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The historical perspective of dryland agriculture: lessons learned from 10 000 years of wheat cultivation

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Abstract

Wheat is one of the founder crops of Western agriculture. This study reconstructs agronomic conditions, potential yields, and kernel weight in the beginnings of cultivation of domesticated free-threshing wheat, *c.* 8000 BC. The carbon and nitrogen stable isotope compositions and the dimensions of fossil grains of naked wheat (*Triticum aestivum/durum*) were analysed. Samples were collected in Tell Halula and Akarçay Tepe, two Neolithic archaeological sites from the Middle Euphrates (the claimed core area for wheat domestication). The samples analysed include the oldest reported remains of naked wheat. Consistently wetter conditions but lower kernel weights were found in the Neolithic compared with the present day. Besides, the estimated yields were clearly beyond what is expected from the gathering of wild stands of cereals. Patterns of phenotypic adaptation achieved by wheat after its diffusion through the Mediterranean were also assessed. On the one hand, the study looked at variation in morphophysiological traits as related to local climate in a set of 68 durum wheat landraces from the Middle Euphrates. On the other hand, an assessment was made of regional adaptation around the Mediterranean Basin in a set of 90 landraces, traditional varieties, and modern cultivars from different origins by character-izing agronomic and morphophysiological variability. Significant relationships were observed between phenotypic variation among landraces from the Middle Euphrates and both minimum temperatures and the ratio of precipitation to potential evapotranspiration of the sites of origin. In addition, consistent differences in grain yield, plant structure, and water status were found among genotypes following both north–south and east–west gradients across the Mediterranean. These differences are associated with contrasting environ-mental and selection pressures.

Key words: Carbon isotope discrimination, Fertile Crescent, fossil grains, grain yield, Holocene, kernel weight, origins of agriculture, *Triticum turgidum durum*, water availability.

Introduction

The adoption and diffusion of agriculture has shaped human societies down to the present day. Western agriculture started around 10 000 BC somewhere along the Fertile Crescent in the Near East (Hillman and Davies, 1990). The origins of agriculture in the Fertile Crescent,

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Abbreviations: *AF*, ash concentration in the flag leaf blade three weeks after anthesis; CIMMYT, Centro Internacional de Mejoramiento de Maíz y Trigo; $\delta^{13}C$ and $\delta^{15}N$, carbon and nitrogen isotope composition; Δk and Δl, carbon isotope discrimination in kernels and penultimate leaf; *DH*, days to heading; *ETP*, potential evapotranspiration; *GY*, grain yield; ICARDA, International Center for Agriculture in the Dry Areas; *KW*, kernel weight; *KS*, kernels spike^{-1}; *LA*, total leaf area; *LG*, leaf greenness of the flag leaf blade 3 weeks after anthesis; M-PPNB and L-PPNB, Middle and Late Pre-Pottery Neolithic B; *P*, seasonal precipitation; *P/E*, ratio of precipitation to potential evapotranspiration; *PH*, plant height; *PN*, Pottery Neolithic; T_{max} and T_{min}, average maximum and minimum temperatures; *TWI*, total water inputs during grain filling.

and the nature of the crops first adopted, along with the selection pressure that was a result of cultural practices, are factors that are intimately related to water. Regions characterized by long drought episodes, such as the Mediterranean savannahs and steppes of the Near East, have favoured plants with large annual seeds, able to survive for long dry periods and germinate when rains occur (Harlan, 1992). In fact, most of the early domesticates were herbaceous annuals capable of selfing (Hancock, 2003), and the starchy cereals, complemented with high-protein legumes, were among the first plants cultivated.

The oldest formal idea about the origins of agriculture is Childe's 'oasis theory' (Childe, 1952). Childe suggested that, after the glaciations, North Africa and South-west Asia became drier and humans began to aggregate in areas where water was available. This theory is an appealing explanation for agriculture's appearance at xeric sites. However, the climate could not have been as harsh as Childe imagined. Other authors suggest that climate in the Fertile Crescent could have shifted from a cool steppe to a warmer and perhaps moister savannah at the beginning of agriculture (Wright, 1968). Alternative factors, either of a global nature, such as the increase in atmospheric levels of CO_2 (Sage, 1995), or a variety of regionally specific forces, including population growth, overhunting, overgathering (Cohen, 1977), religion, or a simple desire for more of something in short supply (Wadley and Martin, 2000) may have pushed people towards farming. Knowledge of specific agronomic conditions in early agriculture, such as plant water status and grain yield, among others, would certainly provide valuable clues to solve this incognita.

The beginnings of agriculture in the Old World are closely associated with cereal domestication (i.e. einkorn and emmer wheats as well as barley). However, there is evidence that cultivation greatly preceded domestication (Moore *et al*., 2000; Tanno and Willcox, 2006), the latter being a very slow adaptive process which took almost 2000 years to be established within the Levant (Mac Key, 2005). Changes associated with domestication could also be relevant for plant adaptation to dry environments. Recurrent (probably unconscious) selection due to sowing and harvesting cereal seeds could have produced a positive selection pressure favouring seedling competition (Allard, 1988). In turn, this could have increased seedling vigour, a well-recognized trait for adaptation of cereals to Mediterranean environments (Richards *et al*., 2002), through an increase in seed size, thus increasing total carbohydrates (Hancock, 2003). In fact, domestication is thought to be present when archaeological plant remains show, among other traits, substantial increases in kernel weight (Salamini *et al*., 2002; Willcox, 2004). Kernel weight is, moreover, one of the three main agronomic components of grain yield in cereals, and it has direct implications for grain quality (Rharrabti *et al*., 2003). Therefore, it may also act as an indicator of the potential quality of food products that could be delivered in ancient times. Inferences on kernel weight values for cultivated cereals at the origins of agriculture would add some clues on the genetic gains already attained at the beginning of crop domestication and since then to the present. Such inferences could also provide helpful information about the agronomic conditions under which crops developed in the past. To our knowledge, however, studies providing such information are lacking because of the fact that, usually, only charred grains are preserved in archaeological sites (Ferrio *et al*., 2004).

Phytogeographical, molecular and archaeological data support the existence of a 'core area' of domestication of several crops in the Fertile Crescent (Lev-Yadun *et al*., 2000; Salamini *et al*., 2002), including einkorn (*Triticum monococcum* L.) (Diamond, 1997; Heun, 1997), emmer [*T. turgidum* L. subsp. *dicoccum* (Schrank ex Schübl.) Thell.] (Elias *et al*., 1996) and, probably, related to free-threshing (i.e. naked) tetraploid wheats. This area, a small region of south-east Turkey and north-east Syria around the Middle Euphrates (average coordinates 37°00′ N, 38°60′ E), might therefore be the cradle of wheat agricultural innovation (Gopher *et al*., 2002; Salamini *et al*., 2002). Adoption of polyploid wheats such as emmer and, later, naked wheats represented an advantage with regard to diploids such as einkorn, not only because of their more favourable harvesting properties but also as a result of their superior adaptation to warm climates (Salamini *et al*., 2002). Of the different tetraploid wheats, the free-threshing durum wheat [*T. turgidum* L. subsp. *durum* (Desf.) Husn.] is, however, the only one that remains widely cultivated today. Moreover, the free-threshings of tetraploid durum wheat and hexaploid bread wheat (*T. aestivum* L.) represent the final steps of wheat domestication (Salamini *et al*., 2002). In this regard, the Pre-Pottery (aceramic) Neolithic B site of Tell Halula is the oldest archaeological site in the Middle Euphrates region where remains of naked wheat (*T. aestivum*/*durum*), dating from the eighth millennium BC, have been conclusively reported (Willcox, 1996; Zohary and Hopf, 2000; Araus *et al*., 2001*b*).

Once plants were domesticated, they were dramatically altered by humans through both conscious and unconscious selection. Probably the total genetic change achieved by farmers over the last 10 000 years was far greater than that achieved by breeders in the last 100 years (Simmonds, 1979). Among the features commonly associated with the domestication process there is also an increase in local adaptation (Hancock, 2003). After domestication, free-threshing wheats spread west through the Mediterranean Basin, reaching its western edge by 5000 BC (Araus and Buxó, 1993, Buxó, 1997; Feldman, 2001). At present, durum wheat is grown mostly in rainfed areas of the Mediterranean region where water stress progressing during grain filling is a common event (Loss and Siddique, 1994). Nevertheless, contrasting climate conditions exist around the Mediterranean Basin. The northern part changes progressively from cold to temperate climates (following the east–west direction), whereas the south of the Mediterranean is characterized by a drier climate, with higher temperatures and more severe terminal drought (http://www.fao.org/sd/Eidirect/climate/Eisp0002.htm). Hence, different adaptation strategies are likely to have occurred during wheat expansion through the Mediterranean Basin, therefore producing material suited to the environmental conditions and agronomic practices of their regions of origin (Moragues *et al*., 2005).

