



Yield formation strategies of durum wheat landraces with distinct pattern of dispersal within the Mediterranean basin I: Yield components

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Abstract

This study was undertaken to ascertain whether the pattern of dispersal of durum wheat within the Mediterranean basin is associated with variation in phenology and yield formation strategies. A set of 52 durum wheat landraces, previously genetically characterized as been dispersed by the north or south of the Mediterranean region, were grown in three rainfed sites in a dry-temperate region (Lleida, NE Spain), and crop phenology, yield and yield components were determined. Northern genotypes had a larger number of stems per unit area, but a lower percentage of fertile tillers and fewer grains per spike than southern landraces. Grain yield for the northern dispersal group was mainly related to variations in thousand-kernel weight, while the number of spikes per m² was the component most highly correlated with yield among southern genotypes. These contrasting yield formation strategies are probably a consequence of the different climates prevalent in the zones of adaptation, and likely conferred adaptive advantages to the genotypes of one or the other group. Our results suggest that gradual changes in yield components occurred during the movement of durum wheat from east to west through the north side of the Mediterranean basin. According to our results, the weight of grains and the number of spikes per unit area may be selection criteria to improve adaptation for the northern and the southern parts of the Mediterranean basin, respectively.

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1. Introduction

Durum wheat (*Triticum turgidum* L. var *durum*) originated in the Fertile Crescent around 10,000 B.P.

(before present). From there it spread west through southern Europe, reaching North Africa around 7000 B.P. (Feldman, 2001). Recently, a second route of dispersal through North Africa, assumed to have occurred during the middle ages, has been reported (Moragues et al., submitted for publication).

At present, durum wheat is grown mostly in rainfed areas of the Mediterranean region under stressful and

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variable environmental conditions. Most rain falls during autumn and winter, and water deficit appears in spring, resulting in a moderate stress for wheat around anthesis, increasing in severity throughout the grain filling period (Edmeades et al., 1989). Nevertheless, different climatic conditions exist in the north and the south of the Mediterranean basin. The north part changes progressively from east to west from cold to temperate climate (classes D and C, respectively, according to Koeppen climate classification) (Leemans and Cramer, 1991; <http://www.fao.org/sd/EI-direct/climate/EIsp0002.htm>), but the south of the Mediterranean is characterized by a dry climate (class B according to the same classification) having temperate climate with terminal drought stress for wheat cultivation. Hence, contrasting adaptation strategies may have occurred during the spread of wheat through the north of the Mediterranean basin (via Turkey, Balkan Peninsula, Greece and Italy) versus those dispersed through the south (via North Africa). Landraces are adapted to the environmental conditions and agronomic practices of their regions of origin; thus, they are a valuable tool for identifying different strategies of adaptation and grain yield formation.

Grain yield can be analyzed in terms of three primary yield components (number of spikes per unit land area, product of number of plants per land area and number of spikes per plant, number of grains per spike and mean grain weight). These components develop sequentially, with later-developing components under control of earlier developing ones (Hamid and Grafius, 1978; García del Moral et al., 1991; Dofing and Knight, 1992). Tillering is one of the first developmental processes; it occurs during early growth and mainly depends on sowing density and the availability of water and nitrogen (García del Moral et al., 1991; Simane et al., 1993). Development of floral primordia happens during rapid vegetative growth; then, competition for limiting resources may take place between vegetative and floral organs (Austin et al., 1980; Miralles et al., 2000). Later, grain filling is maintained by a high contribution from assimilation before and immediately after anthesis and remobilization of vegetative reserves during grain growth (Royo et al., 1999), particularly under water and nitrogen shortage (Simane et al., 1993). Compensation of yield components occurs as a result of

competition for limited resources (Simane et al., 1993; Miralles et al., 2000).

Environment strongly affects yield and its components; moreover, correlation studies in barley (Rasmuson and Cannell, 1970) and durum wheat (García del Moral et al., 2003) provide additional evidence of the important effect that environmental variation has on the relationships among yield components. Drought stress may cause a reduction in all the yield components, but particularly in the number of fertile spikes per unit area and in the number of grains per spike (Giunta et al., 1993; Simane et al., 1993; Abayomi and Wright, 1999), while kernel weight is negatively influenced by high temperatures and drought during ripening (Chmielewski and Kohn, 2000). In addition, genetic divergence correlating to environmental differences have been found for emmer wheat (Li et al., 2000).

