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REVIEW

Geographic distribution and domestication of wild emmer wheat (*Triticum dicoccoides*)

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Abstract The transition from hunting and gathering to agriculture had revolutionary consequences for the development of human societies. Crops such as wheat, barley, lentil, pea and chickpea played a crucial role in the establishment of complex civilizations in south west Asia. Wild emmer wheat (*Triticum dicoccoides*) was one of the first cereals to be domesticated in the Fertile Crescent between c. 12,000 and c. 10,000 years ago. This step provided the key for subsequent bread wheat evolution. Wild emmer is found today in the western Fertile Crescent in Jordan, Syria and Israel, the central part of southeastern Turkey and mountain areas in eastern Iraq and western Iran. In this review, we summarize issues concerning geography and domestication of wild emmer wheat based on published molecular and archaeobotanical data and on our recent findings. We suggest that modern domestic tetraploid wheats derived from wild emmer lines from southeast Turkey. However, our understanding of emmer domestication is not complete. The "dispersed-specific" domestication model proposed for einkorn might well be appropriate also for emmer.

Keywords Archaeobotany · Domestication · Emmer wheat · Evolution · Molecular diversity · *Triticum dicoccoides*

Note: This is the first paper of a series of articles that came out of the international and interdisciplinary workshop "Cereal Diversity, Plant Domestication and Human History in the Fertile Crescent" held at the University of Çukurova, Adana, Turkey at the 10–15 of May 2009 organized by Hakan Özkan (Çukurova University) and Benjamin Kilian (Leibniz Institute of Plant Genetics and Crop Plant Research, IPK). Twenty-three scientists (from ten countries) from different fields of research presented and discussed their ideas. Two days of presentations were followed by a field trip.

This article is dedicated to P. Hanelt's 80th birthday, plant taxonomist and teacher.

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Introduction

Wheat is a staple crop in more than 40 countries (Williams 1993), and one of the founder crops of old

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world agriculture (Harlan 1992; Zohary and Hopf 2000). The crop provides more than 60% of calories in human diet, together with rice and maize (Gill et al. 2004). Wheat was among the first crops to be domesticated between c. 12,000 and c. 10,000 years ago (dates are given in before present calibrated years) in the Fertile Crescent (Nesbitt and Samuel 1996; Tanno and Willcox 2006a). Common present-day wheat cultivars fall into two groups: (1) tetraploid durum wheat, *T. durum* Desf. ($2n = 28$, BBAA) and (2) hexaploid bread wheat, *T. aestivum* L. ($2n = 42$, BBAADD). Cultivated polyploid wheats derive from the wild tetraploid progenitor *T. dicoccoides* (Körn. ex Aschers. et Graebn.) Schweinf.). In this review, the nomenclature and the genome formula given for *Triticum* by Dorofeev et al. (1979) is followed with little changes.

Wild emmer wheat (*T. dicoccoides*) is an annual, predominantly self-pollinated plant with large elongated grains and brittle ears disarticulating at maturity into spikelets. The species has two homologous sets of chromosomes, designated as BBAA (the cytoplasm is from the B genome), resulting most probably from spontaneous hybridization. Two wild diploid grasses have contributed, *T. urartu* Tum. ex Gandil. (AA) as the pollen donor and an unknown species closely related to modern *Aegilops speltoides* Tausch (SS) which contributed the B genome, as the female (Kilian et al. 2007a). Molecular data indicate that wild emmer as a species is about 360,000 years old, resulting from an event which took place somewhere in the Fertile Crescent (Dvorak and Akhunov 2005). According to Feldman and Kislev (2007), the hybridization could have occurred in the vicinity of Mt. Hermon and the catchment area of the Jordan River because of the larger morphological, phenological, biochemical and molecular variation of wild emmer from this region, compared to wild emmer from southeastern Turkey, northern Iraq, and southwestern Iran (Nevo and Beiles 1989; Ozbek et al. 2007).

Wild emmer wheat was recognized in 1873 by Friedrich August Körnicke, a German Agro-Botanist, in the herbarium of the National Museum of Vienna (Körnicke 1889). He found it among specimens of wild barley (*Hordeum spontaneum* K. Koch) that were collected by the botanist Theodor Kotschy in 1855 in Raschaya on the northwestern slope of Mt. Hermon (cited in Aaronsohn 1909). Körnicke described this plant specimen in 1889 as wild emmer wheat (*Triticum vulgare* Vill. var. *dicoccoides* Körn., Körnicke 1889). He also recognized that this plant is the wild progenitor "prototype" of cultivated wheat (Aaronsohn 1910).

It was not until June 18, 1906, that wild emmer was identified in the field by Aaron Aaronsohn who found it growing in a vineyard at Rosh-Pinna, near Safed, Eastern Galilee, Israel (together with Moses Bermann) (Aaronsohn and Schweinfurth 1906). Aaronsohn later found several forms of *T. dicoccoides* at different sites in Palestine and Syria. Körnicke was deeply impressed by the diversity of the new wheat and described 16 forms. Aaronsohn reported that *T. dicoccoides* always grows together with *H. spontaneum* in very poor soils. He also mentioned his aim to cross *H. spontaneum* with *T. dicoccoides*, in order to develop advanced races for future needs.

The discovery of wild emmer wheat in its natural habitat and Aaronsohn's subsequent studies of its geographic distribution and ecological requirements, greatly contributed to our understanding of wheat domestication, human history and wheat improvement (Aaronsohn and Schweinfurth 1906; Schweinfurth 1908; Aaronsohn 1909).

Wild emmer wheat belongs to the first cereals domesticated by humans in the Fertile Crescent and its domesticated form is known as *T. dicoccon* Schrank. Four subspecies were subsequently recognized for *T. dicoccon*: (1) ssp. *maroccanum* Flaksb. (Moroccan emmer); (2) ssp. *abyssinicum* Vav. (Ethiopian emmer); (3) ssp. *europaeum* Vav. = ssp. *dicoccon* (European emmer), and (4) ssp. *asiaticum* Vav. (Eastern emmer) (Gökgöl 1955; Dorofeev et al. 1979; Szabó and Hammer 1996; Teklu et al. 2007). It is this domestication step which provided the key for subsequent bread wheat evolution.

Present-day distributions and habitats

The geographical distribution of wild emmer wheat has been presented by Harlan and Zohary (1966), Johnson (1975), Valkoun et al. (1998) and Zohary and Hopf (2000). Wild emmer still grows in the western Fertile Crescent, the central part of southeastern Turkey and in the mountain areas in eastern Iraq and western Iran (Fig. 1). A center of wild emmer diversity has been reported to exist in the Jordan valley (Harlan and Zohary 1966; Zohary 1973), in an open park forest belt

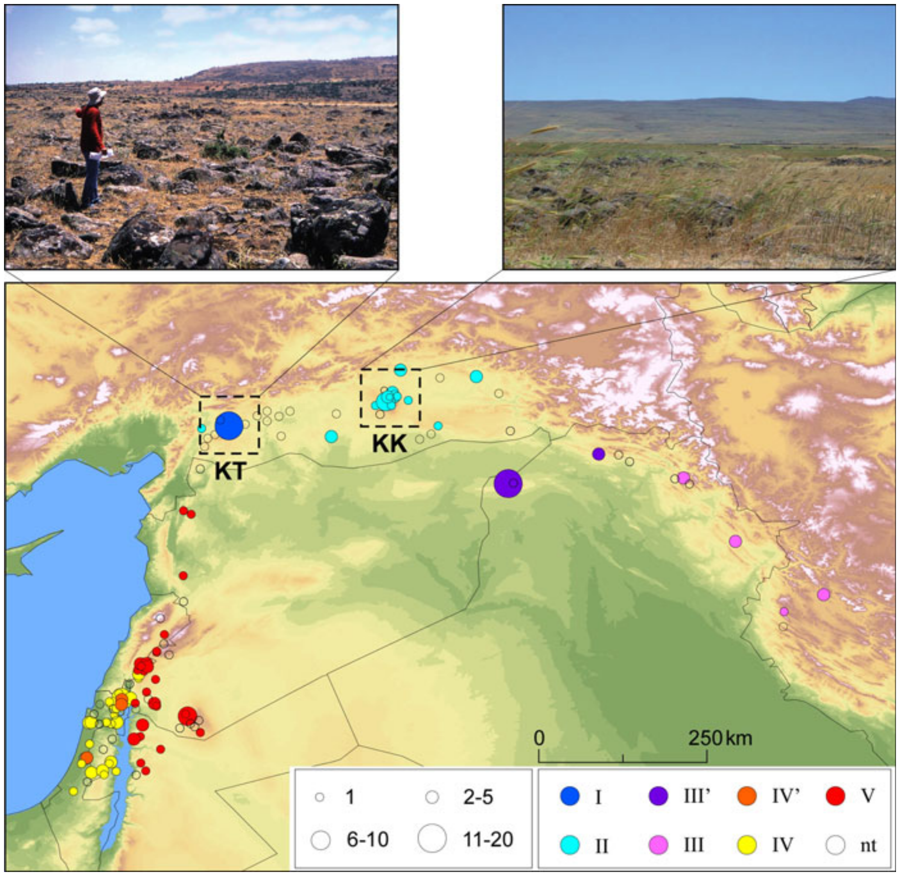

Fig. 1 Natural distribution and region of wild emmer domestication. Geographical information system (GIS) based overview of wild emmer collection sites. Collection site information has been combined from Harlan and Zohary (1966), Johnson (1975), Zohary and Hopf (2000), Nevo et al. (2002) and Ozkan et al. (2005) and recent observations from H. Özkan et al. (unpublished). Race assignments are color-coded and based on Ozkan et al. (2005). The western race consists of three subgroups IV′, IV and V. The central-eastern one comprises subgroups I, II, III′ and III. Other wild emmer collection sites that are not included in Ozkan et al. (2005) are shown without color. Numbers of individuals collected at specific sites (Ozkan et al. 2005) are indicated by a key at the bottom. KK, Karacadağ; KT, Kartal-Karadağ; nt, not tested by Ozkan et al. (2005). The landscapes of the Kartal-Karadağ (*upper left*) and the Karacadağ region (*upper right*) are shown

