Croatia, France, Spain, Greece, Italy, Turkey and Portugal). By contrast, the two lower branches include countries of the southern Mediterranean Basin, from both the east (Egypt, Jordan, Libya, Israel and Syria) and the west (in this case Cyprus and Lebanon jointly with Algeria, Tunisia and Morocco). The ANOVA, conducted to confirm these climatic dissimilarities between regions, showed statistically significant differences among them for all long-term climate traits (Fig. 1B). The comparison of their mean values showed that differences between the two northern regions were greater than those of the southern ones before anthesis, but smaller during the grain-filling period (Fig. 1B). The climatic variables that mostly differentiated the two regions within the northern side were the temperatures and ET_0 before anthesis, which were lower in the north Balkan countries than in the north-coastal ones. By contrast, the greatest differences between the two regions identified on the southern side were temperature, ET_0 and relative humidity during the grain-filling period. A map showing the four climatic regions is shown in Fig. 1C.

3.2. Relationship between climatic regions and agronomic performance

In order to assess whether the agronomic performance of landraces matched with a geographic structure and its possible relationship with the climatic features, a multivariate analysis was conducted with the mean data by country across years of the 14 agronomic traits analysed (Fig. 2). The first two axes of the principal component analysis (PCA) accounted for 68.0% of the variance existing in the agronomic data. PC1 had the largest weight (51.4%), and the position of the eigenvectors indicated that it was positively related to all traits except GFD, which was located in the negative part of this axis, and HI and NGS, which had no effect on it (Fig. 2A). Increases in PC2 were mostly associated with yield, HI, TKW, NGS, GFR and PH, while decreases were related mostly to NS and phenological variables. The points representing the countries of origin of the landraces are depicted in Fig. 2B. The position of points representing countries in the plane formed by the two PC axes followed a trend nearly matching with climatic regions, from the coldest and wettest (north-Balkan) to the warmest and driest (south-east), with some overlapping of the clusters grouping countries of the north-coast and those of the south-west. The results of the ANOVA showed that landraces from the four climatic regions significantly differed in all agronomic traits except for HI, NS, NGS and PH (Table S3). The comparison of the average values of the agronomic traits of landraces adapted to each region showed that those from north-Balkan countries had the longest developmental pattern, followed by those of north-coastal countries, south-western ones and south-eastern ones, which were the earliest (Table 1). North-Balkan landraces headed and flowered 10 days later than south-eastern ones. Yield values followed a similar pattern to that observed for phenological traits, but differences between the two northern zones were not statistically significant (Table 1). The highest and lowest yields were recorded in Romanian and Libyan landraces: 6.58 t ha^{-1} and 3.42 t ha^{-1}, respectively (Table S4). TKW was lowest in landraces from the south-eastern region. The heaviest grains were recorded in the Portuguese landraces (46.2 mg $grain^{-1}$) and the lightest in the Libyan ones (26.9 mg $grain^{-1}$) (Table S4). Cycle length was correlated positively with GFR and negatively with GFD (Table S4). Yield was not correlated with NS or GFD, but it was positively and significantly correlated with NGS, TKW and GFR (Table S5).