The objective of this study was two-fold. Firstly, the aim was to exemplify the methodological steps for reconstructing the agronomic conditions (mainly water status and yield) and the grain characteristics of naked wheat crops at the origins of agriculture. An attempt was also made to get an insight into the current variation present in phenotypic traits responsible for the adaptation of durum wheat to local climates in (i) the 'nuclear' region of the Fertile Crescent where tetraploid wheat was domesticated, and (ii) across the Mediterranean Basin following the spread of agriculture. The reconstruction of agronomic conditions and kernel characteristics in early agriculture was tackled using the different approaches developed by our team (Araus *et al*., 1997*a*, *b*, 1999*a*, *b*, 2003; Ferrio *et al*., 2004, 2005). To this end, stable carbon and nitrogen isotopic compositions and seed size were analysed in fossil kernels of naked wheat (*T. aestivum*/*durum*) recovered from Tell Halula and Akarçay Tepe, two Neolithic sites of the Middle Euphrates. The results were further compared with those of grains harvested in present-day crops in the same region. In addition, differences in adaptative patterns to Mediterranean conditions were assessed at the local and regional scales using two collections of durum wheat provided by ICARDA. One collection consisted of a set of 68 local landraces gathered in the Middle Euphrates region of South Turkey and North Syria, the provenance of the fossil grains. The other collection, made up of a total of 90 genotypes, included a set of landraces and old cultivars from different regions around the Mediterranean Basin as well as advanced lines and new varieties developed by CIMMYT/ICARDA. Carbon isotope discrimination, grain weight, grains per spike, plant size, and phenology were measured in both collections. Grain yield and different physiological traits related to plant water status such as ash concentration, leaf area, and leaf greenness (Araus *et al*., 1997*c*, 1998; 2001*a*; Richards *et al*., 2002; Condon *et al*., 2004) were also monitored in the regional durum wheat collection.

Materials and methods

Archaeological grains

Samples of ancient grains of naked wheat (*T. aestivum*/*durum*, after van Zeist and Bakkers-Heeres, 1982) were collected from two Neolithic archaeological sites from the Middle Euphrates: Tell Halula and Akarçay Tepe. Tell Halula is located about 85 km east of Aleppo and 80 km northwest of Raqqa (Fig. 1). The settlement, an artificial mound 8 m in height and roughly circular (360 m×300 m), is on the west Euphrates river bank, 4 km from the main Euphrates valley (Raqqa province, Syria), and delimited to the south and east by two of its tributaries. Latitude, longitude and altitude above sea level of the settlement are 35°55′ N, 38°30′ E, and 300 m, respectively. This site comprises (to date) three periods: Middle and Late Pre-Pottery Neolithic B (M-PPNB and L-PPNB, respectively), and Pottery Neolithic (PN, pre-Halaf). The site has been excavated by the Universitat Autònoma de Barcelona. The present-day natural vegetation in the region is a degraded steppe, with a total annual rainfall of about 250 mm. At present, the land above the valley floor is extensively used for lamb and goat grazing and rainfed cultivation of barley, whereas durum wheat and horticultural crops are cultivated only where supplementary irrigation is available. The chronology of archaeological samples was based on stratigraphic dating and radiocarbon ages. All radiocarbon determinations were performed in charcoal samples at Beta Analytic Inc. (Miami, Florida, USA). Calibrated ages were determined according to Stuiver and Reimer (1986) by using the computer program CALIBTH3. After calibration, the range of dates for the material studied was 7945 BC to 6400 BC (Table 1).

The site of Akarçay Tepe is situated at the Akarçay village, Bireçik (Urfa province, Turkey) on the left bank of the Euphrates (Fig. 1), on a low alluvial plain. Latitude, longitude, and altitude above sea level of the settlement are 36°55′ N, 38°01′ E and 355 m, respectively. The climate today is continental with cold winters and hot summers. The annual precipitation is about 370 mm and the natural vegetation of the region is steppe-type. Land use at present is similar to that of

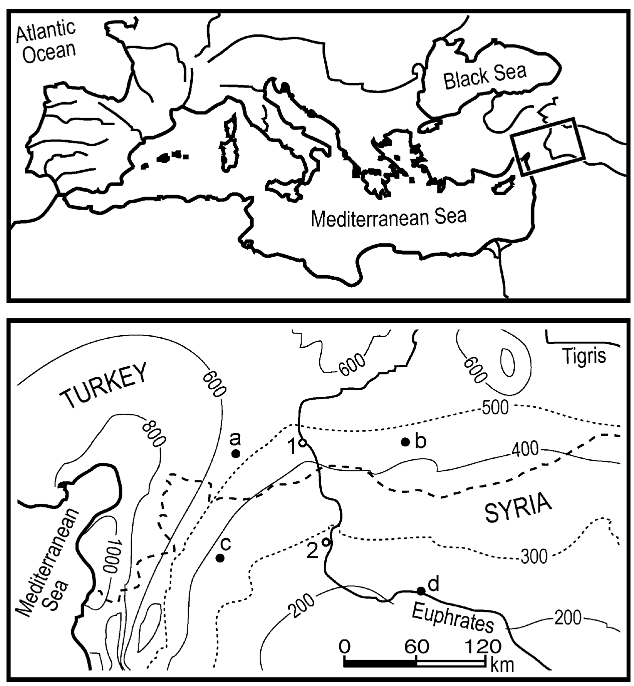

Fig. 1. Map of the Middle Euphrates region showing the archaeological sites where fossil kernels of naked wheat were collected. The map also represents the general area where the durum wheat landraces used in the assessment of local adaptation patterns originated. Empty circles: archaeological sites: (1) Akarçay Tepe, (2) Tell Halula. Filled circles: main cities (capitals of province) in the surroundings of the sites: (a) Gaziantep, (b) Şanliurfa, (c) Aleppo, (d) Raqqa. Isohyets of mean annual precipitation are included for reference.

Table 1. *Main cultural periods for the archaeological sites, with their calibrated ages and estimated carbon isotope composition in atmospheric CO_2 ($\delta^{13}C_{air}$), together with the number of individual grains (N) analysed for each variable*

Δk, Carbon isotope discrimination in kernels; *KW*, kernel weight; δ^{15}N, nitrogen isotope composition in kernels.

Archaeological site	Cultural period	Calibrated age (Years BC)	$\delta^{13}C_{air}$ (‰)	N (Δk)	N (*KW*)	N (δ^{15}N)
Tell Halula	M-PPNB	7945–7550	−6.63	21	5	9
	L-PPNB	7470–7170	−6.56	2	–	2
	PN	7000–6400	−6.54	3	–	4
Akarçay Tepe	M/L-PPNB	7600–7000	−6.55	5	4	5
	L-PPNB	7460–7160	−6.58	13	8	13
	PN	6900–6100	−6.57	10	8	10

Tell Halula, except for a larger contribution of crops under supplementary irrigation. The site is being excavated by the University of Istanbul and the Universitat Autònoma de Barcelona and comprises (to date) two mounds: the eastern one from M-PPNB to L-PPNB, and the western one belonging to the PN. The chronology of the archaeological samples was also based on a combination of stratigraphic dating and radiocarbon ages. Radiocarbon calibrated ages ranged between 7600 BC and 6100 BC (Table 1).

In both sites, cereal grains were found in a carbonized state and were gathered in disparate fashion from domestic fires, cooking ovens, and root floors. Soil samples were treated using a standard flotation tank in the field with 0.3 mm (flotation) and 2.5 mm (wet) sieves. Plant remains were then dried slowly before the transport and sorting of seeds. Prior to stable isotope analysis, archaeological grain samples were cleaned as described elsewhere (Araus *et al*., 1997*a*; Ferrio *et al*., 2004).

Present-day material and local adaptation: durum wheat landraces from the Middle Euphrates

Seeds of 68 landraces of durum wheat [*T. turgidum* L. ssp. *durum* (Desf.) Husn.] collected across different locations from the Middle Euphrates valley (currently North Syria and South Turkey) were provided by the Genetic Resources Unit of the International Center for Agriculture in the Dry Areas (ICARDA) (Table 2). A digitalized climate map of the region was provided by the Natural Resources Unit of ICARDA. Climate conditions for the collecting sites were calculated by interpolating the values of the closest meteorological stations for a 20-year period. Seasonal precipitation (*P*), average maximum and minimum temperatures (T_{max} and T_{min}), potential evapotranspiration (*ETP*), and the ratio of precipitation to potential evapotranspiration (*P*/*E*) were obtained. The range of annual precipitation and annual mean temperature among sites was 269 mm (208 mm–477 mm) and 1.8 °C (16.4 °C–18.2 °C), respectively.