There are numerous diversity studies based on molecular markers that reveal relationships between genotypes, but studies relating this to the agronomic performance of these genotypes are lacking. In a previous study, we analyzed 63 durum wheat landraces from the Mediterranean basin by means of AFLPs and microsatellite markers (Moragues et al., submitted for publication). Non-metric multidimensional scaling clustered the accessions according to their geographical origin, revealing two patterns of dispersal of durum wheat within the Mediterranean region from the Fertile Crescent, one through the north side and a second one through the south. Given that the north and the south of the Mediterranean basin have different climatic conditions and human selection may have act in a different way in the two regions, we conducted this research to ascertain whether the zone of adaptation of the landraces affected their yield formation strategies. This is the first of a series of two papers addressing changes on yield formation and biomass partition and allocation (part II, Moragues et al., 2006) as response to human and natural selection in the two zones of adaptation.

2. Materials and methods

2.1. Plant material and experimental design

Three field experiments were conducted during the 2001–2002 crop season at three sites (Gimenells,

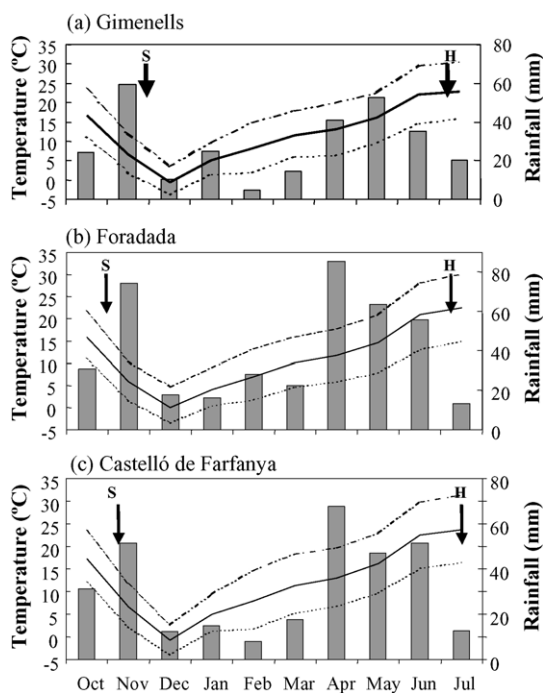


Fig. 1. Monthly rainfall (bars) and maximum (dashed line), mean (solid line) and minimum (dotted line) temperatures during the growth cycle at the experimental sites. S and H indicate sowing and harvesting times, respectively, in 2001–2002.

Castelló de Farfanya and Foradada) of the province of Lleida (north-eastern Spain) (Table 1). The three sites differ in their soils, weather (mostly rain distribution, see Fig. 1) and usual agronomic practices, thus giving contrasting growing conditions that lead to a range of grain yield potentialities. The test sites were located in a temperate-dry area with a climate not as cold as the existing in the north-east of the Mediterranean basin, but not as dry as the north-east African climate. Thus, they may be considered as intermediate between the extreme cold and dry environments existing along the Mediterranean Sea, but similar to the prevalent in some areas of Morocco, Argelia and Tunisia.

From the 63 durum wheat landraces previously characterized genetically, only the 52 that were properly classified by AFLPs and SSR as belonging to one of the two dispersal groups (Moragues et al., submitted for publication) were used in this study. Sixteen and 36 of them corresponded to landraces dispersed through the north and the south of the Mediterranean basin, respectively (Table 2).

In each experiment, landraces were mechanically sown in an alpha-lattice incomplete-block design with three replicates. The seeding rate was adjusted to 250 viable seeds per m^2 . The plot size was 4.8 m^2 (eight rows, 0.15 cm apart and 4 m length). Each plot was divided in two parts of 2 m of length each, one used for destructive sampling and the other for yield determination.

2.2. Components of yield formation

Days from sowing to the principal phenological stages (jointing, E.31; heading, E.55; and physiological maturity, E.91) were determined in each plot using the Zadoks's decimal code (Zadoks et al., 1974). The number of stems per m^2 , the number of spikes per m^2 and the number of grains per spike were determined at maturity from a sample of 1 m of a central row on each plot. Fertile tillering (FTi) was calculated as the number of spikes per m^2 containing grains divided by the total number of stems per m^2 . The number of spikelets per spike was determined as the average spikelet number of 15 spikes randomly selected from the sample. The number of grains per spikelet was the result of dividing the number of grains per spike by spikelets per spike. Thousand-kernel weight (TKW) was also determined in each plot. Plots were mechanically harvested at ripening and yield was expressed at 12% grain moisture content.