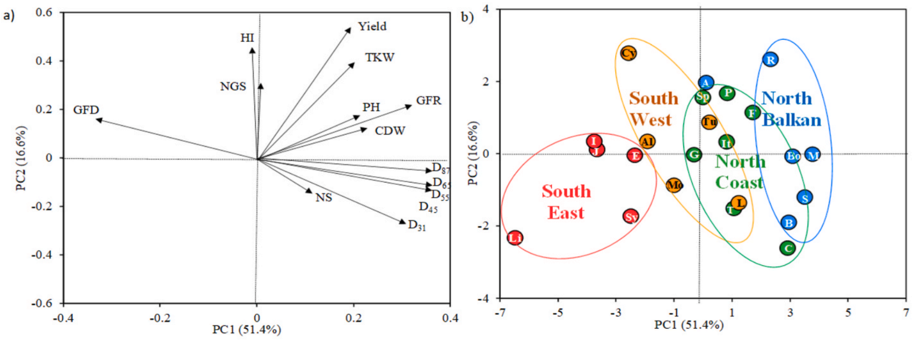


Fig. 2. Biplot of the first two axes of the principal component analysis summarizing the relationships between agronomic traits of landraces collected on each of the 23 countries. a) Eigenvalues of the correlation matrix symbolized as vectors representing agronomical traits. HI harvest index, NGS number of grains per spike, TKW thousand kernel weight, PH plant height, GFR grain filling rate, GFD grain filling duration, CDW crop dry weight, NS number of spikes per m^2, D_{31} days from sowing to the beginning of jointing, D_{45} days from sowing to boots swollen, D_{55} days from sowing to heading, D_{65} days from sowing to anthesis, D_{87} days from sowing to physiological maturity. b) Points representing the 23 countries origin of the landraces. A Albania, Al Algeria, Bo Bosnia & Herzegovina, B Bulgaria, C Croatia, Cy Cyprus, E Egypt, F France, G Greece, I Israel, It Italy, J Jordan, L Lebanon, Li Libya, M Macedonia, Mo Morocco, P Portugal, R Romania, S Serbia, Sp Spain, Sy Syria, Tu Tunisia, T Turkey. Colours correspond to the four climatic regions shown in Fig. 1: blue north-Balkan, green north-coast, orange south-west and red south-east. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Mean values for the 14 agronomic and the 11 grain quality traits of the panel of 153 Mediterranean bread wheat landraces included in the study according to their climatic region of origin. D_{31} days from sowing to the beginning of jointing, D_{45} days from sowing to boots swollen, D_{55} days from sowing to heading, D_{65} days from sowing to anthesis, D_{87} days from sowing to physiological maturity, GFD grain filling duration, GFR grain filling rate, HI harvest index, CDW crop dry weight, NS number of spikes per m^2, NGS number of grains per spike, TKW thousand kernel weight, PH plant height, TW test weight, GH grain hardness index, FY flour yield, GP grain protein, FP flour protein, FS flour strength, MT mixing time, W strength, P/L tenacity/extensibility ratio, LV loaf volume. Data are means across two crop seasons.

Trait	South-East (29)		South-West (46)		North-Coast (58)		North-Balkan (20)	
D31	104.8	c	104.6	c	108.4	b	111.6	a
D45	136.6	d	138.7	c	141.8	b	144.8	a
D55	143.4	d	146.8	c	151.0	b	154.3	a
D65	149.4	d	152.2	c	156.1	b	159.7	a
D87	183.6	d	185.2	c	187.7	b	189.3	a
GFD (days)	34.2	a	32.95	b	31.61	c	29.55	d
GFR (mg day^{-1})	0.99	c	1.18	c	1.28	b	1.37	a
Yield (t ha^{-1})	4.28	d	5.01	b	5.21	ab	5.52	a
HI	0.29	a	0.28	a	0.29	a	0.30	a
CDW (g m^{-2})	15.01	b	16.38	ab	16.19	ab	17.21	a
NS	528	a	541	a	532	a	535	a
NGS	24.73	a	24.85	a	25.81	a	26.66	a
TKW (g)	33.76	b	38.34	a	40.22	a	40.35	a
PH (cm)	121.4	a	122.8	a	123.9	a	126.9	a
TW (kg hL^{-1})	78.05	a	77.82	a	77.77	a	78.14	a
GH	47.12	a	38.40	b	41.22	ab	45.47	ab
FY (%)	63.77	a	63.11	a	63.75	a	64.04	a
GP (%)	12.78	a	13.07	a	12.66	a	12.95	a
FP (%)	10.45	a	10.72	a	10.36	a	10.60	a
FS (mL)	10.23	ab	9.30	c	10.01	b	10.68	a
MT (min)	2.24	a	1.77	b	21.27	a	2.30	a
Peak (%Torque × min)	88.83	a	68.43	c	81.54	b	88.49	a
W (J × 10^{-4})	161.6	b	125.5	d	150.8	c	183.9	a
P/L	1.52	a	1.59	a	1.38	a	1.55	a
LV (mL)	653	a	617	b	651	a	656	a

3.3. Relationship between climatic regions and grain-quality traits

The first two axes of the PCA carried out with the mean grain quality data of each country across years accounted for 68.7% of the variance contained in the data set (Fig. 3). Axis 1 accounted for 41.9% of the variance and was positively related to all the traits except GP and FP, which negatively affected this axis (Fig. 3A). Eigenvectors representing GP and FP were located on the opposite side to the one representing FY, in agreement with the negative correlation coefficients between them (Table S5). The small angle between vectors representing Peak and W and between Peak and MT (Fig. 3A) are a consequence of the close positive relationship between these grain characteristics (Table S5). Significant and positive correlations appeared between LV and FS, MT, Peak and W, and negative correlations appeared between MT and both GP and FP (Table S5). On the other hand, a significant negative relationship was found between LV and P/L, indicating that the higher the gluten extensibility (L), the better the bread-making quality.