characterized by the presence of *Quercus ithaburensis* Decne and *Q. brantii* Lindl. (Nevo et al. 2002). Peripheral western populations of wild emmer wheat are present in *Q. calliprinos* Webb = *Q. coccifera* L. macquis, and in the open park forest with *Ceratonia siliqua* L. Dense natural populations of wild emmer wheat are frequent in the Upper Jordan Valley catchment area. However, elsewhere in the Fertile Crescent wild emmer wheat populations are semi-isolated or isolated, display a patchy distribution (Nevo et al. 2002; Figs. 1, 4), and are frequently mixed with wild einkorn. Johnson (1975) reported that from southeastern Turkey to Iraq and Iran the species is progressively replaced by a close relative, the wild tetraploid wheat species, *T. araraticum* Jakubz. ($2n = 28$, GGAA). In these eastern areas, occasional *T. dicoccoides* populations are present among more frequent stands of *T. araraticum* (Tanaka and Ishii 1973). A further centre of massive stands of wild emmer is found on the basalt slopes of the Karacadağ (Şanlıurfa and Diyarbakır province) and Kartal-Karadağ (Gaziantep province) mountain ranges, in southeast Turkey (Harlan and Zohary 1966). Wild emmer habitats range in altitude from 100 to 150 m below sea level up to 1,600–1,800 m above sea level (Schweinfurth 1908; Aaronsohn 1909; Nevo et al. 2002). They occur in very different climatic regions, from cool and humid Karacadağ mountains to hot and dry valleys in Israel. Wild emmer requires at least 400 mm annual rainfall (Willcox 2005) and it is found mainly in primary habitats (Harlan and Zohary 1966; Nevo et al. 1982, 1984), although in Turkey it occasionally colonizes secondary habitats (H. Özkan et al., unpublished). The species seems to be adapted to various geological conditions (Schweinfurth 1908); today, *T. dicoccoides* grows mainly in basalt areas in Turkey (H. Özkan et al., unpublished), but also on hard limestone bedrocks and on terra rossa soils (Schweinfurth 1908; Nevo et al. 2002). Its distribution in southeast Turkey and northwest Syria is patchy, being rare on calcareous soils (Willcox 2005; Fig. 4).

More needs to be known about wild emmer habitats. At the time of writing, no detailed distribution map exists for the species. We know even less about the past distribution of this important species, because plowing and overgrazing have probably reduced the natural habitats of *T. dicoccoides*.

Archaeobotanical finds of emmer from the Near East

Finds of charred hulled wheats for the early Neolithic archaeological sites in the Near East are given in Table 1. Despite the large number of identifications this provides only a limited picture of the early history of emmer due to incomplete chronological sequences and geographical gaps; in addition there are difficulties in identifying cereals from charred material. We know that wild emmer was gathered by Upper Paleolithic societies c. 23,000 years ago in the southern Levant from the charred grains recovered from the site of Ohalo II on the Sea of Galilee (Table 1; Kislev et al. 1992). Feldman and Kislev (2007) suggest that by c. 11,300 years ago wild emmer was first cultivated in the southern Levant at Netiv Hugdud and neighboring sites in the Jordan valley in the Pre-Pottery Neolithic A levels (PPNA). In the northern Levant wild emmer is absent from early sites, for example Abu Huereyra 1, Mureybet, Tell ‘Abr, Jerf el Ahmar, Tell, and Göbekli Tepe (see Table 1). At Tell Qaramel four grains were found, but the reliability of these finds is in doubt given their low frequencies and the presence of overlying Bronze Age layers. At the northern PPNA sites wild einkorn, barley and rye prevail and were probably cultivated (Willcox et al. 2009). Emmer appears in the northern Levant from the early PPNB (c. 10,500 years ago.) onward, but its status as wild or morphologically domestic is problematic at sites in southeast Turkey such Nevali Cori, Cafer Hüyük, and Cayonü (Table 1). At these sites emmer is associated with einkorn. At about the same time it appears outside its natural habitat at Dja’de in the Euphrates valley, northern Syria, and on the island of Cyprus, with einkorn.

Morphological domestication is best identified from spikelet bases which show the loss of dispersion mechanism resulting in an ear which disarticulates only during threshing (Hammer 1984). This is not easy to identify, because spikelet bases with the abscission scar are often poorly preserved. In addition, for some authorities emmer and einkorn spikelets are difficult to separate. Thus precise identifications are rare and indeterminate identifications more common (see Table 1, columns to the right). A recent reexamination of wheat spikelets bases (Tanno and Willcox 2006a) and a reappraisal (Fuller 2007) of the data, indicate that wild and domestic forms co-existed at sites for millennia. Grain size as opposed to spikelet bases was used as a criterion for morphological domestication at some sites such as Aswad (see below) and Cayönü. We consider this problematical because of phenotypic variation and puffing caused by charring (Braadbaart 2008). At the site of Tell Aswad, excavated in 1973 and situated in the southern Levant (southern Syria), grain size was used to identify emmer domestication which was dated to c. 11,250 years ago (van Zeist and Bakker-Heeres 1982). Subsequently, carbon isotope (AMS) dating directly on the emmer grains in 2003, showed that these seeds date to c. 10,500 years ago (Willcox 2005; Table 1). Recent excavations (Stordeur 2000) at Tell Aswad confirmed this estimate.

So when did emmer populations lose their ability to disperse? Unfortunately the data is too incomplete to be sure. But by the middle PPNB (c. 10,000 years ago) at sites such as Abu Hureyra, Cafer Höyük, Halula, and Aswad spikelet bases have been identified as domesticated. These sites also have naked wheat which is indisputably domesticated in form. Early PPNB material from sites such as Cayönü and Cafer Höyük need to be reexamined.

Archaeobotanical evidence demonstrates that during the PPNA emmer was the only wheat used in the southern Levant. A solitary exception of two grains

Table 1 Identifications of hulled wheats obtained from charred remains from sites in the Near East

Site	Period	Wild einkorn and emmer						
		T. boeoticum/ *S. strictum* grain	*T. boeoticum* glume base	*T. boeoticum* grain (1 g)	*T. boeoticum* spikelet base	*T. boeoticum* grain (2 g)	*T. dicoccoides* spikelet base	*T. dicoccoides* grain
Ohalo II*	Early Epipalaeolithic						9	21
Abu Hureyra	Late Epipalaeolithic	303				252		
Mureybit I	Late Epipalaeolithic					12		
Mureybit II	Khiamian					9		
Mureybit III	PPNA	2,172						
Qaramel	PPNA/Khiamian	1,170		1,108	292			?4
Tell 'Abr	PPNA	2,999		90				
Jerf el Ahmar	PPNA	2,539		67	5			
Göbekli	PPNA					5		
Netiv Hagdud*	PPNA						123	27
Iraq ed Dubb*	PPNA	1				1		
ZAD II*	PPNA						2	4
Gilgal*	PPNA						x	x
Djade	Early PPNB	1,120		302	16			192
Mureybit IV	Early PPNB					7		
Jericho	PPNA/early PPNB							
Wadi Jilat 7*	Early PPNB							
Cayönü	Early PPNB							20
Nevali Cori	Early PPNB							
Cafer Höyük	Early/middle PPNB	23	3		3			4
Asikli Höyük	Middle PPNB			1				
Tell Aswad*	Middle PPNB							
Beidha*	Middle PPNB							
Cayönü	Middle PPNB							
Halula	Middle PPNB			3				
Hacilar	Middle PPNB							
Jericho*	Middle PPNB							x
Abu Hureyra	Middle/late PPNB	7						
Ain Ghazal*	Middle/late PPNB							
Cafer Höyük	Middle/late PPNB	8	1		1			
Cafer Höyük	Middle/late PPNB	5	2					1
Ghoraifé*	Middle/late PPNB							

Table 1 continued

Site	Period	Wild einkorn and emmer						
		T. boeoticum/ *S. strictum* grain	*T. boeoticum* glume base	*T. boeoticum* grain (1 g)	*T. boeoticum* spikelet base	*T. boeoticum* grain (2 g)	*T. dicoccoides* spikelet base	*T. dicoccoides* grain
Nahal Hemar*	Middle/late PPNB							
Wadi Jilat 7*	Middle/late PPNB							2
Abu Hureyra	Middle/late/PPNB	21						
El Kowm I	?Late PPNB							
Basta*	Late PPNB							
Cayönü	Late PPNB							
Dhuweila*	Late PPNB					2		
Ghoraifé*	Late PPNB							
Ramad*	Late PPNB			4				
Ras Shamra	Late PPNB							
Wadi Fidan A*	Late PPNB							
Bouqras	Late PPNB/PN							
El Kowm II	Final PPNB							
Tell Ramad*	Final PPNB			22				
Wadi Fidan C*	Final PPNB					2		
Wadi Jilat 13*	Early late neolithic							
Cayönü	PPNC							
Can Hasan III	Late/final PPNB			3		3		
Catal Höyük	Aceramic							
Catal Höyük	Aceramic							
Catal Höyük	Aceramic			2				
Abu Hureyra	PN							
Cayönü	PN							
Catal Höyük	PN		49	2				
Catal Höyük	PN		51	52				
Catal Höyük	PN		2					
Ohalo II*	Early Epipalaeolithic							
Abu Hureyra	Late Epipalaeolithic							
Mureybit I	Late Epipalaeolithic							
Mureybit II	Khiamian							
Mureybit III	PPNA							
Qaramel	PPNA/Khiamian							