A field experiment was conducted under rainfed conditions in Gimenells (41°38′ N 0°23′ E, 200 m above sea level), a temperate-dry site from Lleida province (north-eastern Spain), during the 2002–2003 crop season. The precipitation and potential evapotranspiration during autumn (82.6 mm and 99.7 mm, respectively), winter (120.8 mm and 119.7 mm), and spring (103.5 mm and 450.2 mm) gave crop seasonal values of 306.9 mm and 669.6 mm, respectively, quite similar to the average for the Fertile Crescent area from where the landraces were collected (380 mm and 769 mm for precipitation and potential evapotranspiration, respectively). The seasonal average temperature for Gimenells (6.4 °C in 2002–2003) was also comparable with that for the Middle Euphrates valley (7.9 °C, mean average temperature for the region), but the minimum temperatures were somewhat lower in Gimenells (albeit without relevant frost episodes compromising crop growth).

Each accession was sown in an unreplicated plot due to the small number of seeds available, with a control plot on either side of it containing bread wheat (*T. aestivum* L.) cv. Soissons. The plot size was 0.40 m^2 and consisted of two 1.0 m length rows spaced 0.20 m apart and seeded at a rate of 350 kg seeds ha^{-1}. All the plots remained unfertilized. Heading date (days to heading, *DH*) was recorded at stage 49 of Zadocks' decimal code (Zadocks *et al*., 1974) and plant height (*PH*, including the peduncle) was measured at maturity. Plots were harvested manually, oven-dried for 48 h at 60 °C and weighed. Kernel weight (*KW*), kernels per spike (*KS*) and carbon isotope discrimination of kernels (Δk) were measured, and the harvest index (*HI*) was calculated.

Present-day material and regional adaptation: durum wheat landraces and cultivars from the Mediterranean Basin

The Durum Core Collection (DCC) of durum wheat, assembled at ICARDA, was cultivated during the 1995–1996 crop season at Tel Hadya (Headquarters of ICARDA, Aleppo, Syria) under rainfed and support irrigation. Growth conditions can be found in Araus *et al.* (1997*c*). From the 125 genotypes of the DCC cultivated that season, a subset of 90 genotypes was chosen comprising landraces and old varieties from seven different countries around the Mediterranean Basin (Syria, Jordan, Morocco, Portugal, Spain, Italy, and Greece) plus modern (released between 1970–1980) and recent cultivars (released from 1985 to 1995) (Table 3). From the array of agronomical and morphophysiological variables measured in Araus *et al.* (1997*c*, 1998), ten were selected that contributed to distinguishing among origin groups (either genetic or geographic). The traits selected were grain yield (*GY*), *KW*, *KS*, some morphometric characteristics, *PH* and total leaf area (*LA*), phenology (*DH*) and several traits related to water status (carbon isotope discrimination of the penultimate leaf (Δl) and of mature kernels (Δk), ash concentration of the flag leaf around anthesis (*AF*), and greenness of the flag leaf blade (*LG*). The procedures used for sampling, measuring and analysing are described in full elsewhere (Araus *et al*., 1997*c*, 1998). In brief, *GY* components and *PH* were measured at maturity, and *DH* was measured when at least half of the spikes of each genotype were fully extruded. *LG* was assessed 3 weeks after anthesis with a portable chlorophyll meter (SPAD-502, Minolta Camera Co., Japan), and leaves were then harvested, the blade area (*LA*) measured and the *AF* determined after burning preweighed dry matter in a furnace at 450 °C for 12 h (Araus *et al*., 1998, 2001*a*).

Stable isotope analyses

Stable isotope composition of carbon (δ^{13}C, referred to VPDB standard) and nitrogen (δ^{15}N, referred to air) was determined by

Table 2. *Durum wheat landraces of the Middle Euphrates region from the ICARDA Genetic Resources Collection*

Country	Province	Site	Latitude	Longitude	ID
Syria	Aleppo	Algamiyi	N36° 26′	E37° 38′	IG-92304, IG-92341, IG-92294
		Ashkan Kbir	N36° 48′ 59″	E38° 27′ 56″	IG-92349
		Befor	N36° 31′ 04″	E37° 55′ 12″	IG-110719
		Tal Al-ain	N36° 00′ 54″	E37° 31′ 43″	IG-92399, IG-92397
	Raqqa	Hamam	N35° 54′ 10″	E38° 46′ 30″	IG-96150
		Mansura	N35° 50′ 35″	E38° 44′ 30″	IG-96149
Turkey	Gaziantep	Nizip	N37° 01′	E37° 48′	IG-84614
		Nizip (surroundings)	N37° 01′	E37° 40′	IG-82771, IG-97453
	Urfa	Akcakale	N36° 44′	E38° 59′	IG-82695, IG-82695, IG-82754, IG-82757, IG-82758, IG-82758, IG-84117, IG-84121, IG-84122, IG-84704, IG-84704, IG-97430, IG-97430
		Babetlhatle	N36° 43′	E38° 57′	IG-84646
		Birecik	N37° 02′	E38° 00′	IG-84776
		Birecik (surroundings)	N37° 03′	E37° 59′	IG-82759, IG-84085, IG-97449
		Germus	N37° 11′	E38° 49′	IG-84580, IG-84610
		Hodja	N37° 07′	E38° 48′	IG-82568, IG-83944, IG-83946
		Ikizce	N36° 44′	E38° 59′	IG-97495
		Karakopru	N37° 11′	E38° 47′	IG-84815
		Mahsara	N36° 55′	E38° 21′	IG-84684
		Mursitpinar	N36° 54′	E38° 21′	IG-84552
		Suruc	N36° 59′	E38° 25′	IG-84611, IG-84612, IG-84613
		Suruc (surroundings)	N36° 59′	E38° 24′	IG-82767, IG-82760, IG-84123, IG-84127, IG-84127, IG-97450, IG-97450, IG-97451, IG-97451, IG-97451
		Tepelihaman	N36° 59′	E38° 17′	IG-84751
		Tibagdat	N36° 43′	E38° 57′	IG-84809
		Şanliurfa	N36° 43′	E38° 57′	IG-84609
		Şanliurfa (surroundings)	N37° 10′	E38° 47′	IG-84680, IG-84760

continuous flow isotope ratio mass spectrometry. The analyses were performed in the 'Serveis Cientifico-Tècnics' of the Universitat de Barcelona (Barcelona, Spain), Iso-Analytical Ltd. (Sandbach, Cheshire, UK), and Isotope Services (Los Alamos, NM, USA). Overall analytical precision was about 0.1‰ and 0.2‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Archaeological kernels are mostly found in the carbonized state; however, carbonization does not appear to alter significantly either the $\delta^{13}C$ (Araus *et al*., 1997*a*; DeNiro and Hastorf, 1985; Ferrio *et al*., 2006*a*) or the $\delta^{15}N$ (JP Ferrio *et al*., unpublished results) of starchy seeds.

Carbon isotope discrimination

Carbon isotope discrimination of archaeological kernels (Δk) was calculated from their $\delta^{13}C$ and from the $\delta^{13}C$ of atmospheric CO_2, as follows:

$$\Delta k(‰) = (\delta^{13}C_{air} - \delta^{13}C_{plant})/[1 + (\delta^{13}C_{plant}/1000)]$$

where $\delta^{13}C_{air}$ and $\delta^{13}C_{plant}$ denote air and plant $\delta^{13}C$, respectively (Farquhar *et al*., 1989).

$\delta^{13}C_{air}$ was inferred by interpolating a range of data from Antarctic ice-core records (Leuenberger *et al*., 1992; Francey *et al*., 1999; Indermühle *et al*., 1999; Eyer *et al*., 2004), together with modern data from two Antarctic stations (Halley Bay and Palmer Station) of the CU-INSTAAR/NOAA-CMDL network for atmospheric CO_2 (ftp://ftp.cmdl.noaa.gov/ccg/co2c13/flask/readme.html), as described in detail in Ferrio *et al*. (2006*b*). The whole $\delta^{13}C_{air}$ data set thus obtained covered the period from 15 600 BC to 2003.