2.3. Statistical analyses

Combined analyses of variance for grain yield, primary and secondary yield components, and phenological traits were performed. Replications nested within sites and incomplete blocks nested within replications and sites were considered as random factors, whereas site, dispersal pattern and genotype nested within dispersal pattern were fixed. The factor "genotype" was divided into "genotype within northern dispersal" and "genotype within southern dispersal". Tukey's test (Hsu, 1996) was performed to determine the significance of the difference between means of dispersal patterns. Principal component analyses were performed on the correlation between adjusted means of each landrace to determine the relationships between yield components. Stepwise regression analyses were

Table 1
Description of experimental sites

	Gimenells	Castelló de Farfanya	Foradada
Coordinates	41°38'N 0°23'E	41°47'N 0°45'E	41°88'N 0°76'E
Altitude (m.a.s.l.)	200	325	580
Soil classification	Calcixerolic xerochrept	Xerolic paleorthid	Gypsic xerochrept
Rainfall (mm)			
From sowing to harvesting	186	281	371
Grain filling period	38.8	58.2	67.0
Average temperatures during growth cycle (°C)	10.9	11.2	9.8
Average temperatures during grain filling period (°C)	19.6	20.8	19.7
Average growing-degree days from sowing to heading	1154	1242	1367
Average number of days from sowing to heading	156	176	196
Range of heading dates	22 April–5 May	21 April–9 May	8–21 May
Fertilizers (kg ha ⁻¹)			
N (seed bed + top dressing)	76 + 110	28 + 105	60 + 105
P	62	23	26
K	118	52	50
Weed control	2,4 D + MCPA Metabenzotiazuron	Tibenuron Metil diclofop	Metabenzotiazuron
Sowing date	26 November 2001	8 November 2001	1 November 2001
Harvest date	5 July 2002	17 July 2002	11 July 2002
Previous crop	Alfalfa	Fallow	Barley

Table 2
Landraces used in this study classified according to their pattern of dispersal determined by molecular markers

Country	Cultivars ^a	Seed source
North dispersal		
Turkey	BGE-018192; BGE-018350; BGE-018351; BGE-018353; BGE-019262; BGE-019264; BGE-019265; BGE-019266; BGE-019269	CRF
Cyprus	IG-82547; IG-82549	ICARDA
Greece	IG-96851	ICARDA
Italy	IG-82555; IG-83905; IG-83920	ICARDA
Portugal	BGE-012329	CRF
South dispersal		
Syria	IG-95841; IG-95931	ICARDA
Lebanon	IG-84856	ICARDA
Egypt	BGE-000168; BGE-012451	CRF
Greece	IG-96802	ICARDA
Algeria	IG-92895; IG-92967; IG-93621; IG-94009	ICARDA
Italy	IG-82551	ICARDA
Morocco	BGE-020916	CRF
Spain	BGE-018632; Andalucía 344; Azulejo de Villa del Río; Recio cañimacizo de Cañete; Enano de Jaén; Alonso de Málaga; Berberisco de Fernan Núñez; Claro de Balazote; Recio Cañimacizo; BGE-018599; BGE-013600; Ruso; Entrelargo de Montijo; BGE-013614; Rubio de Montijo; Rubio de Miajadas; Blanco de Baleares; Blanco; Asolacambre; Farto Cañifino; Morisco de Tenerife	CRF
Portugal	BGE-012409; BGE-012486; BGE-012532	CRF

^a BGE-numbers are codes from Centro de Recursos Fitogenéticos (I.N.I.A., Madrid); IG-numbers are codes from ICARDA bank germplasm; otherwise are cultivar names.

developed for the genotypes belonging to each pattern of dispersal independently, considering yield as the dependent variable and phenological traits and yield components as independent variables. SAS Institute Inc. (2000) procedures and programs were used for these calculations.

3. Results

3.1. Effect of environment and dispersal pattern on yield and related traits

The combined analyses of variance revealed an important environmental effect on all traits evaluated (Table 3), but especially phenological development, TKW and yield. The pattern of dispersal had also a significant effect on the number of stems per m², days to jointing, fertile tillering, days from sowing and jointing to heading, and number of grains per spike.

Significant interactions were found between patterns of dispersal and sites for some traits, but except for yield and TKW they were non cross-over in nature.

Gimenells was the most productive site, followed by Foradada and Castelló de Farfanya (Table 4). Northern genotypes had higher yield and TKW than the southern group at Gimenells, similar at Foradada, but lower at Castelló de Farfanya (Table 4).

The final yield reached by genotypes dispersed by north and south Mediterranean basin was similar (Table 5) given the compensation between primary yield components. Thus, while southern landraces had 4.9% more grains per spike than northern ones, they had 5.5% fewer spikes per m², although the latter difference was not statistically significant according to the Tukey's test. Northern landraces had 9.3% more stems per m² than southern ones, but 6.2% fewer fertile spikes. In spite of being significant, differences in plant phenology were too small (less than 4% in all cases) to have biological sense, and thus, they are not considered further.