Table 1 continued

Site	Period	Domestic einkorn and emmer							
		T. monococcum glume base	*T. monococcum* grain (1/2 g)	*T. monococcum* grain (1 g)	*T. monococcum* spikelet base	*T. monococcum* grain (2 g)	*T. dicoccon* grain	*T. dicoccon* glume base	*T. dicoccon* spikelet base
Tell ʻAbr	PPNA								
Jerf el Ahmar	PPNA								
Göbekli	PPNA								
Netiv Hagdud*	PPNA								
Iraq ed Dubb*	PPNA								
ZAD II*	PPNA								
Gilgal*	PPNA								
Djade	Early PPNB								
Mureybit IV	Early PPNB								
Jericho	PPNA/early PPNB		x				x		
Wadi Jilat 7*	Early PPNB								
Cayönü	Early PPNB			12			9		
Nevali Cori	Early PPNB								
Cafer Höyük	Early/middle PPNB	4	11		4		5	34	17
Asikli Höyük	Middle PPNB		17				33		
Tell Aswad*	Middle PPNB			17			1,905		
Beidha*	Middle PPNB						x		
Cayönü	Middle PPNB			3			3		
Halula	Middle PPNB								
Hacilar	Middle PPNB						x		x
Jericho*	Middle PPNB		68			82	64		
Abu Hureyra	Middle/late PPNB		24				15		
Ain Ghazal*	Middle/late PPNB						x		x
Cafer Höyük	Middle/late PPNB		35				5	38	23
Cafer Höyük	Middle/late PPNB	15	8		15				2
Ghoraifé*	Middle/late PPNB						7		
Nahal Hemar*	Middle/late PPNB						7	14	
Wadi Jilat 7*	Middle/late PPNB	2	6	7	5	22	10		
Abu Hureyra	Middle/late/PPNB	3	16				9		1
El Kowm I	?Late PPNB						14		
Basta*	Late PPNB			1			21		14
Cayönü	Late PPNB			9			37		

Table 1 continued

Site	Period	Domestic einkorn and emmer							
		T. monococcum glume base	*T. monococcum* grain (1/2 g)	*T. monococcum* grain (1 g)	*T. monococcum* spikelet base	*T. monococcum* grain (2 g)	*T. dicoccon* grain	*T. dicoccon* glume base	*T. dicoccon* spikelet base
Dhuweila*	Late PPNB								
Ghoraifé*	Late PPNB		16				114		
Ramad*	Late PPNB		20				281		
Ras Shamra	Late PPNB						6		
Wadi Fidan A*	Late PPNB		1			1	1		
Bouqras	Late PPNB/PN		x				x	13	2
El Kowm II	Final PPNB		10		6		10	16	21
Tell Ramad*	Final PPNB		141				3,926		
Wadi Fidan C*	Final PPNB		2	3		1			
Wadi Jilat 13*	Early late neolithic		1	3		3	3		
Cayönü	PPNC			1			2		
Can Hasan III	Late/final PPNB			9		7	6		
Catal Höyük	Aceramic	136		134			299	1,648	
Catal Höyük	Aceramic	13		16			126	544	
Catal Höyük	Aceramic	22		107			430	1,166	
Abu Hureyra	PN		5				2		
Cayönü	PN		1				16		
Catal Höyük	PN	35		5			13	280	
Catal Höyük	PN	680		125			517	16,729	
Catal Höyük	PN	8		5			2	152	

Site	Period	Domestication status not specified								
		T. boeoticum/monococcum glume base	*T. boeoticum/monococcum* grain	*T. boeoticum/monococcum* spikelet base	*T. dicoccoides/dicoccon* grain	*Triticum* spp. spikelet base	*T. monococcum/dicoccon* glume base	*T. monococcum/dicoccon* grain	*Triticum* sp. glume wheat grain	*T. monococcum/dicoccon* spikelet base
Ohalo II*	Early Epipalaeolithic									
Abu Hureyra	Late Epipalaeolithic									
Mureybit I	Late Epipalaeolithic									
Mureybit II	Khiamian									
Mureybit III	PPNA									
Qaramel	PPNA/Khiamian									
Tell ʻAbr	PPNA									
Jerf el Ahmar	PPNA									

Table 1 continued

Site	Period	Domestication status not specified								
		T. boeoticum/ *monococcum* glume base	*T. boeoticum*/ *monococcum* grain	*T. boeoticum*/ *monococcum* spikelet base	*T. dicoccoides*/ *dicoccon* grain	*Triticum* spp. spikelet base	*T. monococcum*/ *dicoccon* glume base	*T. monococcum*/ *dicoccon* grain	*Triticum* sp. glume wheat grain	*T. monococcum*/ *dicoccon* spikelet base
Göbekli	PPNA									
Netiv Hagdud*	PPNA									
Iraq ed Dubb*	PPNA						35		1	7
ZAD II*	PPNA						18			
Gilgal*	PPNA									
Djade	Early PPNB									
Mureybit IV	Early PPNB									
Jericho	PPNA/early PPNB									
Wadi Jilat 7*	Early PPNB							2	1	
Cayönü	Early PPNB		5		16			1		1,421
Nevali Cori	Early PPNB		661		129	26,002				
Cafer Höyük	Early/middle PPNB	3	14	1			41	16		24
Asikli Höyük	Middle PPNB						528	4		111
Tell Aswad*	Middle PPNB						13,745			7,168
Beidha*	Middle PPNB							1		x
Cayönü	Middle PPNB		2					2		497
Halula	Middle PPNB				163	11				
Hacilar	Middle PPNB			x						
Jericho*	Middle PPNB							5,000		x
Abu Hureyra	Middle/late PPNB		9				2			1
Ain Ghazal*	Middle/late PPNB									
Cafer Höyük	Middle/late PPNB	15	67	5			31			1
Cafer Höyük	Middle/late PPNB		5				54	5		8
Ghoraifé*	Middle/late PPNB						38			28
Nahal Hemar*	Middle/late PPNB									
Wadi Jilat 7*	Middle/late PPNB						27	8	16	1
Abu Hureyra	Middle/late/PPNB		9				11			2
El Kowm I	?Late PPNB									
Basta*	Late PPNB						27			
Cayönü	Late PPNB		1						1	260
Dhuweila*	Late PPNB									
Ghoraifé*	Late PPNB						667			482

Table 1 continued

Site	Period	Domestication status not specified								
		T. boeoticum/*monococcum* glume base	*T. boeoticum*/*monococcum* grain	*T. boeoticum*/*monococcum* spikelet base	*T. dicoccoides*/*dicoccon* grain	*Triticum* spp. spikelet base	*T. monococcum*/*dicoccon* glume base	*T. monococcum*/*dicoccon* grain	*Triticum* sp. glume wheat grain	*T. monococcum*/*dicoccon* spikelet base
Ramad*	Late PPNB						1,212			1,428
Ras Shamra	Late PPNB						9			15
Wadi Fidan A*	Late PPNB						224			13
Bouqras	Late PPNB/PN									
El Kowm II	Final PPNB						534	15		94
Tell Ramad*	Final PPNB						24,843			20,153
Wadi Fidan C*	Final PPNB						1,761	2		512
Wadi Jilat 13*	Early late neolithic						5			1
Cayönü	PPNC									12
Can Hasan III	Late/final PPNB			15						
Catal Höyük	Aceramic						2,749	54		
Catal Höyük	Aceramic						1,291	53		
Catal Höyük	Aceramic						1,971	154		
Abu Hureyra	PN		1				22			4
Cayönü	PN									1,679
Catal Höyük	PN						430			
Catal Höyük	PN						14,108	265		
Catal Höyük	PN						360	5		

Despite the incomplete nature of the data it appears that emmer dominates at sites situated in the southern Levant (southern Syria, Jordan and Israel), which is culturally distinct (sites from this area are distinguished by *) and that einkorn appears about 10,000 years ago. In the north (northern Syria and Turkey) emmer is not found until about 10,500 years ago, prior to this period einkorn is present with rye and barley. Sure identifications of domestic emmer do not appear until about 10,000 years ago, those dated earlier need to be verified, they come from the northern Levant. The strikingly low frequencies of einkorn (less than 10% taking into account the problems of identification) compared to emmer suggest that it may have been a weed in emmer fields (also rye and barley) and not a pure crop. Most information for this table came from the data base compiled as part of AHRB/C funded project, based at the Institute of Archaeology, UCL (2001–2004): 'The origin and spread of Neolithic plant economies in the Near East and Europe' principal investigators: Stephen Shennan and James Conolly; research assistant: Sue Colledge. For these sites we have not to cite the original source (http://ads.ahds.ac.uk/catalogue/collections/blurbs/283.cfm). Sites not included in the data base include Halula (Willcox et al. 2009), Jerf el Ahmar, Dja'de, Qaramel Tell 'Abr (Willcox et al. 2008), Göbekli (Neef 2003), ZAD II (Edwards et al. 2004). Gilgal (Feldman and Kislev 2007). x—Presence, *—sites situated in the southern Levant, 1 g—one-grained forms, 2 g—two-grained forms of einkorn reported from the PPNA site at Iraq "ed Dubb" should be treated with caution. In the north einkorn wheat occurs during the PPNA (Tell Qaramel) and early PPNB (Nevali Çori). Feldman and Kislev (2007), on the basis of archaeobotanical data, suggest that emmer cultivation spread from the southern Levantine Corridor to the northern Levantine Corridor and during a period of several hundred years multiple domestication events occurred independently at different locations. By the early PPNB emmer wheat appears in the north and by the middle PPNB it becomes dominant over einkorn, while in the south einkorn appears as an introduced but minor component. Could it be that einkorn was introduced to the south with crops coming from the north?

Emmer identifications from the middle PPNB onwards (Table 1) out number by 90% those of einkorn, even when the problems of identification are taken into account. This proportion resembles einkorn's role as weed of cultivation in traditional wheat fields observed in the Near East today. We also suppose that einkorn was a weed of emmer fields during the Neolithic. Indeed to date there is no archaeobotanical evidence that in the Near East einkorn was grown as a separate crop from emmer (van Zeist and Buitenhuis 1983). At later sites as agriculture spread west into Europe, emmer continued to be dominant but einkorn became a major component at some sites in Europe (Jacomet 2007) and in Central Asia (Charles 2007).