The position of the points representing the 23 countries in the plane formed by the first two PC axes showed no geographical pattern related to the four climatic regions for the grain quality characteristics (Fig. 3B). Comparisons of the mean values of the quality traits recorded in landraces from the four climatic regions confirmed that differences were not statistically significant for TW, FY, GP, FP and P/L (Table S3), and a clear pattern was not observed for the remaining grain quality traits (Table 1). Nevertheless, landraces from south-western Mediterranean countries were clearly distinguishable from those of the other three climatic regions by their significantly lower values for FS, MT, Peak, W and LV, while north-Balkan landraces had the strongest gluten overall. The distribution of the points representing countries in Fig. 3B allowed three main clusters to be differentiated. The first one (1), placed in the upper-right part of the figure, included the points corresponding to Bosnia & Herzegovina, Bulgaria, Romania, Turkey and Syria. The closeness of the point corresponding to Bosnia & Herzegovina to the vector representing FS is indicative of the higher FS of the landraces from this country, which almost doubled the values of Libyan landraces (Table S6). Bulgarian and Romanian accessions showed the highest values for LV (500 mL) and GH (60.39), respectively. The second cluster (2) in Fig. 3B, located in the negative part of PC2, included points corresponding to Cyprus, Lebanon and Jordan, commonly characterized by their low FS values. Finally, the third cluster (3), located close to the origin of the axes, grouped all the remaining countries except Libya, whose position resulted from its low values for GP and FP. On this cluster the point corresponding to Croatia was detached from the rest in the direction of the vectors representing GP and FP because of the high values recorded for these two traits in Croatian landraces (13.80% and 11.38%, respectively, Table S6).

Correlation coefficients between agronomic and grain quality traits are shown in Table S5. Protein content, either in grain or flour, was positively correlated with cycle length and PH, but negatively correlated with GFD, yield, HI and NGS. Positive correlations were also obtained between phenological traits and both FS and LV, but kernel weight was negatively associated with GH, Peak, W and LV.

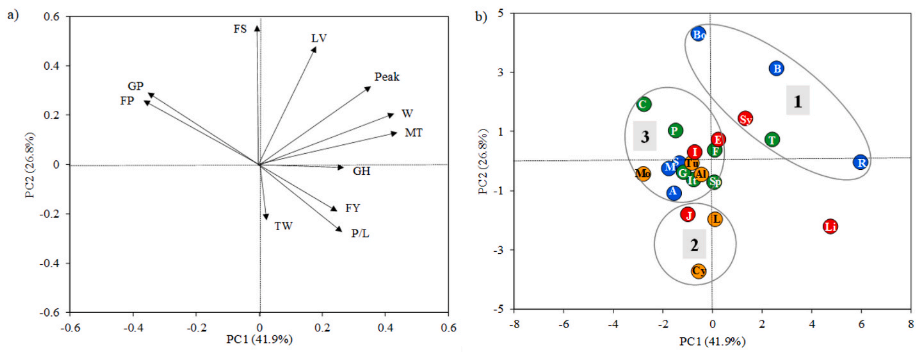


Fig. 3. Biplot of the first two axes of the principal component analysis summarizing the relationships between grain quality traits of landraces collected on each of the 23 countries. a) Eigenvalues of the correlation matrix symbolized as vectors representing grain quality traits. TW test weight, GH grain hardness index, FY flour yield, GP grain protein, FP flour protein, FS flour sedimentation, MT mixing time, W strength, P/L tenacity/extensibility ratio, LV loaf volume. b) Points representing the 23 countries origin of the landraces. A Albania, Al Algeria, Bo Bosnia & Herzegovina, B Bulgaria, C Croatia, Cy Cyprus, E Egypt, F France, G Greece, I Israel, It Italy, J Jordan, L Lebanon, Li Libya, M Macedonia, Mo Morocco, P Portugal, R Romania, S Serbia, Sp Spain, Sy Syria, Tu Tunisia, T Turkey. Colours correspond to the four climatic regions shown in Fig. 1: blue north-Balkan, green north-coast, orange south-west and red south-east. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.4. Genetic relationships among countries

The neighbor-joining dendrogram with genetic data showed two main clusters (Fig. 4A). The first cluster included the eastern and south-eastern countries, represented by all of the countries from the climatic zone 'South-East', and, Turkey and Lebanon. The second cluster included the countries from the 'North-Balkan' climatic zone and, France and Croatia. Finally the rest of the countries from the 'North-Coast' and 'South-West' climatic zones located in the centre of the dendrogram in undefined clusters.