Differences between landraces were significant for all yield components (Table 3). Moreover, genotypic variability within dispersal patterns existed for all the traits analyzed. Landraces from the north showed greater variability than those from the south in fertile tillering, days from sowing to jointing, number of grains per spikelet, spikes per m² and grains per spike (Tables 3 and 5). In contrast, greater variation in the

Table 3
F values of the combined ANOVA for yield and yield components of 52 durum wheat genotypes with different patterns of dispersal (north and south) through the Mediterranean basin and evaluated in three sites during 2001–2002

Source of variation	d.f.	Yield	Spikes per m ²	Grains per spikelet	Thousand-kernel weight	Stems per m ²	Fertile tillering	Spikelets per spike	Grains per spikelet	Days from sowing to		Days from jointing heading	Days from filling period
										Jointing	Heading		
Site	2	140****	24.1**	12.4**	212****	29.6****	22.5**	31.6****	23.8**	2959****	10857****	217****	31.9****
Dispersal	1	0.01	3.14	4.68*	0.3	14.0****	13.0****	1.6	3.51	13.5**	9.02**	7.92**	0.82
Site × dispersal	2	8.34***	0.11	6.70**	7.72**	0.48	0.67	2.81	5.89**	0.28	3.31*	0.61	0.71
Genotype (dispersal)	50	5.79****	2.07***	2.13****	5.01****	2.46	2.05	4.67****	1.54*	1.79**	24.15****	2.53****	3.79****
Within north	15	3.58***	3.10****	3.05****	5.21****	1.60	4.42	4.48****	2.07*	3.80****	26.43****	3.60****	4.09****
Within south	35	6.65****	1.67*	1.73*	4.99****	2.84	0.96	4.75****	2.16	0.94	23.13****	2.08****	3.67****
Site × genotype (dispersal)	100	1.70	1.22	1.01	1.30	1.38	1.62**	2.04****	1.23	1.29	1.53**	1.30	1.55**
Environment × within north	30	1.28	1.32	1.87**	1.71*	1.41	2.10**	1.96*	1.31**	2.96****	1.33	2.48****	1.51
Environment × within south	70	1.90	1.17	0.64	1.13	1.37*	1.44*	2.07****	0.83	0.57	1.63**	0.77	1.52

* P < 0.05.

** P < 0.01.

*** P < 0.001.

**** P < 0.0001.

Table 4
Yield and thousand-kernel weight for each dispersal group at each site

	Northern dispersal	Southern dispersal	Average
Grain yield (t ha ⁻¹)			
Gimenells	3.57 a	3.38 b	3.47
Foradada	2.25 a	2.24 a	2.24
Castelló de Farfanya	1.38 b	1.59 a	1.48
Thousand-kernel weight (g)			
Gimenells	50.6 a	49.3 b	49.9
Foradada	40.7 a	40.4 a	40.5
Castelló de Farfanya	37.4 b	39.5 a	38.4

Site means within rows with different letters (a and b) are significantly different at 5%.

number of stems per m² and grain yield was detected in southern genotypes.

3.2. Relationships between yield and its components as affected by dispersal pattern

Principal component analyses were performed independently for each dispersal group of genotypes to determine the relationships between yield and its components. The first two axes of the principal component analysis for the northern dispersal group explained 38.5 and 19.9%, respectively, of the variability found. Given that most of the variation could be explained by considering these two axes, we used the projections of the data points on the planes

determined by the axes 1 and 2. The (a) graphs of Figs. 2 and 3 represent the eigenvectors of the characteristics that most influence each axis. The length of the projection of each of them on each principal component axis (PC1 and PC2) measures the weight (loading or eigenvalue) of its influence on that axis, whereas the cosine of the angle between any two vectors is inversely proportional to their correlation. The first axis of Fig. 2a was positively related to the number of spikes per m² and its components, i.e., stems per m² and percent of fertile spikes, while it was negatively related to the number of grains per spike and its components, i.e., spikelets per spike and grains per spikelet. The second axis was mainly related to yield and the length of grain filling period on its positive values and the stem elongation period duration on its negative. Fig. 2a shows a strong relationship between yield and TKW and the duration of grain filling period, whereas the length of the stem elongation period and days to heading were negatively correlated to grain yield, because the vectors form an angle between 90° and 180°, with a negative cosine.

The (b) graphs of Figs. 2 and 3 represent the projection on the planes 1 and 2 of the points representing the mean genotype values across environments. Fig. 2b shows that genotypes from Turkey and Cyprus clustered together and separately from the Italian genotypes. The clusters were formed following a westward direction on the eigenvectors corresponding to spikelets per spike and stems per m².