Other than einkorn, emmer was the major wheat crop during the Neolithic in the Near East, it was also the major wheat in ancient Mesopotamia and Egypt. In Turkey it started to decline during the Bronze Age about 5,000 years ago when it was replaced by naked wheats (*T. durum* and/or *T. aestivum*). In Europe this change occurred later (for more details see Nesbitt and Samuel 1996). Emmer wheat cultivation continued its decline becoming rarer and rarer. Today it can be found only in some isolated traditional farming communities, in Turkey, Iran, Armenia, Ethiopia, Oman, Italy and Spain (Perrino et al. 1996; Hammer et al. 2004; Teklu and Hammer 2006. In recent years emmer wheat has been re-discovered by the organic food industry where it is used for bread and cookie production (Caballero et al. 2008; Fares et al. 2008; Serpen et al. 2008). The importance of *T. dicoccon* landraces has been themed by Teklu et al. (2007).

Molecular studies of emmer domestication

Previous studies have shown that wild emmer has a wide range of morphological and genetic variation (Aaronsohn 1909; summarized in Xie and Nevo 2008). In natural habitats of wild emmer, two main races, namely a western Palestine race and a central-eastern Turkish-Iraqi race, have been recognized (Harlan and Zohary 1966; Mori et al. 2003; Ozkan et al. 2005; Luo et al. 2007). The two races are geographically (Figs. 1, 4), morphologically and genetically distinct (Kawahara et al. 1993; Nishikawa et al. 1994; Joppa et al. 1995; Kawahara and Nevo 1996; Ozkan et al. 2005; Luo et al. 2007; Poyarkova 1988; Figs. 2, 3). *T. dicoccoides* and *T. araraticum* are morphologically very similar but not interfertile (Maan 1973; Zohary and Hopf 2000).

Molecular marker-based studies of crop domestication have provided important details on taxonomy, genetic diversity, evolution and domestication history of wheat (Salamini et al. 2002; Dubcovsky and Dvorak 2007; Kilian et al. 2009). In addition, DNA markers offer excellent opportunities for narrowing down the putative area of crop domestication, as well as for tracing the spread of these crops. New molecular fingerprinting techniques allow screening of large germplasm collections at multiple loci. These approaches involve comparing wild and domesticated populations based on genome-wide estimates of genetic similarity (Martin and Salamini 2000). Such studies rely on the assumption that the genetic structure of modern wild populations has not been significantly altered during the past 10,000 years. Heun et al. (1997) used the AFLP (Amplified Fragment Length Polymorphism) technique and compared 261 wild einkorn lines (*T. boeoticum* Boiss.) still growing in the Fertile Crescent, with 68 lines of cultivated einkorn wheat (*T. monococcum* L.). In their study, a genetically distinct group of 11 wild einkorn lines from the Karacadağ mountain range in southeast Turkey was identified. These lines were more similar to cultivated einkorn than any other wild line studied. Therefore, Heun et al. (1997) suggested the Karacadağ mountain range in southeast Turkey as the site of einkorn domestication. This study pioneered the search for the origin of crop domestication using large germplasm collections and considering a large set of marker loci.

At the beginning of this century the history of tetraploid wheat domestication started to get scrutinized using AFLP molecular markers. Ozkan et al.

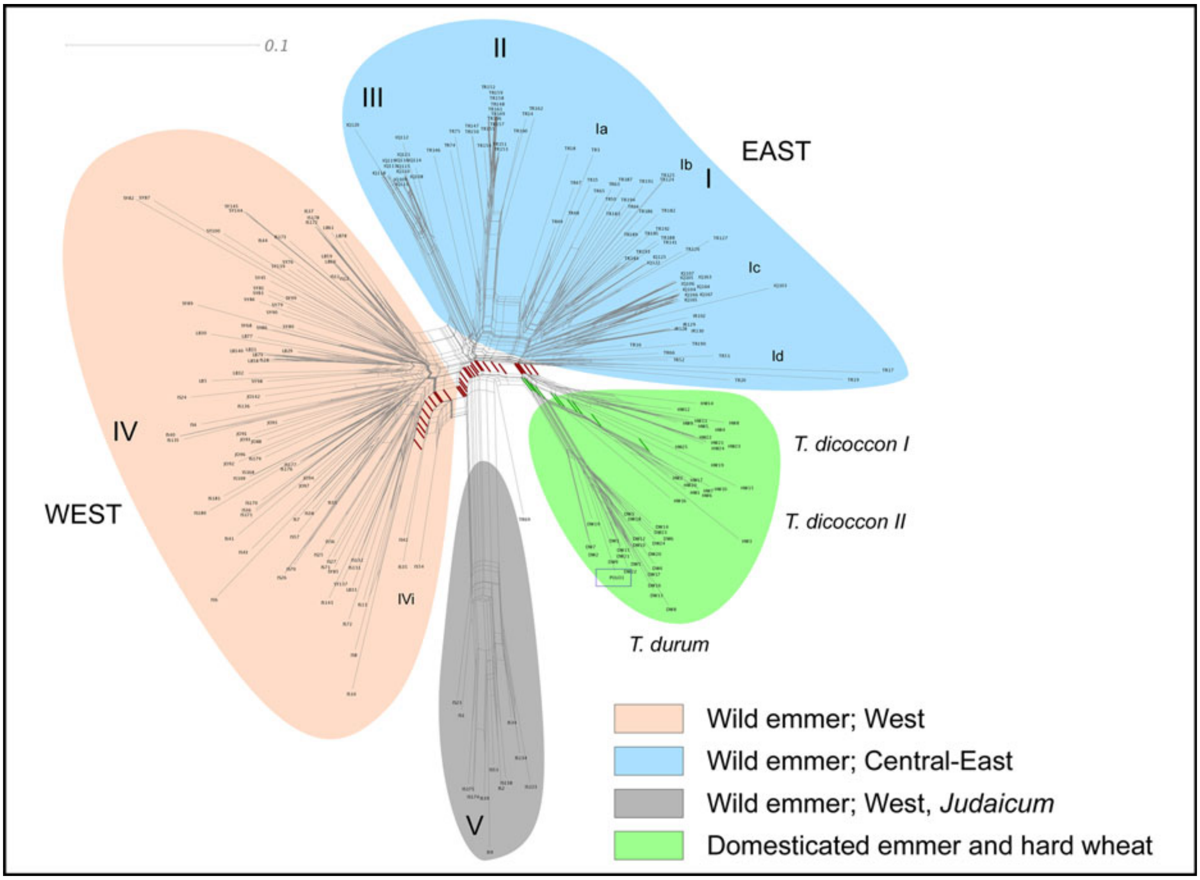

Fig. 2 Genetic diversity among wheat accessions considered in Ozkan et al. (2005). NeighborNet (NNet) planar graph of 234 wheat individuals based on 175 polymorphic AFLP chromosome markers and Dice distances between individuals

(2002) compared wild and domesticated emmer wheats and studied a collection of 99 wild emmer wheats sampled from primary habitats, included 43 domesticated wheat lines (19 hulled emmer lines and 24 free-threshing durum wheat lines). The most important findings were that 15 out of 19 wild emmer lines from the Karacadağ mountain range were more closely related to domesticated emmer and durum wheat than any other wild emmer lines. They concluded that the southeastern Turkish populations were more closely related to domesticated tetraploid wheats than any other wild emmer populations. This was the basis to propose a "monophyletic" origin of domesticated emmer wheat. The authors further reported that domesticated, hulled emmer lines (*T. dicoccon*) and free-threshing hard wheat lines (*T. durum*) were separated in phylogenetic trees, although these two wheat groups originated probably from one common progenitor. However, due to the lack of wild emmer populations from several regions in Turkey and elsewhere (Kartal-Karadağ mountains, Gaziantep region and Şanlıurfa plateau in Turkey or regions in Iraq and Iran), it was not possible to be sure of the precise region of emmer domestication. In addition, Allaby and Brown (2003, 2004) claimed that a monophyletic origin of domestication might be erroneously inferred when populations are examined by AFLP genotyping and neighbor-joining analysis. They argued that the combination of hybridization among populations, migration, and genetic drift might affect the shape of phylogenetic trees, which cannot be used to reconstruct correctly the history of the relationship between domesticated and wild populations (Allaby and Brown 2004). Based on the comment of Allaby and Brown (2003), Salamini et al. (2004) re-analyzed AFLP data using the Principal Coordinate Analysis (PCA). Ordination methods such as PCA (Hotelling 1933), like tree-building procedures,