The same approach was used to calculate Δk for present-day genotypes. Thus, for the DCC cultivated in the 1995–1996 season, $\delta^{13}C_{air}$= –7.83‰, and for the set of the Fertile Crescent Landraces cultivated in 2002–2003, $\delta^{13}C_{air}$= –8.05‰. For the DCC, recalculated Δk and Δl values were somewhat higher that those previously reported by Araus *et al*. (1998) using a $\delta^{13}C_{air}$ of –8.00‰ after Farquhar *et al*. (1989).

Reconstruction of early agriculture conditions

The carbon isotope discrimination of archaeological grains allows the reconstruction of plant water status and yield of ancient wheat crops. The procedure stems from the strong association between Δk

Table 3. *Durum wheat genotypes from the Mediterranean Basin included in the different groups*

Origin (geographic or genetic)	
Group 1. Landraces and old cultivars (ICARDA Durum Wheat Core Collection)[a]	
Greece	Atsiki 3 (L), Iraklion (L), Mavragani-Iraklio (L), Moundrous 2 (L), Romanou 2 (L)
Italy	Cannizzara (C), Scorsonera (L), Senatore Cappelli (C), Sicilia Lutri (L), Trinakria (L), Tripolino (C)
Jordan	Jordan Coll86 No 17 (L), Jordan Coll86 No 21 (L), Jordan Coll86 No 42 (L), Jordan Coll86 No 44 (L), Jordan Coll86 No 53 (L), Jordan Coll86 No 80 (L)
Morocco	M 10 (L), M 1084 (L), M 1086 (L), M 1090 (L), M 11 (L), M 1150 (L), M 13 (L), M 15 (L), M 20 (L), M 21 (L), M 3 (L)
Portugal	Amarelo de barba (C), Arrancada No 7710 (C), Camadi Abdu 173 N (C), Candeal da Grao Escuro (C), Casablanca No 758 (L), Corado 11639 v91 (L), Entrelargo de Montijo (L), Mourisco Fino v80 (L), Rubiao 9053 v49 N (L), Santa Marta 2442 (C)
Spain	Barba de Lobo (L), Caravaca Colorado (L), Recio Raspinegro (L), Roqueño (C)
Syria	Akbash (L), Baladia Hamra (L), Hamari Ahmar (L), Haurani (L), Haurani Nawani (C), Haurani 27 (C), Kishk (L), Normal Haurani (L)
Group 2. CIMMYT–ICARDA modern cultivars	
Released 1970–1980	Guerou 1, Hazar, Jordan, Loukos 1, Nile, Siliana, Zeroud 1
Released 1985–1995	Belikh 2, Bicre, Blk 2//134×S-69–18, Brachoua, Brch/*KS*79238–2/Ch, Chahba 88, Cham 1, Daki, Deraa, Furat 1, Gedifla, Heider, Kabir 1, Karasu, Khabur 1, Korifla, Lahn, Massara 1, Om Rabi 14, Om Rabi 17, Om Rabi 5, Omlahn 3, Omruf 2, Omsnima 1, Oronte 1, Po, Quassel-1/4/Buc/C, Saada 3/Dds/Mtl 1, Sabil 1, Sebou, Telset-5, Tensift 1, Wadalmez 1

[a] C, cultivar; L, landrace.

and both total water inputs during grain filling (*TWI*; Araus *et al.*, 1997*b*, 1999*a*; Ferrio *et al.*, 2005) and *GY* (Araus *et al.*, 1999*b*, 2001*b*, 2003) observed in present-day wheat crops, provided that a wide range of genotypes and Mediterranean conditions are considered. Initial estimates of ancient *TWI* or *GY* were then obtained by applying Δk values of archaeological grains to the present day-derived relationships. *GY* estimates were subsequently corrected to take into consideration the two main differences between ancient and modern crops not accounted for by the Δk of ancient samples: atmospheric CO_2 levels and harvest index (*HI*). Soil fertility and/or the occurrence of fallow were investigated from the $\delta^{15}N$ values of grains. Kernel weight (*KW*) of archaeological samples prior to carbonization was estimated using a model based on the length×breadth and length×thickness products of charred grains as described in Ferrio *et al.* (2004).

Current precipitation during grain filling at the two archaeological sites was estimated from historical records of rainfall from the meteorological stations closest to both sites. Present-day *GY* (means of 1987–1996) of wheat landraces cultivated under rainfed conditions in Raqqa and Aleppo provinces were obtained from the Syrian Ministry of Agriculture and Agrarian Reform (The Annual Agricultural Statistical Abstract, 1996). In addition, values of Δk, *KW*, and $\delta^{15}N$ from present-day wheat crops cultivated in the region were also included for comparison.

Statistical analysis

Data for the set of morphophysiological traits measured in the collection of landraces from the Middle Euphrates were summarized by means of box-and-whisker plots. Relationships among morphophysiological variables were examined by principal component analysis. The number of principal components to extract was decided based upon the proportion of total variance accounted for by each component. Information on adaptive patterns in the set of landraces was examined by means of simple correlations calculated between the principal components scores and several climate variables characterizing the collecting sites.

Data for the DCC genotypes were first subjected to mixed model analyses of variance (ANOVA). To this end, the genotype effect was considered as the random factor and the environment (i.e. trial) as the fixed one, so variance components could be estimated for genotype (*G*) and genotype by environment interaction (*GE*) terms. Thereafter, the ratio of *GE* to *G* variance components was calculated for each variable as a way to quantify the magnitude of *G* and *GE* effects. An additional ANOVA model was also fitted to the data, in which landraces and old cultivars were grouped by country of origin (Table 2), with single genotypes considered as random replications of the fixed factor 'origin'. This was done in order to evaluate possible differences among geographic origins for the traits under study. The same model was also applied, including the two additional groups of modern CIMMYT–ICARDA cultivars, in the ANOVA. The objective was to assess additional variation brought about by modern material. Canonical analysis was then applied to the set of 10 variables that showed significant *F*-values for group means comparison. Because of the large *GE*-to-*G* variance ratio associated with grain yield (implying changes in ranking among groups owing to the environment), this trait was included in the analysis independently for each trial. Otherwise, genotype means were used across trials as input for the canonical analysis. A graphical representation was subsequently performed, thus allowing between-groups differences to be shown using a two-dimensional graph.

Results

Wheat cultivation in early agriculture

A comparison between early agriculture and present-day values for Δk, *TWI*, *GY*, *KW*, and kernel $\delta^{15}N$ is displayed in Table 4. Fossil kernels from both archaeological sites showed Δk values about 3‰ higher than those of present-day durum and bread wheats cultivated under rainfed conditions in the surroundings of Tell Halula and in Breda, an experimental field station of ICARDA with a similar climate to Tell Halula. *TWI* during grain filling as inferred from Δk of fossil kernels was 2–3-fold higher than *TWI* estimates from Δk of present-day wheat rainfed crops, as well as from the averaged values of the meteorological stations closest to both sites. Potential yields, also inferred

Table 4. *Comparison between archaeological and modern reference data (means ±standard deviation)*

Δ*k*, carbon isotope discrimination in kernels; *TWI*, total water inputs during grain filling; *GY*, grain yield; *KW*, kernel weight; $\delta^{15}N$, nitrogen isotope composition in kernels.

Site	Period	Δ*k* (‰)	*TWI* (mm)	*GY* (kg ha^{-1})	*KW* (mg)	$\delta^{15}N$ (‰)
Archaeological data						
Tell Halula	M-PPNB	17.40±1.05	126±55[a]	1752±865[a]	11.6±6.7[a]	7.8±0.8
	L-PPNB	17.34±0.84	123±40[a]	1710±625[a]		11.7±6.6
	PN	16.80±0.87	102±30[a]	1378±448[a]		
Akarçay Tepe	M/L-PPNB	16.77±0.45	100±9[a]	1360±132[a]	10.5±2.7[a]	3.4±1.0
	L-PPNB	17.25±0.73	120±10[a]	1651±141[a]	19.8±8.4[a]	6.0±2.3
	PN	17.03±0.79	110±11[a]	1509±167[a]	21.8±7.1[a]	3.8±1.4
Reference data						
Breda DCC[b]		14.33±0.23	41±5[a]	1469±319	41.4±4.4	
Breda *T.a.*[c]		14.68±0.34	47±7[a]	1428±133	22.4±2.1	1.8±0.5
Tell Halula[d]		13.73	33[a]		35.0	0.8
Raqqa[e]				1100		
Aleppo[e]				1200		
Halula[f]			31			
Akarçay[f]			35			