A multiple linear regression (Table 2) was carried out to quantify the relation between climatic data and population structure based on the PCoA (Fig. 4B) during the periods from sowing to anthesis (SA) and anthesis to maturity (AM). Most of the climatic conditions explaining population structure during SA showed high values of R^2 (above 0.7) except Rh and rainfall, this last with a value of 0.0199, being Tmax and Tmean the highest values (0.8259 and 0.843 respectively). When the period AM was analysed half of the climatic conditions showed R^2 values above 0.6, being in this case the rain one of the most important conditions explaining the genetic structure (R^2 = 6708), with maximum values for Sunshine (0.6974) and radiation (0.6853).

Table 2
Relationship between climatic data and population structure revealed by PCoA for the 153 Mediterranean landraces.

Climatic variable	R^2 (SA)	R^2 (AM)
ET_0	0.7166	0.5502
Rh	0.5175	0.2814
Rad	0.8053	0.6853
Rain	0.0199	0.6708
Sunshine	0.8032	0.6974
Tmax	0.8259	0.5672
Tmean	0.8143	0.6175
Tmin	0.7604	0.5808

ET_0, accumulated potential evapotranspiration; Rh, average daily relative humidity; Rad, average daily solar radiation; Rain, average daily rainfall; Tmax, average maximum daily temperature; Tmean, average mean daily temperature; Tmin, average minimum daily temperature.

4. Discussion

Assessment of the phenotypic diversity of wheat landraces evolving from their centre of origin to environments climatically distant from it may deliver significant information for the release of next-generation wheat varieties resilient to the negative effects of climate change. The current study presents a comprehensive phenotypic characterization of 153 bread wheat landraces collected in 23 Mediterranean countries for relevant agronomic and grain quality traits and analyses the relationship of the phenotypic performance and the climate of the regions where landraces are well adapted.

As country is a political concept, the first step consisted in identifying regions with similar climates within the Mediterranean Basin according to Royo et al. (2014). The multivariate analysis conducted with the long-term climate data of the main wheat-growing areas within each country revealed a geographic structure that clearly separated countries located on the northern side from those situated on the southern side of the Mediterranean Sea. The northern countries were characterized by lower temperatures, sunshine, radiation and ET_0, but higher rain and

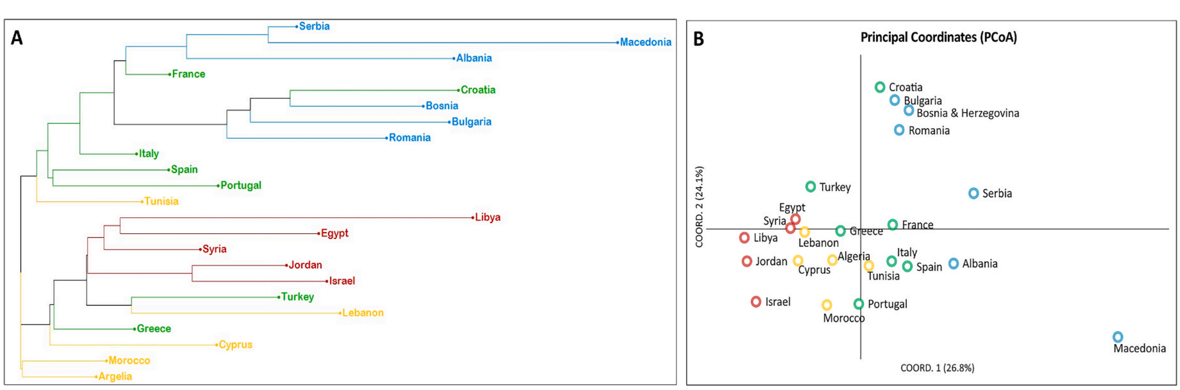


Fig. 4. A) Neighbor joining tree and B) Principal Coordinate Analysis of the 23 Mediterranean countries based on genotypic data of 153 Mediterranean landraces. Colour code correspond with the climatic regions: Blue, North Balkan; Green, North Coast; Orange, South West; Red, South East. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

relative humidity during the whole crop season than the southern ones. This differentiation is in agreement with that established by Köppen's climate classification, which identifies different climates on the northern and the southern shores of the Mediterranean Basin. Thus, landraces collected in northern Mediterranean countries are adapted to colder temperatures during the whole growth cycle and to more water availability, particularly during the grain-filling period, than those collected in southern-Mediterranean ones. Temperatures and ET_0 were the climatic variables that most contributed to distinguishing two climatic zones within countries of each coast, with the greatest differences between them being found during the pre-anthesis period on the northern side and during grain-filling on the southern side.