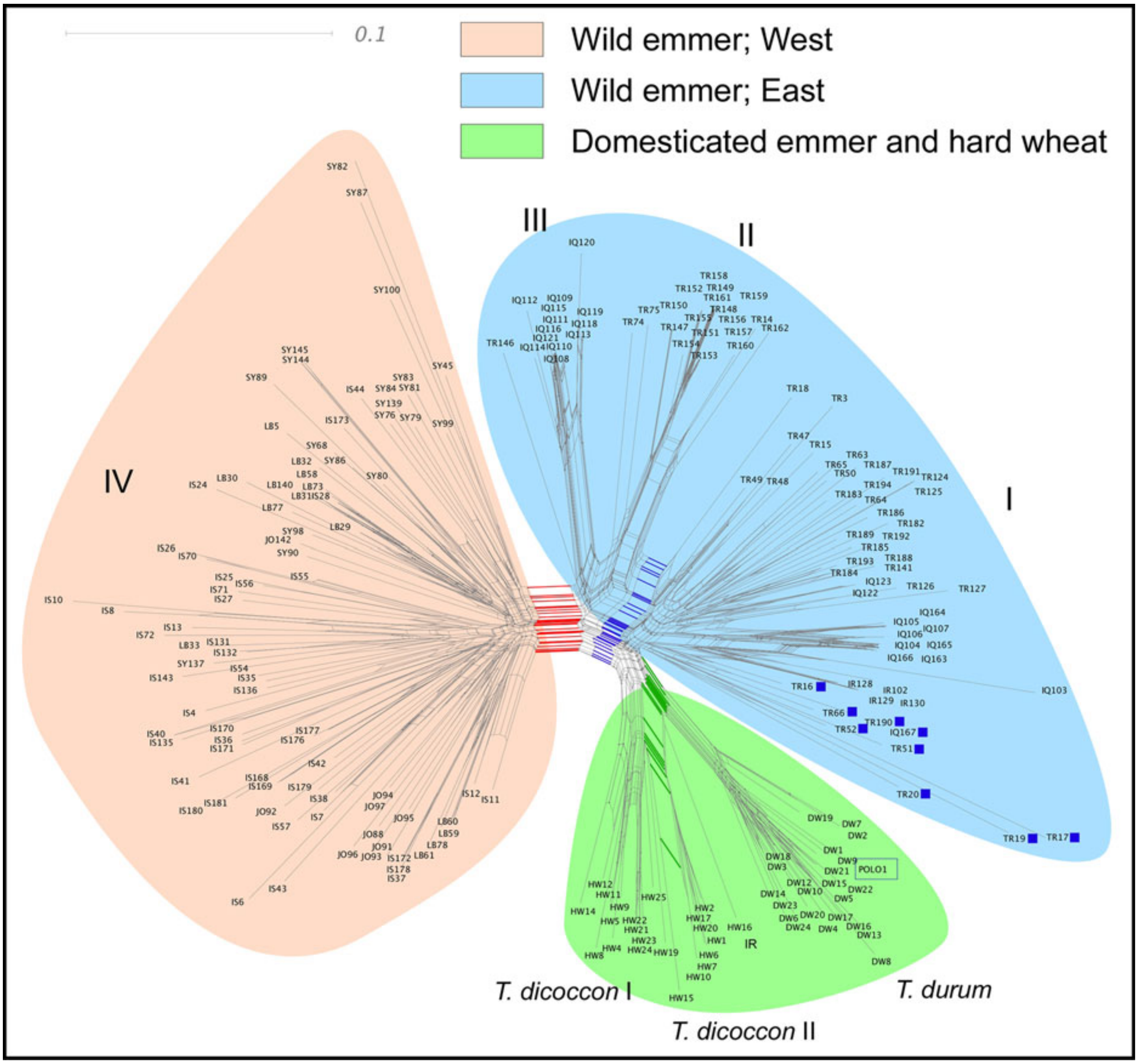

Fig. 3 Genetic diversity study among wheats as described in Fig. 2. NeighborNet (NNet) planar graph of 219 wheat individuals based on 175 polymorphic AFLP chromosome markers and Dice distances between individuals

simplify the presentation of multivariate data. The logic of this analysis is the existence of different degrees of correlation between allelic frequencies in paired populations. The extent of the correlation measures the history of the populations in terms of their common descent (Cavalli-Sforza et al. 1994). The PCA results (Salamini et al. 2004) supported the previous results of Ozkan et al. (2002), that domesticated tetraploid wheats are most closely related to wild emmer lines sampled in southeastern Turkey, particularly from the Karacadağ area/Diyarbakır region.

In 2003, Mori et al. published a paper on chloroplast (cp) microsatellite variation in a collection of wild and domesticated tetraploid wheats. They detected a large number of cpDNA haplotypes within two broad emmer lineages. Haplotype 10, belonging to lineage I, was present in 39.6% of domesticated emmer (*T. dicoccon*) accessions and in 90% of bread wheat varieties (*T. aestivum*). This haplotype was present only in three wild emmer accessions from the Kartal-Karadağ mountain region in southeast Turkey (around 280 km west of the Karacadağ mountains). These lines represented 4%

of the total number of wild emmer accessions investigated. Furthermore, the unique haplotypes 22 and 59 were found in domesticated emmer lineage II and in bread wheat lines, but not in wild emmer. Based on these results, Mori et al. (2003) concluded that wild emmer was independently domesticated, once in the Kartal-Karadağ mountain region and also once somewhere else in Fertile Crescent.

The findings of Ozkan et al. (2002) and Mori et al. (2003) provided a new vision of emmer domestication which nevertheless remained contradictory and unresolved. In order to understand the source for the discrepancy between nuclear and chloroplast DNA markers results, Ozkan et al. (2005) studied again the genetic variability in wild and domesticated emmer, considering more accessions and more sampling locations. In their experiment the authors used a collection of 226 wild and domesticated emmer lines and amplified 169 polymorphic AFLP loci. This collection included all 69 wild emmer lines considered by Mori et al. (2003). The main aim of this experiment was to narrow down the region in which wild emmer was brought into domestication. In this study, Ozkan et al. (2005) showed that two different genetic taxa of *T. dicoccoides* exist, the western one, from Israel, Jordan, Syria and Lebanon, and the central-eastern one, which has been sampled in Turkey, Iraq and Iran (Fig. 1). The authors concluded that the central-eastern race played the key role during wild emmer domestication and was therefore to be considered the progenitor of domesticated emmer wheat. Wild emmer populations, particularly from the Karacadağ mountain range, were again genetically more related to domesticated emmer compared with other wild emmer lines from other regions. The Turkish Kartal-Karadağ population belongs genetically to the central-eastern *T. dicoccoides* race, but is less related at the nuclear DNA level (AFLP marker loci) to the domesticated gene pool of emmer wheat. Nevertheless, a discrepancy remains on the smaller (local) geographical scale, reflecting the difficulty of studying events which took place in the Neolithic some 10,000 years ago; the cpDNA data indicate the Kartal-Karadağ mountains, while AFLP fingerprinting points to the Karacadağ range as the putative site of tetraploid wheat domestication. In 2006, Abbo et al. reinterpreted recent DNA polymorphism data (Ozkan et al. 2002, 2005; Mori et al. 2003) to detect genetic ripples left by the earlier wave of Neolithic wheat farming. They proposed that the close genetic affinity between domesticated stocks and wild emmer from the Karacadağ and the Kartal-Karadağ mountains (western border) and Iraq-Iran (eastern border) defines the area where mixed cultivation of local wild genotypes and imported genotypes may have taken place prior to the emergence of the non-shattering mutant(s) (considered a sign of domestication). Later, such mutants established in the incipient seed stocks and may have later spread across the Neolithic cultural horizons of the Near East. According to them, this model can corroborate the theory regarding the hub of the Neolithic "Big (agricultural) Bang" in southeastern Turkey already suggested by Lev-Yadun et al. (2000) and Gopher et al. (2001).

One year later, Luo et al. (2007) revisited emmer domestication using restriction fragment length polymorphisms (RFLP) at 131 loci in 277 accessions of wild emmer, 186 domesticated emmer landraces and 55 landraces of durum wheat. Their aim was to understand the population structure in wild and domesticated emmer. Their results support that wild emmer consists of two genetically distinct populations, each further subdivided as previously suggested by Ozkan et al. (2005). Luo et al. (2007) found that gene flow between wild and domesticated emmer occurred across the entire area of wild emmer distribution. Based on these results, they concluded that either (1) emmer was domesticated in the Diyarbakır region in southeastern Turkey, which was followed by subsequent hybridization and introgression from wild to domesticated emmer in southern Levant. The wild emmer gene pool in the Levant was partly absorbed into the gene pool of domesticated emmer diffusing from southeastern Turkey, or (but less likely, according to authors)—(2) emmer was domesticated independently in the Diyarbakır region and also in the southern Levant.

Based on a direct estimation of mutation rates for microsatellite loci and re-sequencing candidate loci, Thuillet et al. (2002, 2005) and Haudry et al. (2007) have discussed the occurrence of bottlenecks during tetraploid wheat domestication and breeding. A continuous decrease in effective population size is evident, indicating the action of severe bottlenecks, associated in particular to breeding. However, Thuillet et al. (2005) reporting that the bottleneck of domestication was relatively low—which in terms of Nei's heterozygosity corresponds to the presence of 95% of the variation of *T. dicoccoides* in *T. dicoccon*. This situation is remarkably similar to the one reported for einkorn by Kilian et al. (2007b). On the other hand, a considerable loss of nucleotide diversity is reported at 21 loci when comparing domesticated lines of *T. dicoccon* and *T. durum* to the wild *T. dicoccoides* (Haudry et al. 2007). In this experiment, however, it is difficult to separate recent bottlenecks from the loss of diversity due only to domestication. Haudry et al. (2007) analyzed 21 nuclear loci in 101 individuals representing four *Triticum* species (28 lines of *T. dicoccoides*, 12 *T. dicoccon*, 20 *T. durum* and 41 *T. aestivum*) to unravel their evolutionary history and to quantify their genetic diversity. Unfortunately, the wild emmer group was too small and not sufficiently polymorphic to build a population structure as previously done by Ozkan et al. (2005) and Luo et al. (2007). Thus, a significant correlation between genetic and geographic distances was not obtained. Haudry et al. (2007) performed multilocus analyses combining all gene-fragments studied, and found that the general topology of their tree support the conclusion that all cultivar forms are subsets of the *T. dicoccoides* group, as expected from a single domestication event. Interestingly, they also reported that three *T. dicoccoides* accessions grouped together with cultivated bread wheat, a case explained by gene flow from wild emmer to cultivated bread wheat also reported by Luo et al. (2007). Starting from here, Feldman and Kislev (2007) suggested that the studies on genetic relationship between wild and domesticated emmer wheat must include the analysis of genetic contacts between the two groups. Based on this idea, they concluded that without this knowledge it is difficult, if not impossible, to identify the ancestral wild emmer populations of domestic emmer. Poyarkova and Gerechter-Amitai (1991) reported that one large grained form of wild emmer that closely resembles domesticated wheats in many other aspects grows in the upper Jordan valley. The observation of Poyarkova and Gerechter-Amitai (1991) fits very well to the results of Luo et al. (2007). Blumler (1998) argued that morphological similarity between wild and cultivated emmer found by Poyarkova and Gerechter-Amitai (1991) could result from introgression of *T. durum* genes into wild emmer growing together in this region. Interestingly, Aaronsohn found wild emmer wheat neither in cultivated wheat nor in cultivated emmer fields during his surveys in 1906–1909 (Aaronsohn and Schweinfurth 1906; Aaronsohn 1909). However, the findings of our recent revised analysis presented below (Figs. 2, 3) clearly support the view of Blumler (1998).