Table 5

Mean values of yield and yield components of durum wheat landraces with different patterns of dispersal across the Mediterranean basin

	Northern dispersal		Southern dispersal		Difference	
	Mean (a)	Range	Mean (b)	Range	a – b	(a – b)/a × 100 (%)
Yield (t ha ⁻¹)	2.40	2.05–2.89	2.40	1.57–3.04	0.00	0.0
Number of spikes per m ²	237	152–325	224	157–285	13	5.5
Number of grains per spike	28.8	24.2–50.0	30.2	22.7–35.7	–1.4*	–4.9
Thousand-kernel weight (g)	42.9	35.7–48.4	43.1	36.8–50.2	–0.2	–0.5
Number of stems per m ²	313	258–377	283	195–360	30***	9.3
Fertile tillering (%)	73.7	54.7–89.5	78.3	68.9–87.4	4.6***	–6.2
Number of spikelets per spike	17.4	15.1–19.3	17.6	14.9–21.5	–0.2	–1.1
Number of grains per spikelet	1.66	1.50–2.21	1.73	1.54–2.06	–0.07	–4.0
Days to heading	176.4	167–180	175.9	170–181	0.5**	0.3
Days to jointing	144	139–154	142	139–145	2***	1.3
Days from jointing to heading	41.3	32.5–45.9	42.9	31.4–48.4	–1.6**	–3.9
Grain filling duration (days)	37.9	34.2–41.7	38.2	34.6–43.1	–0.3	–0.8

* P < 0.05.

** P < 0.01

*** P < 0.001 according to Tukey's test.

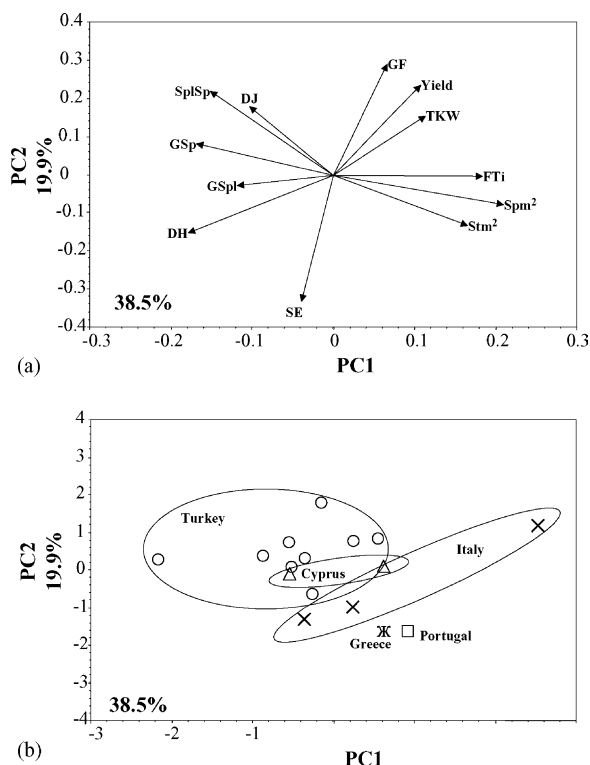


Fig. 2. Principal component analysis (PCA) projections on axes 1 and 2, accounting for 58.4% of total variance, for 16 northern dispersal Mediterranean durum wheat genotypes. (a) The eigenvalues of the correlation matrix are symbolized as vectors representing yield, number of spikes per m^2 (Spm^2), number of grains per spike (GSp), thousand-kernel weight (TKW), number of stems per m^2 (Stm^2), fertile tillering (FTi), number of spikelets per spike (Sp1Sp), number of grains per spikelet (GSp1), days to jointing (DJ), days to heading (DH), stem elongation period duration (SE) and grain filling duration (GF). (b) Plot of the points corresponding to genotypes from Turkey (○), Cyprus (△), Greece (⌘), Italy (×) and Portugal (□).

Thus, clusters for Turkish and Cypriot genotypes were located in the left upper quadrant, whereas the ones from Italy and the points corresponding to the Portuguese and Greek genotypes were in the lower right quadrant.

The first two axes of the PCA for southern dispersal group of genotypes explained 30.2 and 28.0% of the total variation, respectively (Fig. 3). The first axis was related to the number of grains per spike, the number of grains per spikelet and the grain weight in a positive direction and to the number of spikes per m^2 and stems per m^2 in a negative direction. The second axis was