[a] Estimated values, derived either from $\Delta^{13}C$ or grain measurements.
[b] Durum wheat landraces (only from Syria and Jordan) cultivated at Breda (Syria) (*n*=12). See details in Araus *et al.* (1997*c*).
[c] Bread wheat (*T. aestivum* L.) cultivars (*n*=24) grown in Breda (1999).
[d] Data from several spikes of rainfed wheat, collected around the archaeological site in 2003, and pooled together for the analysis.
[e] Average yields for wheat landraces under rainfed conditions (1987–1996) in the provinces of Raqqa and Aleppo.
[f] Average precipitation during grain filling (here considered: ½ April+May, after Araus *et al.*, 1999*a*).

from Δ*k* of fossil kernels, were well beyond 1 Mg ha^{-1}. They were comparable to those achieved at the experimental rainfed trial of Breda, and even somewhat higher than the average rainfed yields for the Syrian provinces of Raqqa (in which Tell Halula is included) and Aleppo (with an average precipitation similar to that of Akarçay Tepe). The estimated *KW* from the oldest levels of both archaeological sites was well below present-day values for wheat crops, with Akarçay Tepe showing a trend of increasing *KW* with time. Values of $\delta^{15}N$ in fossil kernels were higher (particularly for Tell Halula) than those achieved today in the surroundings of Tell Halula or in Breda without applying nitrogen fertilization.

Present-day material and local adaptation: durum wheat landraces from the Middle Euphrates

Box-and-whisker plots for the set of morphophysiological traits measured in Gimenells (NE Spain) are shown in Fig. 2. The collection exhibited a large variability in *PH*, *KS*, *HI*, and *KW*, as also shown by their corresponding coefficients of variation (*CV*) (*PH*=13.1%; *KS*=21.1%; *HI*=12.9%; *KW*=11.1%). Likewise, the range of variability for Δk was considerable (about 2‰; *CV*=3.5%). The trait showing the least variation was *DH*, with a difference of 7 d between extreme landraces (*CV*=1.9%). The first three axes of a principal component (PC) analysis explained 46%, 18%, and 17% of the original variability, respectively (Table 5). The first axis was positively related to *PH*, *DH*, and GW, and negatively to Δ*k*, whereas variation along the second axis was mainly (positively) related to *HI*. The third axis was positively related to *GS* and, to a lesser extent, to *DH* and, negatively, to GW.

The role of climate in determining phenotypic variability was studied by means of simple correlations between the main climate variables and the landraces scores for the three first PC axes (Table 6). As a result, a number of correlations with PC1 were significant, suggesting that only those traits associated to PC1 bore adaptive relevance, at least for the climate variables monitored. Overall, the average minimum temperature (T_{min}) was the variable best correlated (positively) with PC1, followed by *P*/*E* and precipitation. *ETP* was also (negatively) related with PC1. The largest correlations were usually attained for either the whole cropping season or spring, although in some cases large correlations were also obtained for other seasons (e.g. autumn or winter for T_{min}).

Present-day material and regional adaptation: durum wheat landraces and cultivars from the Mediterranean Basin

The overall mean values and dispersion statistics of landrances-old cultivars (thereafter termed landraces) and modern material for the set of 10 agronomic and morphophysiological variables are shown in Table 7. Most traits showed statistically significant differences (P <0.05) between landraces and modern material, with the exception of Δ*l*, leaf area, and leaf greenness (data not shown). Modern cultivars exhibited higher yields in both rainfed (*THR*) and irrigated (*THI*) conditions, a higher *KW* (around 2 mg) and four more kernels per spike on average, as well as

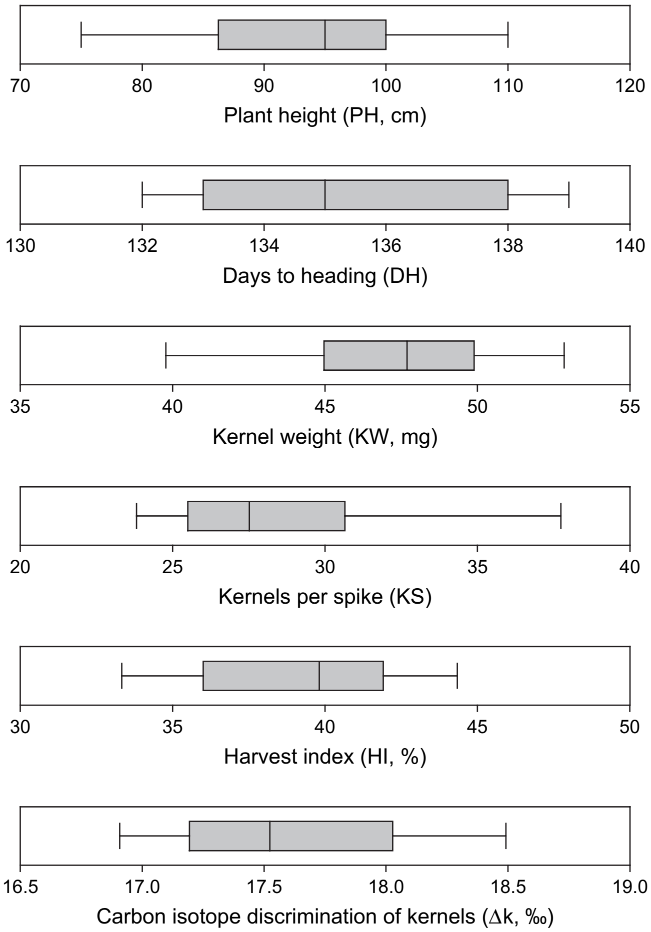

Fig. 2. Box-and-whisker plots for the different morphophysiological traits measured in the set of 68 durum wheat landraces from the Middle Euphrates. Genotypes were grown in an experimental field in Gimenells (Lleida province, NE Spain). The boundary of the box closest to zero indicates the 25th percentile, the line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whisker caps above and below the box indicate the 90th and 10th percentiles.

larger Δk and *AF* values. On the contrary, landraces flowered on average 1 d later (see *DH*) and were about 20 cm taller (*PH*) than their modern counterparts. Despite the lack of differences in *LA* and *LG*, modern cultivars showed larger minimum values in both variables (Table 7).

The origin (either geographic or genetic) mean values, the ratio of estimated *GE* to *G* variance components and *F*-values of the univariate ANOVA for each trait are reported in Table 8. The estimated yield variance component for *GE* was considerably larger than the estimate for *G*, and the corresponding variance components ratio for grain yield exceeded those for the other traits, with important changes in yield ranking among origins depending on the trial (Table 8). Except for *KW* and *LG*, differences among landraces of different origin were significant for all traits (Table 8). When the modern cultivars CI(1) and CI(2) were added to the comparison, differences became significant for all traits. Overall, landrances from Portugal and Spain were the least productive, having lower *KS* and *KW*. Landraces from Morocco and Jordan (under rainfed conditions) and from Greece and Jordan (under irrigated conditions) yielded the most, and also tended to exhibit the highest *KW* and *KS*. The most productive geographic origins, under both irrigated and rainfed conditions, were those shorter in phenology and exhibiting larger Δk and *AF* values. *PH* did not appear to have a crucial role determining *GY*, since either tall or short material exhibited indistinctly high or low yields. However, when including

Table 5. *Eigenvectors for the three first principal components (PC) obtained from the PC analysis of a set of variables measured in 68 ecotypes of durum wheat from the Middle Euphrates valley sown in an experimental field in Gimenells (Lleida province, NE Spain)*

Morphophysiological variable	PC1 (46%)	PC2 (18%)	PC3 (17%)
Plant height (*PH*)	0.52	0.10	0.06
Days to heading (*DH*)	0.48	−0.05	0.40
Kernel weight (*KW*)	0.40	0.35	−0.45
Kernels/spike (*KS*)	−0.24	0.37	0.75
Harvest index (*HI*)	−0.16	0.85	−0.15
δ^{13}C kernels (Δk)	−0.51	−0.11	−0.21

Table 6. *Simple correlation coefficients (n=68) between climatic variables for the Middle Euphrates sites where durum wheat landraces were collected and the landrace scores for the three first principal component (PC) axes*

The average values of climate variables across sites included in the upper and lower 5% percentile of PC1 are also shown.