In this article we also report recent analyses based on results by Ozkan et al. (2005). In the first step (Fig. 2) we conducted NeighborNet (NNet) analysis for 234 wheat individuals based on 175 polymorphic AFLP chromosome markers and Dice distances between individuals with SplitsTree 4.8 (Huson and Bryant 2006). AFLP data circumscribe 187 wild *T. dicoccoides* lines, 23 domesticated *T. dicoccon* lines, 23 *T. durum* lines and one *T. polonicum* L. line. Details of *Triticum* accessions used in this study and comparison of phylogenetic results (Ozkan et al. 2005 vs. NeighborNet (NNet) analysis presented here) of wild emmer groups are presented in Table 2. This new analysis enables to clearly distinguish between the two wild emmer races and leads to several conclusions: (1) The wild western emmer race (group IV in Figs. 2, 3, 4) comprises all accessions sampled in Israel, Jordan, Lebanon and Syria. The western populations are connected and intermixed. No clear population structure can be detected. (2) The wild eastern race (groups I, II, III) consists of all plants collected in Turkey, Iraq and Iran. Three main groups can be recognized among the eastern group: Group I with four subgroups: Ia—Karacadağ; Ib—southeast Turkey and north Iraq; Ic—Iraq and Iran; Id—Karacadağ. Group II comprises exclusively lines collected in the Kartal-Karadağ mountain range and group III lines collected only at the Jabal Sinjar mountain range in Iraq. The populations of the eastern race are more isolated from each other and genetically more separated, however they harbor a great genetic diversity comparable with the diversity present in the western wild race. (3) The wild eastern emmer race appears to be closer related to domesticated tetraploid wheats. Its group Id from the Karacadağ is the closest related wild emmer group to domesticated emmer. (4) One split highlighted in brown separates the domesticated tetraploid wheats and few wild emmer accessions from northern Israel (group V, highlighted in green in Fig. 4; and three lines considered as group IVi, highlighted in yellow in Fig. 4) to the exclusion of all other wild emmer lines. Group V consists of emmer race “*judaicum*” (in total 12 accessions, see Table 2) expected to be of hybrid origin of wild western emmer and durum wheat (Blumler 1998). Morphological characters investigated and presented

Table 2 Overview of available data for wild (*T. dicoccoides*) and domesticated (*T. dicoccon* and *T. durum*) accessions and comparison of their phylogenetic grouping based on Ozkan et al. (2005) and our recent NNet analysis present here

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
TR3	PGR0006	Turkey, Karacadag	37 40 18	39 49 52	1,853	II	I	a	85.00	9.50	12.50	+		10.00	19.40	3.00
TR15	PI 428018	Turkey, 36.2 km west of Diyarbakir in the Karacadag	37 53 00	39 52 00	1,200	II	I	a	70.00	–	–	+		12.50	12.75	1.00
TR18	PI 428063	Turkey, 51 km west of Diyarbakir in the Karacadag	37 48 00	39 46 00	1,400	II	I	a	60.00	6.75	14.00	+		11.50	14.43	1.00
TR47	PI 538626	Turkey, 36.2 km west of Diyarbakir in the Karacadag	37 53 00	39 52 00	1,200	II	I	a	80.00	6.75	16.75		+	13.75	19.71	3.00
TR48	PI 538633	Turkey, 32.6 km west of Diyarbakir in the Karacadag	37 52 00	39 53 00	1,200	II	I	a	70.00	6.75	13.50	+		8.50	22.21	1.00
TR49	PI 538651	Turkey, 44 km west of Diyarbakir in the Karacadag	37 50 00	39 49 00	1,400	II	I	a	85.00	9.75	16.75	+		11.25	16.43	1.00
TR65	PI 554582	Turkey, Urfa, Junction of Karacadag Mt. road and highway	37 47 00	39 46 00	775	II	I	a	80.00	8.75	10.75		+	10.25	16.43	1.00
Group Ia									**75.71**	**8.04**	**14.04**			**11.11**	**17.34**	**1.57**
IQ122	8821A	Iraq, 15.3 km ENE from Dohuk to Amadiyah	36 53 11	43 08 10	1,000	III′	I	b	–	–	–			–	–	–
IQ123	8821C	Iraq, 15.3 km ENE from Dohuk to Amadiyah	36 53 11	43 08 10	1,000	III′	I	b	–	–	–			–	–	–

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
TR50	PI 538656	Turkey, 52.6 km west of Diyarbakir in the Karacadag	37 47 00	39 46 00	1,560	II	I	b	75.00	9.00	14.75	+		11.50	19.40	3.00
TR63	PI 554580	Turkey, Urfa, Junction of Mt. Karacadag road and Diyarbakir highway	37 47 00	39 46 00	1,220	II	I	b	85.00	9.50	11.50		+	9.50	18.57	1.00
TR64	PI 554581	Turkey, 25 km southwest of Diyarbakir	37 45 00	40 06 00	1,000	II	I	b	80.00	7.25	13.50		+	12.25	15.71	3.00
TR124	8915A	Turkey, 17.3 E from Silvan to Bitlis	38 07 30	41 11 06	865	II	I	b	–	–	–			–	–	–
TR125	8915B	Turkey, 17.3 E from Silvan to Bitlis	38 07 30	41 11 06	865	II	I	b	–	–	–			–	–	–
TR126	8935	Turkey, 9.3 km SE from Ergani to Diyarbakir	38 13 37	39 58 01	900	II	I	b	–	–	–			–	–	–
TR127	8937B	Turkey, 9.3 km SE from Ergani to Diyarbakir	38 13 37	39 58 01	900	II	I	b	–	–	–			–	–	–
TR141	TA 1138	Turkey, Karacadag	37 40 00	39 35 00	1,000	II	I	b	–	–	–			–	–	–
TR182	TR 03396	Turkey, Karacadag	37 44 00	39 43 00	1,100	II	I	b	–	–	–			–	–	–
TR183	TR 03369	Turkey, Karacadag	37 44 00	39 43 00	1,100	II	I	b	–	–	–			–	–	–
TR184	TR 03358	Turkey, Karacadag	37 44 00	39 43 00	1,100	Deleted	I	b	–	–	–			–	–	–
TR185	TR 03376	Turkey, Karacadag	37 44 00	39 43 00	1,100	II	I	b	–	–	–			–	–	–
TR186	TR 03371	Turkey, Karacadag	37 44 00	39 43 00	1,100	II	I	b	–	–	–			–	–	–

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
TR187	TR 00842	Turkey, Sanliurfa, near Karacadag	37 12 00	38 53 00	600	II	I	b	–	–	–			–	–	–
TR188	TR 03402	Turkey, Karacadag	37 44 00	39 43 00	1,100	II	I	b	–	–	–			–	–	–
TR189	TR 03362	Turkey, Karacadag	37 44 00	39 43 00	1,100	II	I	b	–	–	–			–	–	–
TR191	TR 02637	Turkey, Sanliurfa, near Karacadag	37 12 00	38 53 00	600	II	I	b	–	–	–			–	–	–
TR192	TR 03388	Turkey, Karacadag	37 44 00	39 43 00	1,100	II	I	b	–	–	–			–	–	–
TR193	TR 03346	Turkey, Karacadag	37 44 00	39 43 00	1,100	II	I	b	–	–	–			–	–	–
TR194	TR 03391	Turkey, Karacadag	37 44 00	39 43 00	1,100	II	I	b	–	–	–			–	–	–
Group Ib									**80.00**	**8.58**	**13.25**			**11.08**	**17.89**	**2.33**
IQ103	TTD 151	Iraq	Not specified	Not specified	Not specified	III	I	c	–	–	–			–	–	–
IQ105	8736A	Iraq, SSW of Rowanduz	36 33 46	44 28 35	1,000	III	I	c	–	–	–			–	–	–
IQ106	8736B	Iraq, SSW of Rowanduz	36 33 46	44 28 35	1,000	III	I	c	–	–	–			–	–	–
IQ107	8737	Iraq, SSW of Rowanduz	36 33 46	44 28 35	1,000	III	I	c	–	–	–			–	–	–
IQ163	8536	Iraq, 20.3 km S from Sulaymaniyah to Qara Dagh	35 29 31	45 19 31	1,000	III	I	c	–	–	–			–	–	–
IQ164	8537	Iraq, 20.3 km S from Sulaymaniyah to Qara Dagh	35 29 31	45 19 31	1,000	III	I	c	–	–	–			–	–	–
IQ165	8538	Iraq, 20.3 km S from Sulaymaniyah to Qara Dagh	35 29 31	45 19 31	1,000	III	I	c	–	–	–			–	–	–

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
IQ166	8539	Iraq, 20.3 km S from Sulaymaniyah to Qara Dagh	35 29 31	45 19 31	1,000	III	I	c	–	–	–			–	–	–
IQ167	8541	Iraq, 20.3 km S from Sulaymaniyah to Qara Dagh	35 29 31	45 19 31	1,000	III	I	c	–	–	–			–	–	–
IR102	PI 428016	Iran, Bakhtaran, 50 km west of Shahaba	34 22 00	46 06 00	1,721	III	I	c	–	–	–			–	–	–
IR128	8941	Iran, 58.8 km N from Kermanshah to Ravansar	34 38 35	46 44 40	1,500	III	I	c	–	–	–			–	–	–
IR129	8942	Iran, 58.8 km N from Kermanshah to Ravansar	34 38 35	46 44 40	1,500	III	I	c	–	–	–			–	–	–
IR130	8943	Iran, 58.8 km N from Kermanshah to Ravansar	34 38 35	46 44 40	1,500	III	I	c	–	–	–			–	–	–
Group Ic									**–**	**–**	**–**			**–**	**–**	**–**
TR16	PI 428053	Turkey, 44.0 km west of Diyarbakir in the Karacadag	37 50 00	39 49 00	1,400	Deleted	I	d	80.00	8.00	11.25	+		12.75	27.00	1.00
TR17	PI 428054	Turkey, 44.0 km west of Diyarbakir in the Karacadag	37 50 00	39 49 00	1,400	II	I	d	70.00	8.75	16.00	+		10.75	19.43	1.00
TR19	PI 428069	Turkey, 33.6 km west of Diyarbakir in the Karacadag	37 52 00	39 53 00	886	II	I	d	65.00	8.00	15.50	+		12.25	20.57	1.00