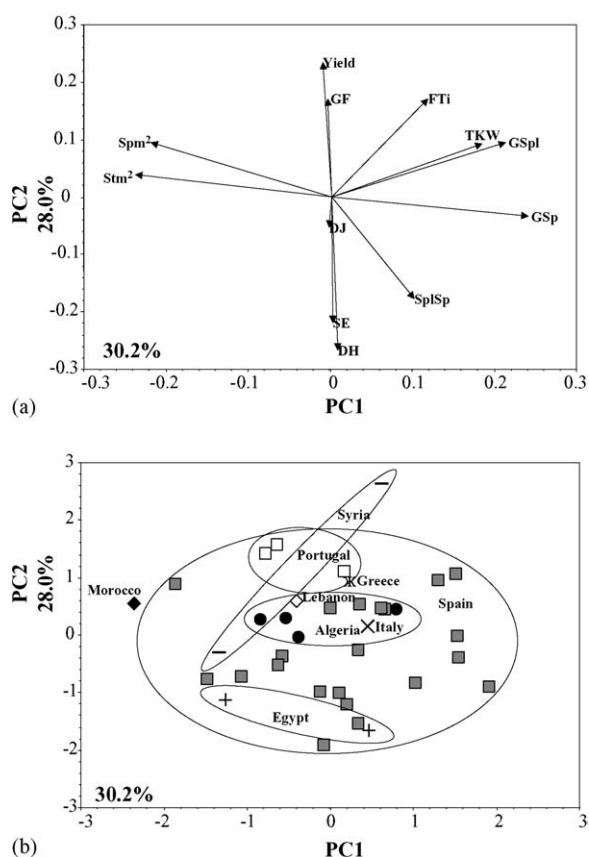


Fig. 3. Principal component analysis (PCA) projections on axes 1 and 2, accounting for 58.2% of total variance, for 36 southern dispersal Mediterranean durum wheat genotypes. (a) The eigenvalues of the correlation matrix are symbolized as vectors representing yield, number of spikes per m^2 (Spm^2), number of grains per spike (GSp), thousand-kernel weight (TKW), number of stems per m^2 (Stm^2), fertile tillering (FTi), number of spikelets per spike (Sp1Sp), number of grains per spikelet (GSp1), days to jointing (DJ), days to heading (DH), stem elongation period duration (SE) and grain filling duration (GF). (b) Plot of the points corresponding to genotypes from Syria (—), Lebanon (◇), Egypt (+), Greece (⌘), Italy (×), Algeria (●), Morocco (◆), Spain (■) and Portugal (□).

related to yield and the duration of grain filling period on a positive side, and to the remaining phenological traits on a negative side. Fig. 3a shows a strong association between yield and the length of grain filling period for the southern group of genotypes. All the traits related to cycle length until heading were negatively associated with productivity. Grain yield was also positively associated with fertile tillering, the number of spikes per m^2 and TKW. Yield, yield

components and phenological traits did not group southern genotypes into any geographical pattern (Fig. 3b).

There was no association between the number of spikes per m² and the percentage of fertile spikes within the southern group, while within the northern group these two traits were strongly and positively related to each other ($r = 0.80$, $P < 0.001$). Similarly, contrasting relationships were observed between the number of stems per m² and the percentage of fertile spikes within both groups of genotypes, since the two traits were positively associated in the northern group, but negative in the southern group.

To assess which traits contributed more to yield in each group, stepwise regression analyses were carried out independently for each of them. When phenological traits were included in the analysis jointly with yield components, days to heading explained 41% of yield variation for both northern and southern genotypes, but for the former it was the only variable that entered in the model (upper part of Table 6). For the southern group days to heading was also the most important trait in explaining variation in yield, but the number of stems per m², TKW and the number of grains per spikelet were also significant in the model, explaining 73% of the variation in yield. Further

regression analyses were performed considering only yield components in order to remove the important effect of phenological development. The results indicated that for the northern dispersal group TKW was the only trait that was significant in the model, explaining 37% of variations in grain yield, whereas for the southern group the number of spikes per m² explained the largest percentage of variation in grain yield (24%, lower part of Table 6).

4. Discussion

It is hypothesized that, apart from the contribution of selection made by humans, differences in climatic conditions prevalent in the north and south of the Mediterranean basin have given rise to contrasting patterns of yield formation in genotypes that have evolved in one or the other region. According to Leemans and Cramer (1991) and FAO (1997) two types of climates, C and D of the Koeppen's climate classification, can be found in the northern coastal regions of the Mediterranean Sea. The average temperature in this region ranges from -4.5 to 22 °C and the rainfall ranges from 300 to 1100 mm year⁻¹. In contrast, most of the southern

Table 6

Linear regression equations for the relationship between yield (Y) as dependent variable and yield components and phenological traits as independent variables, for northern and southern dispersal group

Regression equation		Partial R^2	Model R^2	P
Yield components and phenology				
Northern				
$Y = 12.06 - 0.055 \text{ DH}$	DH	0.41	0.41	0.0080
Southern				
$Y = 6.79 - 0.054 \text{ DH} + 0.005 \text{ Stm}^2 + 0.059 \text{ TKW} + 0.718 \text{ GSp1}$	DH	0.41	0.41	0.0001
	Stm ²	0.18	0.59	0.0002
	TKW	0.10	0.69	0.0129
	GSp1	0.04	0.73	0.0309
Yield components				
Northern				
$Y = -0.028 + 0.057 \text{ TKW}$	TKW	0.37	0.37	0.0128
Southern				
$Y = -2.07 + 0.007 \text{ Spm}^2 + 0.066 \text{ TKW} - 0.078 \text{ Sp1Sp} + 0.806 \text{ GSp1}$	Spm ²	0.24	0.24	0.0001
	TKW	0.19	0.43	0.0031
	Sp1Sp	0.18	0.61	0.0102
	GSp1	0.06	0.67	0.0209