The PCA conducted with the field data revealed that the agronomic performance of the landraces was related to the geographic structure arising from the prevalent climate in each country of origin. The traits that best differentiated between climatic regions were those related to crop phenology, whose length increased steadily from the warmest and driest zone (south-east) to the coldest and wettest one (north-Balkan). This result is consistent with the reduction in flowering time induced in wheat by high mean temperatures and drought during the growing period (Gooding et al., 2003). From south-eastern landraces to north-Balkan ones, time to anthesis increased but GFD decreased in accordance with the positive relationship found in this and other studies between late anthesis and short grain fill (Tewolde et al., 2006). A negative relationship was observed in the current study between GFD and GFR, with the latter being significantly higher in northern landraces. Although the higher temperatures during grain filling experienced in southern countries could enhance the movement of photosynthates from the flag leaf to the spike, they did not increase the GFR of the landraces, probably because high respiratory losses of C also occur at high temperatures (Wardlaw et al., 1980). For this reason, high temperatures during grain filling decrease the grain weight of wheat, in agreement with the results of the current study. GFR was strongly and positively correlated with TKW ($r = 0.88$, $P < 0.001$), which accounted for 25% of the yield variations and was lowest in south-eastern landraces. This is a plausible result given the results of previous studies that have shown that grain weight is the most stable yield component (Royo et al., 2006; Patil et al., 2013), is highly heritable and has a positive effect on yield formation (Maccaferri et al., 2011). Our results support the conclusions of Royo et al. (2006) and Lin et al. (2020) about the critical role of GFR in grain weight and yield determination.

Although the yield obtained in landraces from the two northern climatic regions was similar, yield decreased from the coldest and wettest region to the warmest and driest one, as north-Balkan landraces outyielded south-western ones by 10% and south-eastern ones by 29%. The high yields recorded, considering the rainfed conditions of the field trials, could be attributed to the high soil fertility (~3% of organic matter) and the superficial subsoil water layer at this site. Previous studies (Annicchiarico et al., 1995; Royo et al., 2014) reported that drought stress and high temperature at the collecting site of landraces shortened cycle length, thus affecting their yield potential. Our results showed that late flowering landraces collected in wetter zones produced more biomass at ripening than those collected in drier zones, in agreement with the negative effects of water scarcity on the growth of wheat reported by Villegas et al. (2001) and Royo et al. (2004).

In contrast with the results relative to agronomic performance, the grain quality of Mediterranean landraces did not follow a pattern related to the climate of the regions where they originated. Cluster (1) in Fig. 3B (which includes points corresponding to Bosnia & Herzegovina, Bulgaria, Romania, Syria and Turkey), may be associated with the route of wheat expansion to the north-east from the domestication region in the south of Turkey and Syria to the west Balkan countries (Feldman, 2001). It can be hypothesized that during this migration landraces evolved, probably mediated by humans, to adapt their grain characteristics to the preferences of local populations. A second hypothesis that would explain the partition of north-Balkan countries into two different clusters, one including Bosnia & Herzegovina, Bulgaria and Romania and the other combining Albania, Macedonia and Serbia with Greece, would be a different origin of the Balkan landraces in clusters (1) and (3). Previous studies have suggested that wheats from Bulgaria and other Balkan countries may have their origin on the steppes of southern Russia and in the Volga region (Melnikova et al., 2010). This hypothesis is supported by the different grain quality found in durum wheat landraces from the north Balkan areas and that found in those collected in other Mediterranean zones (Nazco et al., 2012). Whatever the case, the results of the current study show that landraces from Bosnia & Herzegovina, Bulgaria and Romania have higher gluten strength overall than those from other Mediterranean countries. This may be related to a preference in this region for leavened breads, which require a certain gluten strength to obtain a desirable volume and texture.