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
TR20	PI 428077	Turkey, 52.5 km west of Diyarbakir in the Karacadag	37 47 00	39 46 00	1,400	II	I	d	55.00	6.75	–		+	11.00	12.65	1.00
TR51	PI 538657	Turkey, 51 km west of Diyarbakir in the Karacadag	37 48 00	39 46 00	1,400	II	I	d	70.00	8.25	16.25		+	11.50	17.00	3.00
TR52	PI 538659	Turkey, 52.5 km west of Diyarbakir in the Karacadag	37 47 00	39 46 00	1,400	II	I	d	85.00	7.00	18.25		+	11.25	20.43	3.00
TR66	PI 554583	Turkey, Urfa, 3 km southeast of Junction of Karacadag Mt. road and Diyarbakir highway	37 47 00	39 47 00	1,350	II	I	d	80.00	8.50	15.50		+	10.75	21.28	1.00
TR190	TR 03399	Turkey, Karacadag	37 44 00	39 43 00	1,100	II	I	d								
Group Id									**72.14**	**7.89**	**15.46**			**11.46**	**19.76**	**1.57**
TR14	PI 428017	Turkey, 40 km south of Maras	37 18 00	36 48 00	800	II	II		80.00	–	–		+	14.50	19.57	3.00
TR74	IG 116173	Turkey, Gaziantep, Kartal	37 17 00	37 14 00	840	I	II		60.00	6.00	6.50		+	5.50	–	1.00
TR75	IG 116184	Turkey, Gaziantep, Kartal	37 17 01	37 14 01	840	I	II		85.00	8.25	15.00		+	12.50	23.14	3.00
TR147	1945	Turkey, 45 km SE of Maras (Maras—Gaziantep) (Kartal)	37 17 36	37 14 31	843	I	II		–	–	–			–	–	–

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
TR148	1947	Turkey, 45 km SE of Maras (Maras—Gaziantep) (Kartal)	37 17 36	37 14 31	843	I	II		–	–	–			–	–	–
TR149	1948	Turkey, 45 km SE of Maras (Maras—Gaziantep) (Kartal)	37 17 36	37 14 31	843	I	II		–	–	–			–	–	–
TR150	1949	Turkey, 45 km SE of Maras (Maras—Gaziantep) (Kartal)	37 17 36	37 14 31	843	I	II		–	–	–			–	–	–
TR151	1951	Turkey, 45 km SE of Maras (Maras—Gaziantep) (Kartal)	37 17 36	37 14 31	843	I	II		–	–	–			–	–	–
TR152	1952	Turkey, 45 km SE of Maras (Maras—Gaziantep) (Kartal)	37 17 36	37 14 31	843	I	II		–	–	–			–	–	–
TR153	1953	Turkey, 45 km SE of Maras (Maras—Gaziantep) (Kartal)	37 17 36	37 14 31	843	I	II		–	–	–			–	–	–

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
TR154	1955	Turkey, 45 km SE of Maras (Maras—Gaziantep) (Kartal)	37 17 36	37 14 31	843	I	II		–	–	–			–	–	–
TR155	1957	Turkey, 45 km SE of Maras (Maras—Gaziantep) (Kartal)	37 17 36	37 14 31	843	I	II		–	–	–			–	–	–
TR156	1959A	Turkey, 45 km SE of Maras (Maras—Gaziantep) (Kartal)	37 17 36	37 14 31	843	I	II		–	–	–			–	–	–
TR157	1959B	Turkey, 45 km SE of Maras (Maras—Gaziantep) (Kartal)	37 17 36	37 14 31	843	I	II		–	–	–			–	–	–
TR158	1972B	Turkey, 45 km SE of Maras (Maras—Gaziantep) (Kartal)	37 17 36	37 14 31	843	I	II		–	–	–			–	–	–
TR159	1974	Turkey, 45 km SE of Maras (Maras—Gaziantep) (Kartal)	37 17 36	37 14 31	843	I	II		–	–	–			–	–	–

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
TR160	1976B	Turkey, 45 km SE of Maras (Maras—Gaziantep) (Kartal)	37 17 36	37 14 31	843	I	II		–	–	–			–	–	–
TR161	1978B	Turkey, 45 km SE of Maras (Maras—Gaziantep) (Kartal)	37 17 36	37 14 31	843	I	II		–	–	–			–	–	–
TR162	1991	Turkey, 45 km SE of Maras (Maras—Gaziantep) (Kartal)	37 17 36	37 14 31	843	I	II		–	–	–			–	–	–
Group II									**75.00**	**7.13**	**10.75**			**10.83**	**21.35**	**2.33**
TR146[d]	1921	Turkey, 15.5 km W of Mardin (Urfa—Mardin)	37 20 38	40 34 46	850	II	II–III									
IQ108	8804	Iraq, North slope of Jabal Sinjar N of Kursi	36 23 23	41 41 44	850	III′	III		–	–	–			–	–	–
IQ109	8805	Iraq, North slope of Jabal Sinjar N of Kursi	36 23 23	41 41 44	850	III′	III		–	–	–			–	–	–
IQ110	8806	Iraq, North slope of Jabal Sinjar N of Kursi	36 23 23	41 41 44	850	III′	III		–	–	–			–	–	–
IQ111	8807	Iraq, North slope of Jabal Sinjar N of Kursi	36 23 23	41 41 44	850	III′	III		–	–	–			–	–	–

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
IQ112	8808	Iraq, North slope of Jabal Sinjar N of Kursi	36 23 23	41 41 44	850	III′	III		–	–	–			–	–	–
IQ113	8809	Iraq, North slope of Jabal Sinjar N of Kursi	36 23 23	41 41 44	850	III′	III		–	–	–			–	–	–
IQ114	8810	Iraq, North slope of Jabal Sinjar N of Kursi	36 23 23	41 41 44	850	III′	III		–	–	–			–	–	–
IQ115	8811	Iraq, North slope of Jabal Sinjar N of Kursi	36 23 23	41 41 44	850	III′	III		–	–	–			–	–	–
IQ116	8812	Iraq, North slope of Jabal Sinjar N of Kursi	36 23 23	41 41 44	850	III′	III		–	–	–			–	–	–
IQ118	8815	Iraq, North slope of Jabal Sinjar N of Kursi	36 23 23	41 41 44	850	III′	III		–	–	–			–	–	–
IQ119	8816A	Iraq, North slope of Jabal Sinjar N of Kursi	36 23 23	41 41 44	850	III′	III		–	–	–			–	–	–
IQ120	8816B	Iraq, North slope of Jabal Sinjar N of Kursi	36 23 23	41 41 44	850	III′	III		–	–	–			–	–	–
IQ121	8817	Iraq, North slope of Jabal Sinjar N of Kursi	36 23 23	41 41 44	850	III′	III		–	–	–			–	–	–
Group III									**–**	**–**	**–**			**–**	**–**	**–**
Eastern group									**75.71**	**7.91**	**13.38**			**11.12**	**19.10**	**1.95**
IS4	PI 233288	Israel	31 30 00	34 45 00	Not specified	IV	IV		80.00	7.25	11.75		±	10.25	30.30	3.00

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
IS6	PI 414718	Israel, Northern, Almagor, Korazim Sill, Jordan Valley	32 54 37	35 35 52	−122	IV	IV		75.00	8.75	11.00		±	10.00	27.28	1.00
IS7	PI 414719	Israel, Northern, Bet Qeshet, Lower Galilee	32 43 10	35 23 55	119	IV	IV		75.00	8.00	15.25	+		11.75	24.40	3.00
IS8	PI 414720	Israel, Haifa, Bat Shelomo, Samarian Mountains	32 35 48	35 00 07	128	IV	IV		70.00	7.25	13.75	+		10.50	30.43	1.00
IS10	PI 414722	Israel, Northern, Zefat, Upper Galilee	32 58 00	35 29 00	713	IV	IV		65.00	–	–		+	14.25	21.10	3.00
IS11	PI 428013	Israel, Northern, Rosh Pinna, Galilee	32 58 00	35 32 00	713	IV	IV		80.00	7.50	17.25	+		12.75	45.80	3.00
IS12	PI 428014	Israel, 20 km west of Jerusalem	31 47 00	35 14 00	500	IV	IV		65.00	7.00	13.25		±	10.75	23.29	1.00
IS13	PI 428015	Israel, Northern, 3 km east of Safad	32 58 00	35 30 00	700	IV	IV		60.00	7.50	14.25		+	14.25	22.00	1.00
IS24	PI 428097	Israel, Northern, 1 km east of junction of Almagor	32 54 00	35 23 00	538	IV	IV		65.00	7.50	19.75		±	15.00	30.90	1.00
IS25	PI 428099	Israel, Northern, 1 km east of junction to Almagor	32 54 00	35 23 00	538	IV	IV		60.00	6.50	13.00		±	10.25	21.50	1.00

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
IS26	PI 428100	Israel, Northern, 3 km south of Rosh Pinna	32 58 00	35 32 00	713	IV	IV		65.00	7.25	12.50	+		12.75	25.71	1.00
IS27	PI 428105	Israel, Northern, 1–2 km south of Rosh Pinna towards Safad	32 58 00	35 32 00	713	IV	IV		65.00	6.50	10.75		+	11.00	19.86	1.00
IS28	PI 428119	Israel, Northern, city limits of Safad on road to Rosh Pinna	32 58 00	35 29 00	713	IV	IV		65.00	10.50	21.50		+	18.25	13.80	1.00
IS36	PI 466955	Israel, Haifa, Bat Shelomo	32 35 48	35 00 07	128	IV	IV		75.00	7.50	11.50	+		12.75	29.00	1.00
IS37	PI 466981	Israel, Jerusalem, Bet Me'ir	31 48 00	35 02 00	390	IV	IV		75.00	6.50	12.25	+		10.50	22.86	1.00
IS38	PI 466991	Israel, Al Qunaytirah, Mt. Dov (Golan Heights)	33 18 00	35 48 00	1,974	IV	IV		70.00	10.00	13.50		+	10.25	27.28	3.00
IS40	PI 467004	Israel, Northern, Tabigha	32 52 00	35 32 00	36	IV	IV		65.00	7.00	14.50	+		14.50	26.57	3.00
IS41	PI 470988	Israel, Northern, Rosh Pinna	32 58 00	35 32 00	713	IV	IV		80.00	7.00	17.00		+	14.25	18.43	3.00
IS43	PI 471035	Israel, West Bank, Kokhav haShahar	31 57 00	35 20 00	727	IV	IV		60.00	7.00	16.75		+	13.00	20.71	3.00
IS44	PI 479780	Israel, Northern, Gilboa	32 32 50	35 21 30	348	IV	IV		60.00	7.00	12.50		+	10.50	23.71	1.00
IS55	PI 538685	Israel, Rosh Pinna, 1–2 km south towards Safad	32 58 00	35 32 00	600	Deleted	IV		55.00	7.25	14.00		+	11.00	20.57	3.00