Yield components were the only traits included in the model models shown in the lower part of the table. Only variables that met the 0.05 significance level were included in the model. DH, days to heading; Stm², number of stems per m²; TKW, thousand-kernel weight; GSp1, number of grains per spikelet; Spm², number of spikes per m²; Sp1Sp, number of spikelets per spike.

coastal regions of the Mediterranean Sea present climate of class B. This class is characterized by an annual evapotranspiration exceeding the annual precipitation, and the presence of a marked dry season during spring and summer. The average temperature ranges from 10.5 to 30.5 °C and the rainfall varies from 35 up to 725 mm year⁻¹, the latter occurring in a small northern region of Morocco.

Data were recorded in this study in three sites of intermediate climate characteristics between the coldest and driest areas of the Mediterranean basin. However, they differed in terms of productivity, since the average yield at the most productive site was more than double than that of the poorest. In terms of water availability, it seemed unlikely that Gimennells could be the most productive site, since it had the lowest overall (186 mm) and during grain filling (38.8 mm) rainfall. However, the upper yields at Gimennells may be explained by its higher soil fertility (3.18% of organic matter at Gimennells versus 1.58% at Foradada), and the superficial sub-soil water layer at this site.

The results of this study show that the dispersal pattern of durum wheat genotypes within the Mediterranean basin affected some of the agronomic traits evaluated herein, because it accounted for significant part of the observed variation in yield and yield components. Northern and southern dispersal groups had similar yields across experiments, but the significant crossover interaction appeared between dispersal group and site suggests a different pattern of adaptation to the test environments. Northern landraces yielded 5.6% more than the southern in the most productive site, similar to them in the intermediate one and 13.2% less in the poorest site. These results may indicate that northern landraces were the best adapted to the most productive environment, while southern ones fit better in the poorest.

Genotypes from the north versus the south of the Mediterranean basin differed for some yield components. Northern genotypes had larger number of stems and spikes per unit area than southern landraces, which in turn showed higher fertile tillering and number of grains per spike. These results are in accordance with the climatic conditions prevalent on both regions, because tillering and spikes per m² are favored by low temperatures and high water supply (García del Moral et al., 2003).

The larger tillering capacity and lower number of grains per spike of northern landraces may indicate a higher yield potential, according to the findings of Duggan et al. (2000). The larger seed set of southern landraces could be consequence of a higher tolerance to drought and heat stresses, as a result of natural selection. The lower values of fertile tillering and number of grains per spike in northern landraces compared with the southern group suggest that grain setting was more susceptible to drought in the northern group than in the southern one. This susceptibility could be partially attributed to the profligate use of carbon and water by the larger population of tillers in the northern group during the spikelet formation and flowering period.

Our results also showed that the pattern of dispersal of genotypes affected the relationships between grain yield and its related traits. PCA and regression analyses revealed that grain weight was the yield component most important in defining grain yield for the genotypes evolved in the north of the Mediterranean basin, while for those adapted to warmer and dryer conditions (i.e., southern dispersal group), grain yield was more based on the number of spikes per m². Grain weight was less important for grain yield formation in the south than in the north. It has been reported that under cooler conditions grain yield in durum wheat is mainly influenced by grain weight. However, this yield component is less important when compared to the number of spikes per m² under warmer conditions (García del Moral et al., 2003). These results suggest that the environmental conditions in which genotypes evolved influenced the relative weight of yield components on grain yield formation.

As it has been mentioned above, the three test sites have intermediate characteristics, in terms of temperature and drought, between the two zones of adaptation. Differences in yield and yield components would be probably enhanced if genotypes would be tested in more extreme environmental conditions, favoring southern genotypes when cultivated under severe heat and drought stress and northern genotypes when evaluated under cold and more humid environments. Nevertheless, days to heading was the most important trait in explaining variations in grain yield in both groups of germplasm, since it explained about 40% of total variability, reflecting the stress conditions

experienced in the test sites. The importance of phenological adjustment under Mediterranean conditions has been highlighted in several studies (Loss and Siddique, 1994).

The negative relationships among the three principal yield components, i.e., spikes per m², the number of grains per spike and thousand-kernel weight, have already been described (Slafer et al., 1996). Those compensatory effects between the number of spikes per m² through the number of grains per spike, showed by the different direction of their eigenvectors, were observed in both northern and southern Mediterranean genotypes. They may be due to the inverse relationship between tiller production and apical development, presumably deriving from the negative allometry between these traits during plant development (Hamid and Grafius, 1978; Miralles and Slafer, 1999), causing competition for assimilates among different plant structures.