Variable[a]		Correlation coefficients (r)[b]			Average	
		PC1	PC2	PC3	Low PC1	High PC1
P (mm)	Autumn	0.34**	0.02	−0.17	95	145
	Winter	0.31**	0.02	−0.14	149	206
	Spring	0.39***	0.01	−0.02	54	79
	Season	0.35**	0.02	−0.14	298	429
T_{max} (°C)	Autumn	0.00	−0.02	−0.06	19.8	19.5
	Winter	−0.09	−0.02	0.04	13.5	12.8
	Spring	0.23	−0.01	−0.14	28.5	28.8
	Season	0.06	−0.02	−0.06	20.6	20.4
T_{min} (°C)	Autumn	0.54***	0.00	−0.13	6.3	8.0
	Winter	0.43***	−0.03	−0.11	2.5	2.9
	Spring	0.49***	0.03	−0.17	12.8	13.9
	Season	0.58***	0.01	−0.16	7.2	8.3
ETP (mm)	Autumn	−0.12	0.03	−0.02	156	151
	Winter	−0.35**	0.03	−0.05	127	116
	Spring	−0.35**	0.04	−0.03	563	514
	Season	−0.29*	0.04	−0.03	846	781
P/E	Autumn	0.42***	−0.01	−0.16	0.61	0.96
	Winter	0.39***	0.01	−0.12	1.17	1.78
	Spring	0.45***	0.00	0.00	0.10	0.15
	Season	0.45***	0.00	−0.12	0.35	0.55

[a] *P*, precipitation; T_{max}, average maximum temperature; T_{min}, average minimum temperature; *ETP*, potential evapotranspiration; *P/E*, ratio of precipitation to potential evapotranspiration.
[b] * P <0.05, ** P <0.01, *** P <0.001.

Table 7. *Descriptive statistics for ten agronomic and morpho-physiological traits (including grain yield under rainfed and irrigated conditions) used in the classification of the Durum Core Collection (DCC-ICARDA), which includes durum wheat landraces and old cultivars from different origins of the Mediterranean Basin plus modern material released by CIMMYT–ICARDA from 1970 onwards*

Variables[a]		Min	Max	Mean	Std
THI	Landraces	2480	8373	5777	1416
	Modern	4187	9507	7012	1140
THR	Landraces	1700	3417	2462	419
	Modern	1867	3667	2717	474
KW	Landraces	34.6	55.0	45.0	4.5
	Modern	39.7	55.5	46.9	4.1
KS	Landraces	21.7	44.6	33.4	6.1
	Modern	22.9	49.5	37.4	6.0
DH	Landraces	108.7	115.9	111.4	1.1
	Modern	108.4	112.4	110.5	1.7
PH	Landraces	78.8	135.0	103.2	13.3
	Modern	78.8	113.8	92.2	7.1
Δl	Landraces	19.11	21.18	20.24	0.51
	Modern	19.37	21.32	20.20	0.42
Δk	Landraces	14.70	17.00	16.07	0.49
	Modern	15.79	16.97	16.30	0.26
AF	Landraces	8.08	12.74	10.63	1.01
	Modern	8.98	12.82	11.22	0.94
LA	Landraces	18.7	37.4	28.6	3.9
	Modern	22.5	37.8	29.1	3.8
LG	Landraces	39.1	52.2	47.2	3.0
	Modern	43.8	52.1	47.9	1.8

[a] *THI*, yield at Tel Hadya (irrigated) (kg ha^{-1}); *THR*, yield at Tel Hadya (rainfed) (kg ha^{-1}); *KW*, thousand kernel weight (g); *KS*, kernels per spike; *DH*, days to heading; *PH*, plant height (cm); Δl, carbon isotope discrimination of the penultimate leaf (‰); Δk, carbon isotope discrimination of kernels (‰); *AF*, ash concentration in the flag leaf blade three weeks after anthesis (%); *LA*, leaf area of the flag leaf blade (cm^2); *LG*, leaf greenness of the flag leaf blade three weeks after anthesis (SPAD units).

the modern material in the analysis, the reduced *PH* was probably the most important factor contributing to its *GY* superiority over the set of landraces. In fact, modern cultivars behaved better in terms of *GY*, particularly under irrigation, and showed a similar pattern of short phenology and high Δk and *AF* already exhibited by the most productive landrace groups.

The canonical discriminant analysis aided to reveal between-origins differences in overall performance among landraces (Fig. 3a), and among landraces and modern material (Fig. 3b). In both cases, most of the between-groups to within-groups variability could be explained by the first two canonical axes (CAN1 and CAN2). The discriminant loadings for each variable (or simple correlations of the variable and the discriminant scores for each axis), imposed on the plot representation as attribute points, provided a more complete interpretation of the analysis. When comparing landraces only, the centroids of the origin means for the Iberian Peninsula (Portugal and Spain) clustered closely together in the left

Table 8. *Mean values of nine geographic origins for the traits used in the classification of the Durum Core Collection (DCC–ICARDA)*

Coding and units of traits as in Table 7.

Origin[a]	N	*THI*	*THR*	*KW*	*KS*	*DH*	*PH*	Δl	Δk	*AF*	*LA*	*LG*
GRE	5	6680	2410	48.1	33.7	−0.7	106.8	20.23	16.02	10.75	28.6	46.9
ITA	6	6171	2531	46.9	34.4	−0.3	102.1	20.27	16.00	11.15	29.9	47.5
JOR	6	6573	2603	46.8	37.0	−0.1	93.5	20.31	16.42	11.37	28.7	48.1
MOR	11	6400	2792	45.4	36.7	−1.0	95.3	20.62	16.31	11.04	26.3	48.0
POR	10	4288	2118	41.5	28.6	2.2	110.8	19.74	15.76	10.03	30.6	47.1
SPA	4	4613	2296	43.4	27.7	3.1	110.0	19.75	15.48	9.08	32.1	49.3
SYR	8	5908	2398	44.7	33.8	0.1	107.2	20.55	16.26	10.59	26.4	44.7
CI(1)	7	6735	2469	50.5	33.9	−0.5	86.4	20.05	16.16	11.44	30.7	47.7
CI(2)	33	7071	2770	46.1	38.1	−0.4	93.4	20.24	16.33	11.17	28.8	48.0
$\sigma^2_{G\times E} / \sigma^2_G$ [b]		2.31		0.61	0.90	1.38	0.53	1.36	0.60	1.54	1.25	1.60
F_L [c]		5.10	3.25	2.05	3.32	13.58	2.41	6.20	3.69	4.87	2.55	2.01
		(0.0005)	(0.0102)	(0.0794)	(0.0090)	(<0.0001)	(0.0429)	(<0.0001)	(0.0048)	(0.0007)	(0.0334)	(0.0843)
F_T [d]		7.10 (<0.0001)	3.32 (0.0025)	3.14 (0.0038)	4.08 (0.0004)	10.52 (<0.0001)	6.36 (<0.0001)	4.58 (<0.0001)	5.34 (<0.0001)	4.51 (0.0001)	2.11 (0.0442)	2.12 (0.0434)

[a] GRE, Greece; ITA, Italy; JOR, Jordan; MOR, Morocco; POR, Portugal; SPA, Spain; SYR, Syria; CI(1), CIMMYT-ICARDA 1970's modern cultivars; CI(2), CIMMYT-ICARDA 1985 onwards modern cultivars.

[b] Ratio of estimated variance components for genotypexenvironment interation and genotype effect including landraces and modern cultivars.

[c] *F* value of the univariate analysis of variance for comparing landrace origins.

[d] *F* value of the univariate analysis of variance for comparing origins including landraces and modern cultivars.