The closeness of the points corresponding to Jordan, Cyprus and Lebanon may also suggest specific quality requirements in these geographically near countries that the current research revealed to be mostly associated with low FS and LV. Libyan landraces were not included in any cluster, but their primary characteristic was the low protein content of their grains and flour. Given that these countries are very important consumers of durum wheat, it is conceivable that the bread-making quality of bread wheat did not receive great attention because durum is often used for that purpose. The lower values for GH, MT, Peak, W and LV found in landraces from south-western Mediterranean countries may be due to the same reason or to the preference in this region for flat breads, which require less gluten strength.

Crop phenology was weakly related to grain quality. Though the number of days needed to reach growth stages from booting to physiological maturity was positive and significantly correlated with protein content, FS and LV, none of those phenological variables accounted for more than 9% of the variation for these quality traits. The negative correlation coefficient found in this study between yield and GP has been widely reported in the literature and has been a primary reason for the low improvements observed in grain protein content of high yielding varieties (Blanco et al., 2012).

The use of molecular markers revealed a more complex clustering with higher level of admixture among the landraces in the genetic classification than the reported by climatic data, suggesting genetic exchange during the migration process. Only landraces from the south-east of the Mediterranean basin are all grouped in the same cluster without landraces from other areas. When the North Balkan countries were considered differences were found between the climatic and genetic relationships. According to the genetic structure countries were grouped following a geographic pattern with north and eastern countries grouping together in one cluster (Bosnia and Herzegovina, Romania and Bulgaria) and south-eastern countries separated in another one (Albania, Macedonia and Serbia) probably due to higher trade exchange between closer countries. Croatia, grouped by climatic data within North-Coast cluster, was grouped genetically with the North-Balkan landraces from Bosnia and Herzegovina, Bulgaria and Romania, whereas French landraces were genetically more related to those from Albania, Macedonia and Serbia. North-Coast and South-West clusters were better defined by climatic similarities than genetic structure, that according to Rufo et al. (2019) landraces from these countries showed higher level of admixture mainly due to genetic exchange during the migration process.

Multiple regression analysis between climatic data and genetic structure of Mediterranean landraces grouped by their country of origin showed the relevance of the high temperatures before anthesis and rainfall, solar radiation and sunshine after anthesis in population differentiation.

5. Conclusions

The results of the current study highlight the great variability within Mediterranean bread wheat landraces for traits associated with field performance and grain quality characteristics. Clear discrepancies have been identified in the agronomic performance of landraces collected on the northern and southern sides of the Mediterranean Sea. The contrasting crop phenology, yield, grain weight and grain-filling rate of landraces that originated in each of the four climatic regions identified within the Mediterranean Basin reveals a great association of local climate on the configuration of these agronomic traits. The similar plant height, harvest index, number of spikes per unit area and number of grains per spike of landraces that originated in regions with a contrasting climate suggest that these traits play a minor role in the pattern of adaptation of wheat landraces to the local conditions within the Mediterranean Basin.

In contrast with the agronomic performance, grain quality characteristics were not related to the climate prevalent in the regions of origin of the landraces. Though large differences were not found in the grain quality of bread wheat landraces from most countries surrounding the Mediterranean Sea, some of them showed specific quality features. Landraces from Bosnia-Herzegovina, Bulgaria and Romania differed from the rest in their strong gluten and high loaf volume, mixing time and grain hardness, while the opposite attributes were found in those from Jordan, Lebanon and Cyprus.

Genetic relationships using molecular markers found higher levels of admixture within the North-Coast and South-West regions of the Mediterranean basin, mainly due to the germplasm exchange during the migration process from the Fertile Crescent.

This study allowed the identification of landraces suitable to be used in breeding programmes because of their outstanding agronomic and/or grain quality characteristics. Among them, crosses between higher yield and grain protein content have special interest. The landraces Santareno, TRI 14046 and Bladette de Puylaurens present high yield, TKW and GP, whereas the landraces CGN06247 and CGN06255 showed high yield, NS and GP. The detection of allele variants and QTLs associated with them will facilitate their introgression in adapted phenotypes, thus increasing the genetic background of modern cultivars, their resilience to climate change and the fulfilment of consumer's quality requirements.

Author contributions

Conxita Royo: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Resources; Validation; Roles/Writing - original draft; Writing - review & editing. Jose Miguel Soriano: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Supervision; Roles/Writing - original draft; Writing - review & editing. Rubén Rufo: Data curation; Formal analysis; Investigation; Methodology; Writing - review & editing. Carlos Guzmán: Data curation; Formal analysis; Investigation; Methodology; Resources; Validation; Writing - review & editing.

Declaration of interests

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jcs.2022.103478.

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