North and south dispersal groups had different strategies for the determination of the number of spikes per m². This yield component is the product of the number of the stems per m² and fertile tillering. Whereas positive correlation coefficients existed between the three traits for the genotypes from the north (Fig. 2a), within the genotypes from the south the number of spikes per m² was positively correlated with the number of stems per m² ($r = 0.94$, $P < 0.001$), but not with fertile tillering (Fig. 3a). Therefore, a stronger competition between tillers for assimilates was observed in the southern than in the northern groups, indicating a higher sink limitation in southern landraces and supporting the hypothesis of a different strategy for grain yield formation. This result is in agreement with the reported major effect exerted by the capacity of producing tillers on the number of spikes per m² rather than on fertile tillering under rainfed conditions (Y. Rharrabi, personal communication 2004).

The role of non-reproductive tillers on crop performance is not clearly understood (Sharma, 1995). The non-reproductive tillers have been found to be positive in terms of their assimilate accumulation (Lupton and Pinthus, 1969), while on the other hand, they may have a negative effect as competitors for assimilates and plant nutrients (Langer and Dougherty, 1976). Our results show that the non-reproductive tillers had a positive effect on grain weight for the

genotypes from the north, but a negative effect on the ones from the south. Thus, Fig. 2a shows a positive relationship between the total number of stems per m² and TKW within the north dispersal group, suggesting a positive contribution of all plant stems to grain filling. In contrast, within the south dispersal group the relationship between grain weight and the number of stems per m² was negative (Fig. 3a), indicating that within southern landraces a higher tiller production lead to higher number of spikes, but with smaller and lighter grains. The important role of dry matter translocation on grain yield production under Mediterranean environments, where grain filling generally takes place under hot and dry conditions that limit photosynthesis, has been highlighted in different field crops (Papakosta and Gagianas, 1991; Royo et al., 1999; Davies et al., 2000).

The clusters of genotypes formed by the first and second PC axes showed that for the northern genotypes, the geographical pattern of dispersal could be associated with changes in yield components. Fig. 2b shows that, except for the Greek landrace, the spread of durum wheat from the east (Turkey), close to the center of diversity of wheat, to the west of the Mediterranean basin (Portugal) entailed an increase in the number of stems and spikes per unit area, as well as a decrease in the number of spikelets and grains per spike as well as a reduction of the cycle duration until jointing. The position of the clusters for different countries in Fig. 2b (Turkey, Cyprus, Italy and Portugal following the direction upper-left to lower-right) suggests that these changes occurred gradually during the spread of durum wheat through the northern region of the Mediterranean basin. These results may indicate that during the human and natural selection process, landraces evolved through the northern part of the Mediterranean basin steadily increased their tillering capacity and the percentage of tillers able to produce grains. The natural consequence of this was a reduction of grain set in terms of spikelets and grains per spike. Moreover, the reduction of the cycle until jointing resulted likely from the advance from the cold eastern areas to the temperate areas of western Mediterranean basin. Human selection may have act in the same way than natural selection, given that increases in tiller number and fertile tillering would lead to improvements in grain and straw productions, the two end uses of durum wheat. In contrast, none

geographical pattern was observed within the southern dispersal group (Fig. 3b), probably because the spread of durum wheat through the south of the Mediterranean basin has occurred much more recently than in the north. Nonetheless, with adequate time for natural and human selection, southern landraces would probably have evolved to highlight the most efficient mechanisms for yield production under warm and dry conditions.

5. Concluding remarks

The results of this study showed that the pattern of dispersal of durum wheat within the Mediterranean region, determined by genetically characterizing landraces from various countries, led to contrasting yield formation strategies, as a consequence of differences in the prevalent climatic conditions of the areas where they were being cultivated and likely the human selection. Landraces originating from the north of the Mediterranean Sea based their yield on weight per grain, while the number of spikes per m² was a major yield component for the southern dispersal group. Both traits that likely were favored by natural and human selection during centuries, can be useful to design the selection strategies of breeding programs in order to improve adaptation to the target areas. According to our results, the weight of grains and the number of spikes per unit area could be useful selection criteria for grain yield improvement under northern and southern parts of the Mediterranean basin, respectively. Nevertheless, cycle length until heading was the most important trait affecting grain yield in both groups of genotypes, stressing the implication of phenological adjustment on wheat yield under Mediterranean conditions.

Northern landraces evolved a higher tillering capacity, fewer grains per spike and less fertile tillering than those from the south. Our results support the hypothesis that during the Neolithic dispersal of durum wheat from the Fertile Crescent to southern Europe, significant and gradual changes in yield component structure of populations occurred.

Experiments under extreme testing environments along the Mediterranean basin, including coldest and driest areas, should be carried out to validate our results in the widest range of environmental conditions.

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