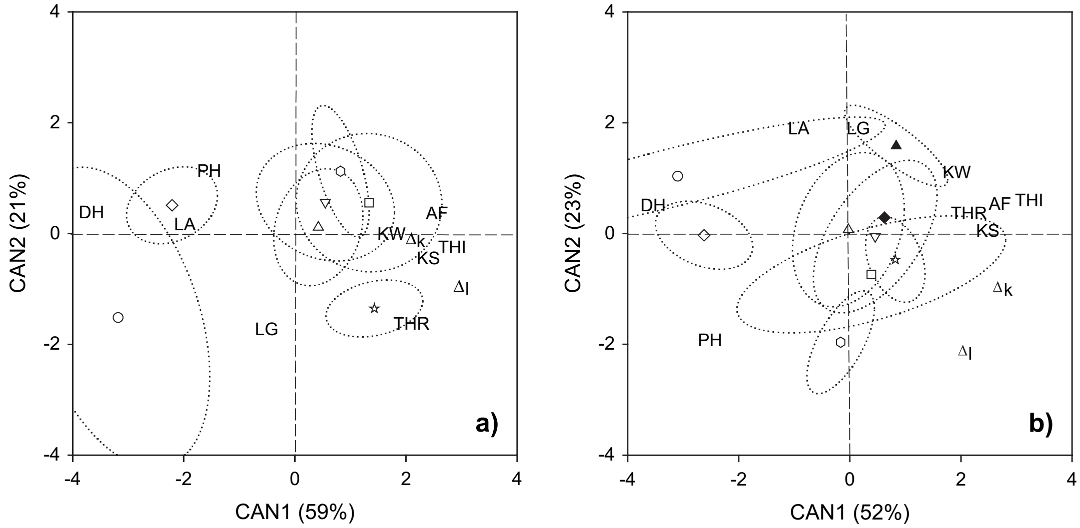

Fig. 3. Plot of the centroids (population means) and their 85% confidence ellipses for the first two canonical variables for durum wheat: (a) landraces and old cultivars from different origins of the Mediterranean Basin; (b) landraces and old cultivars plus modern material released by CIMMYT–ICARDA during the last three decades. (Legend: open square, Greece; open triangle, Italy; inverted open triangle, Jordan; star, Morocco; diamond, Portugal; open circle, Spain; open hexagon, Syria; closed triangle, 1970–1980 modern cultivars; closed diamond, 1985-onwards modern cultivars). Rescaled discriminant loadings of the explanatory variables are included in the plots. Coding of traits and origins as in Tables 7 and 8, respectively.

quadrants and separately from the rest of the geographic origins. Following the direction denoted by the attribute points, these landraces were longer in phenology (*DH*) and taller in height, exhibiting lower *GY* under rainfed and, especially, irrigated conditions as well as lower Δk, Δl, and *AF* than the other geographic origins, which clustered closely in the top-right quadrant. The exception was Morocco, which occupied the bottom-right quadrant, suggesting that this material particularly benefited from rainfed conditions in terms of grain yield (Table 8). The inclusion of the two sets of modern cultivars brought about some changes in the arrangement of the old material, although the Iberian Peninsula landraces still clustered closely together in the left quadrants (Fig. 3b). All other landraces tended to cluster in the bottom-right quadrant, close to the position of the more modern CI(2) CIMMYT–ICARDA material. The position of CI(2), alongside the positive part of CAN1, suggested a superiority in terms of *GY* under both rainfed and irrigated conditions, owing to larger *KW* and *KS* as well as higher *AF* and Δk values. On the other hand, the CI(1) position in the top-right quadrant indicated that these cultivars were characterized by large *KW* and *LG* values along with low *PH*, but also relatively high *GY*.

Discussion

Water conditions in early agriculture

These results suggest that, during early agriculture, wheat was cultivated under much better water status than that expected from present-day (rainfed) conditions in the same area. This agrees with previous δ^{13}C results of barley and wheat kernels recovered from early agricultural sites in the Fertile Crescent (Middle Euphrates) and the Iberian Peninsula (Araus *et al*., 1997*b*, 1999*a*; Ferrio *et al*., 2005). Moreover, fossil seeds of flax (*Linum usitatissimum* L.) have been found in the same PPNB levels of Tell Halula (Araus *et al*., 1999*a*) and Akarçay Tepe (R Buxó, unpublished results) as the fossil wheat kernels of this study. This species grows under wet conditions, and probably first appeared as a weed within cereal crops.

Cultivation under moister conditions could have been possible as a result of more humid environmental conditions prevailing at this time or by planting in alluvial areas (Bar-Yosef and Kislev, 1989). Thus, archaeobotanical evidence supports the possibility that environmental conditions in the Near East during early agriculture were cooler and moister than today (Harlan, 1998; Willcox, 1996). However, under conditions of low demographic pressure, selective exploitation of the more favourable areas (e.g. those depending on the flooding of patches of alluvial soil), cannot be discarded (Hillman, 1996). Moreover, water harvesting is an old practice, allowing deep-rooted plants to grow with the water accumulated. Through experiments in the Negev desert, Evenari (1980) has demonstrated that annuals such as wheat are able to develop and reproduce at a yearly precipitation below 100 mm. Cultivation in wetter soils may indirectly have helped selection of a higher rate of germination, a plant trait related to crop domestication (Hancock, 2003).

Potential yields and implications for the adoption of agriculture

Studies on different harvest techniques in dense stands of either wild einkorn or *T. dicoccoides* indicate the feasibility of obtaining yields in the range between 0.5–1.0 Mg ha^{-1} (Evans, 1998; Harlan, 1990; Hillman and Davies, 1990; Zohary, 1969). These values are below the potential yields (i.e. assuming small losses due to pest and/or diseases) suggested by the ^{13}C signature of plant remains for these early agricultural sites. Previous δ^{13}C results for barley and naked wheat cultivated in early agricultural sites of the Middle Euphrates (Araus *et al*., 2001*b*, 2003) and the Iberian Peninsula (Araus *et al*., 1999*a*) also suggest yields of at least 1 Mg ha^{-1}.

The old hypothesis of Childe (1952) on the role of the Younger Dryas, an episode characterized by a cool, dry climate, which is contemporary with the beginning of cultivation (*c*. 10 000 BC) in the region, is supported by recent studies from archaeological sites of the Middle Euphrates region (Bar-Yosef, 1998; Moore *et al*., 2000; Zohary and Hopf, 2000). As gathering from natural stands of wild cereals is subject to the vagaries of nature, this may in some way or another have resulted in a stimulus to increase yields from local stands. This would explain why early crops were cultivated under wet conditions, therefore increasing productivity and yield stability beyond that attained by gathering.

From the beginnings to the spread of agriculture: some environmental implications

The high δ^{15}N values of archaeological kernels suggest that soils in early agriculture were also fertile (Hörgberg, 1997), probably with high levels of organic matter and of nitrogen derived from mineralization. Either planting in natural wet soils (e.g. flooding of patches of alluvial soils), supplying organic manure (Wilkinson, 1982), or practising fallow (an agronomic practice that seems to be already present in early agriculture; Hillman, 1973), may have been responsible for keeping an adequate soil fertility (Wilkinson, 1994). Whatever the cause, such conditions of wet and fertile soils might have been possible provided that agriculture was restricted to limited areas. In fact, and according to our inferences, the relatively high yields presumably attained at the beginning of agriculture (*c*. 1 Mg ha^{-1}) were quite similar to the averaged yields achieved globally at the beginning of the 20th century (Calderini and Slafer, 1998). This denotes that the increased demands produced by the growing population since the Neolithic (some 4–10 million people; Minc and Vandermeer, 1990) to 1900 (more than 1 billion people; Evans 1998) were chiefly satisfied by an enlargement of the total cultivated land. The spread of agriculture and the subsequent increase in agricultural land may have implied a recurrent cultivation in less-than-optimal conditions, so as to expose crops to the particular environments of the new areas. In such a context, local and/or regional plant adaptations to water and temperature limitations, the two main stress factors in the Mediterranean Basin, may have been triggered.

Written evidences available from historical times for the Near East and the Mediterranean Basin about high cereal yields (post-dating of course the Neolithic Age) are scarce, the topmost being *c*. 4 Mg ha^{-1} for wheat in the Roman province of Syria at the beginning of the Christian era (Amir and Sinclair, 1994). Moreover, most of the evidence refers to cultivation under (natural or artificial) irrigation. Thus, yields of naked wheat under irrigation in ancient Mesopotamia (*c*. 2400 BC) have been calculated at around 1.5 Mg ha^{-1} (considering a hectolitre weight of 75 kg), being of nearly 2 Mg ha^{-1} for emmer (hectolitre weight of around 50 kg) (Adams, 1965). However, by *c*. 2100 BC wheat crops had all but disappeared because of salinization (Jacobsen and Adams, 1958). In Egypt, during the Dynastic Period (2700–435 BC), the yields of wheat (mostly emmer) under the natural flooding of the Nile were estimated to be in the range of 1.2–2.0 Mg ha^{-1} (Butzer, 1976; Kemp, 1989).

Grain weight in early domesticated wheats

Larger seeds are probably among the most important changes associated with domestication. The *KW*s of these early domesticates were probably higher than that reported for wild cereals cultivated prior to domestication (Willcox, 2004). The weight differences detected between archaeological and current material were not limited to modern cultivars, but were also applicable to traditional landraces, suggesting that increases to present-day *KW* were already achieved centuries ago (Cascón, 1934; Austin *et al*., 1989). Domesticated tetraploid wheats like durum wheat tend to have a comparatively low tillering capacity, making them more dependent on the early developed, deeper reaching seminal root system (Mac Key, 2005). In such a context, a correlation exists between *KW* and seminal root system. This may have a clear adaptive role.

KW is under complex polygenic control, and alleles having both positive and negative effects on the trait have been mapped (Cantrell and Joppa, 1991; Elias *et al*., 1996). In fact, the polygenic basis of *KW* and (perhaps) seed dormancy probably prevented a fast and conscious selection of plants with a favourable trait expression. By contrast, unconscious selection during a long phase of wild-plant cultivation can easily account for changes in traits with polygenic inheritance (Salamini *et al*., 2002) such as seed size (Willcox, 2004). Although strongly genetically determined, *KW* also depends on environmental constraints such as water availability or high temperatures during grain filling (Gooding *et al*., 2003; Rharrabti *et al*., 2003). However, the high Δk of archaeological kernels suggests that their low *KW* was not caused by drought stress during grain filling. Moreover, even under the harshest conditions in which wheat can grow in North Syria (Araus *et al*., 1998) or in other dry regions (Gooding *et al*., 2003), the values of grain weight are usually over 30 mg.

Diversity and local adaptation in durum wheat landraces from the Middle Euphrates

These results indicate that the landraces originated from areas with higher T_{min} and *P*/*E* values during the crop cycle are characterized by higher *PH* and *KW*, later heading date and by lower Δk. The most influential seasons on these traits were autumn (for T_{min}) and spring (for *P*/*E*). Therefore, the temperature pattern, together with the incidence of drought stress (especially at the end of the crop period), appeared as relevant ecogeographical factors shaping the evolutionary adaptive patterns of the Middle Euphrates durum wheat gene pool. In particular, genotypes from areas with higher T_{min} could sustain a larger growth, particularly in the initial phases of the crop, and could probably have evolved to require a larger accumulation of growing degree days than genotypes from colder areas, hence delaying their flowering date. Notably, T_{max} (i.e. heat stress) does not seem to play a major adaptive role contributing to the ecological fitness of the Fertile Crescent gene pool examined. This finding contrasts with results reported by Damania *et al.* (1996) when comparing a collection of 2420 Turkish durum wheat accessions at Tel Hadya (Aleppo, Syria). Those authors found a negative correlation between spring T_{max} and *DH*, although the particularly harsh conditions of the evaluation trial as compared with the conditions of the collecting sites could have driven this relationship. In addition to T_{min}, the occurrence of a higher *P*/*E* during the crop season, and particularly during spring, may have further acted to lengthen the crop life cycle. As a result, landraces growing in warmer (with regard to T_{min}) and less-droughted sites may have evolved towards a larger vegetative growth and, consequently, a higher *PH* and enhanced sink strength (*KW*). Probably, these landraces would have been exposed to terminal stress for the climatic conditions of this study (Gimenells 2002–2003), which resemble the average climate for the whole Middle Euphrates area prospected. This would explain their observed lower Δk, while early-flowering, high-Δk landraces would have behaved in the opposite manner owing a strategy to escape drought. Other studies have also revealed that climatic features of collecting sites in the Near East area can influence adaptive and morphological traits of cultivated winter cereals as well as their wild progenitors. For example, Annicchiarico *et al.* (1995) for durum wheat landraces and Peleg *et al.* (2005) for wild emmer reported significant relationships involving drought stress and high temperatures among climate variables and earliness of heading among agronomic traits. Damania *et al.* (1996) concluded that temperature, but not rainfall, provides strong selection force in shaping phenological characteristics in Turkish durum wheat landraces. All together, these studies reveal that tetraploid wheats have accumulated a large genetic diversity for adaptation to the local conditions of the Fertile Crescent area during a long evolutionary history from the dawn of agriculture.

Regional diversification of durum wheat around the Mediterranean Basin

The dispersal patterns of durum wheat within the Mediterranean region have led to the emergence of contrasting genetic material that exhibits clear differences in *GY* performance under rainfed or irrigated conditions, owing to a set of features as regards plant structure and water status. Differences were mainly observed between genotypes from the eastern and western parts of the Mediterranean Basin. Such variation is probably the result of specific adaptive patterns to the particular climate of the areas where durum wheat has been cultivated. In particular, western landraces (from Portugal and Spain), characterized by fewer *KS*, larger *PH*, and longer phenology (*DH*) than the eastern material, have evolved under relatively favourable climatic conditions (low maximum temperatures and mild water stress) and, therefore, the poor *GY* performance in the rainfed Tel Hadya trial was somewhat to be expected. In regard to this, Δ (both Δk and Δl) and *AF* were lower in western landraces, suggesting an enhanced water-use efficiency linked to low transpiration rates (Araus *et al.*, 2001*a*). However, current evidence (Condon *et al.*, 2004) indicates that low-Δ genotypes tend to be conservative in their growth rate, particularly if differences in Δ are the result of changes in stomatal conductance. On the other hand, the low Δ and *AF* of western genotypes may be just the consequence of greater exposure to the terminal water stress because of their long *DH* (Araus *et al.*, 1998, 2002). Remarkably, the morphological attributes of western genotypes did not translate into higher *GY* under irrigation, since lodging susceptibility and an extended growth period may have impaired their performance. Conscious human selection may also have played an important role in determining the contrasting morphological characteristics of durum wheat (Moragues *et al.*, 2005), since an increase in *PH* and tiller number are also relevant to improve straw production, the other end-use of this crop. The natural consequence of an increase in *PH* may have been a reduction in *KS*, a component that has a crucial contribution to the *GY* of durum wheat, especially under drought (García del Moral *et al.*, 2003).

Changes in *GY* top-ranking landrances could be partly attributed to contrasting morphophysiological features among geographic origins. In particular, landraces from Morocco (overall, the best-yielding material in the rainfed trial) flowered earlier, were shorter and had a reduced *LA* compared with the other origins. These are well-known attributes providing *GY* advantage, particularly the former, in drought-prone areas. Likewise, the Greek landraces (overall the best-yielding material under irrigation) had the largest *KW* among all origins. *KW* is the most important

GY component in durum wheat landraces originating from the north Mediterranean Basin (Moragues *et al*., 2005), an area characterized by moderate terminal water stress that resembles the conditions found in the irrigated Tel Hadya trial.

Modern genotypes exhibited a clear *GY* superiority over the set of landraces as a consequence of breeding efforts resulting in reduced *PH*, probably without significant decreases in total biomass, and improved partitioning (i.e. increased *HI*). Similar changes as a result of breeding have been reported elsewhere for durum wheat (Villegas *et al*., 2000; Koç *et al*., 2003; Motzo *et al*., 2004). The initial breeding material released by CIMMYT–ICARDA during the 1970s is clearly differentiated from the rest of the landraces as well as from the group of more recent cultivars. Overall, it displayed the highest *KW* and the shortest *PH*, which contrasted with a relatively low number of *KS*. Whether this observation is accurate or a consequence of a biased selection of sampled material remains to be elucidated. In addition, modern cultivars showed larger minimum values in *LA* and *LG*, probably as a result of positive selection pressures pushing towards increased photosynthetic performance (Araus *et al*., 1997*c*). On the other hand, the CI(2) cultivars shared similar features with the eastern Mediterranean landraces (cf. Fig 3b), although exhibiting the highest *GY* under both irrigated and rainfed conditions. In this regard, the patterns of water use in the modern material, pointing towards a low leaf-level water-use efficiency (high Δ) and high transpiration rates (high *AF*) (Araus *et al*., 2002; Villegas *et al*., 2000), did not seem to differ essentially from those displayed in the Near East landraces.

Concluding remarks

Durum wheat, widely cultivated today in rainfed conditions along the Mediterranean Basin, is a good example of a 'founder' crop in Western agriculture. Neolithic agricultural practices, probably including growing in natural wet soils, seem to have produced relatively high yields, which most likely enabled the global transition from gathering to cultivation to take place. Grain weight of early domesticated wheats was consistently lower than nowadays. Because of the good water (and fertility) conditions of early agriculture, the greater grain weight of current genotypes is largely attributable to more recent genetic improvements. After its domestication *c*. 8000 BC, durum wheat moved during the following millennia through the Mediterranean Basin. The spread of agriculture, together with the need to intensify its activity, putting into cultivation less favourable areas, triggered regional and local adaptations of wheat to a wide array of environmental conditions. The relationships found in landraces from the Middle Euphrates between their phenotypic variability and the particular climate where they were collected illustrate the local adaptedness of this species. At the regional level, consistent differences in grain yield, plant structure and water status among genotypes following both north–south and east–west gradients across the Mediterranean were probably driven by contrasting environmental and selection pressures.

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