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
IS56	PI 538690	Israel, Northern, near Safad on road to Rosh Pinna	32 58 00	35 29 40	800	IV	IV		60.00	8.00	14.50		+	13.00	31.71	3.00
IS57	PI 538699	Israel, West Bank, between Ramla and Jericho, ca. 6 km east of Taibe	31 50 00	35 27 00	90	IV	IV		100.00	7.75	12.25		+	10.75	17.71	1.00
IS70	PI 503312	Israel, Northern, Towards Safad, 1–2 km S of Rosh Pinna	32 58 00	35 32 00	713	IV	IV		60.00	5.50	12.75		+	10.50	18.43	1.00
IS71	PI 503314	Israel, Northern, City limits of Safad, on road to Rosh Pinna	32 58 00	35 29 40	713	IV	IV		70.00	7.50	16.75		+	15.50	20.28	3.00
IS72	PI 503315	Israel, Northern, between ‘En haShofet and Daliyya	32 36 00	35 05 00	128	IV	IV		75.00	7.25	13.00		±	9.75	25.00	1.00
IS131	14401	Israel, Katzrin	32 59 35	35 41 14	302	IV	IV		–	–	–			–	–	–
IS132	14403	Israel, Katzrin	32 59 35	35 41 14	302	IV	IV		–	–	–			–	–	–
IS135	14427	Israel, Rosh Pina	32 58 00	35 31 60	369	IV′	IV		–	–	–			–	–	–
IS136	14429	Israel, Rosh Pina	32 58 00	35 31 60	369	IV′	IV		–	–	–			–	–	–
IS143	TA 1404	Israel, Nahef	32 55 60	35 19 00	277	IV	IV		–	–	–			–	–	–
IS168	14443	Israel, Sanhedriya	31 48 00	35 13 00	748	IV	IV		–	–	–			–	–	–
IS169	14445	Israel, Sanhedriya	31 48 00	35 13 00	748	IV	IV		–	–	–			–	–	–
IS170	14451	Israel, Bet Meir	31 48 00	35 01 60	637	IV	IV		–	–	–			–	–	–
IS171	14453	Israel, Bet Meir	31 48 00	35 01 60	637	IV	IV		–	–	–			–	–	–

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
IS172	14462	Israel, Mt. Hermon	33 24 04	35 50 58	2,814	IV	IV		–	–	–			–	–	–
IS173	14464	Israel, Mt. Hermon	33 24 04	35 50 58	2,814	IV	IV		–	–	–			–	–	–
IS176	14490	Israel, Bat Shlomo	32 35 48	35 01 10	165	IV	IV		–	–	–			–	–	–
IS177	14492	Israel, Bat Shlomo	32 35 48	35 01 10	165	IV	IV		–	–	–			–	–	–
IS178	14505	Israel, Tayiba	32 36 00	35 27 00	137	IV	IV		–	–	–			–	–	–
IS179	14507	Israel, Tayiba	32 36 00	35 27 00	137	IV	IV		–	–	–			–	–	–
IS180	14517	Israel, Kochav Hashahar	31 57 36	35 20 46	557	IV	IV		–	–	–			–	–	–
IS181	14519	Israel, Kochav Hashahar	31 57 36	35 20 46	557	IV	IV		–	–	–			–	–	–
JO88	IG 46320	Jordan, Ebbien (‘Ibbin, ‘Ebbin)	32 22 00	35 49 00	1,050	V	IV		60.00	7.00	12.25	+		9.25	18.85	1.00
JO91	IG 45726	Jordan, Irbid	32 33 20	35 51 00	580	V	IV		70.00	8.50	12.50		+	10.50	23.20	1.00
JO92	IG 46323	Jordan, Balqa (Salt)	32 20 00	35 43 00	760	V	IV		75.00	5.75	10.50		±	12.25	28.71	1.00
JO93	IG 45676	Jordan, Irbid	32 33 20	35 51 00	580	V	IV		75.00	7.50	11.75		+	12.00	25.14	1.00
JO94	IG 46324	Jordan, Amman	31 56 60	35 55 60	760	V	IV		55.00	7.25	10.00		+	11.25	20.20	1.00
JO95	IG 46352	Jordan, Irbid	32 33 20	35 51 00	580	V	IV		70.00	7.25	11.75		+	13.00	23.28	1.00
JO96	IG 45964	Jordan, Balqa (Salt)	32 20 00	35 43 00	760	V	IV		65.00	6.50	16.00		+	11.50	22.28	1.00
JO97	IG 46386	Jordan, Amman	31 56 60	35 55 60	760	V	IV		60.00	6.25	12.00		+	12.50	28.28	1.00
JO142	TA 1181	Jordan, As Samirah (Es Samra)	32 08 00	36 16 00	600	V	IV		–	–	–			–	–	–
LB5	PI 352322	Lebanon, Nabatiye, Mt. Hermon	33 25 00	35 52 00	1,579	V	IV		80.00	7.25	8.50		±	9.50	28.85	1.00
LB29	PI 428126	Lebanon, Rashaya, 1,000 m	32 30 04	35 50 32	1,000	Deleted	IV		60.00	8.25	11.75		+	13.50	19.71	1.00
LB30	PI 428127	Lebanon, El Beqaa, Aiha-Kfarkouk, above ‘sahlet’	33 31 00	35 52 00	1,508	Deleted	IV		85.00	8.25	11.50	+		14.00	19.57	3.00

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
LB31	PI 428132	Lebanon, El Beqaa, Aiha-Kfarkouk, above 'sahlet'	33 31 00	35 52 00	1,508	V	IV		65.00	7.25	11.75	+		13.50	17.14	1.00
LB32	PI 428135	Lebanon, El Beqaa, Aiha-Kfarkouk, above 'sahlet'	33 31 00	35 52 00	1,508	V	IV		60.00	8.25	9.50		±	13.50	16.71	1.00
LB33	PI 428143	Lebanon, El Beqaa, between Rashaya and Aiha	33 30 00	35 50 00	1,000	V	IV		80.00	9.50	12.50		+	11.00	24.57	3.00
LB58	PI 538700	Lebanon, El Beqaa, near Rashaya	33 30 04	35 50 22	1,000	V	IV		70.00	8.25	11.00		+	13.50	16.14	3.00
LB59	PI 538705	Lebenon, El Beqaa, between Aiha and Kfarkouk, ca. 1 km from Aiha	33 30 00	35 52 00	1,508	V	IV		–	–	–			–	–	–
LB60	PI 538708	Lebenon, El Beqaa, between Aiha and Kfarkouk, ca. 1 km from Aiha	33 30 00	35 52 00	1,508	V	IV		70.00	8.75	12.25		+	11.00	–	1.00
LB61	PI 538713	Lebanon, El Beqaa, between Ain Harsch and Ain Ata	33 26 00	35 46 00	1,725	V	IV		–	–	–			–	–	–
LB73	PI 503316	Lebanon, El Beqaa, Outskirts of Rashaya	33 30 04	35 50 22	1,000	V	IV		75.00	8.25	12.25		±	12.25	20.71	1.00
LB77	IG 110815	Lebanon, Biqaa Al Gharbi	34 00 00	36 12 00	1,100	V	IV		65.00	7.75	11.50		+	9.50	18.85	1.00
LB78	IG 46526	Lebanon, Rachaiya,	33 30 04	35 50 22	1,000	V	IV		60.00	7.50	8.50		+	11.75	20.71	1.00
LB140	TA 1071	Lebanon	33 33 00	35 53 00	1,400	V	IV									

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
SY45	PI 487252	Syria, As Suwayda', Salkhad	32 26 40	36 47 00	1,180	V	IV		60.00	8.50	16.00		+	9.00	23.85	1.00
SY68	PI 487255	Syria, Dimashq, Zabadani, 1 km from Zabadani to north, Damascus Province	33 44 00	36 05 00	1,240	V	IV		80.00	8.25	9.50		+	12.75	18.86	3.00
SY76	IG 110737	Syria, Sweida	32 42 00	36 34 00	1,089	V	IV		70.00	6.75	11.50		+	8.25	17.00	1.00
SY79	IG 46504	Syria, May Saloun (Majdouliye?)	33 04 30	35 55 02	780	V	IV		80.00	8.25	11.50		+	9.50	20.86	3.00
SY80	IG 46473	Syria, Rawda (Rawdah?)	35 53 60	39 48 30	340	V	IV		60.00	8.25	9.75		+	10.00	18.14	1.00
SY81	IG 46466	Syria, Sweida	32 42 00	36 34 00	1,089	V	IV		75.00	7.25	10.00		+	11.50	16.28	1.00
SY82	IG 45492	Syria, Darà, Nawa	32 52 60	36 02 60	640	V	IV		65.00	8.25	15.00		+	10.75	19.57	1.00
SY83	IG 46476	Syria, Damascus province, 4 km NW Sarghaya	33 50 05	36 08 37	Not specified	Deleted	IV		60.00	7.75	7.50		+	8.50	12.10	1.00
SY84	IG 45490	Syria, Sweida	32 42 00	36 34 00	1,089	V	IV		85.00	9.00	11.00		±	12.50	26.57	1.00
SY85	IG 45493	Syria, Darà, Nawa	32 52 60	36 02 60	640	V	IV		55.00	8.00	15.00		+	12.75	18.57	1.00
SY86	IG 45494	Syria, Zabadani	33 43 00	36 04 60	1,100	V	IV		85.00	8.00	9.25		+	12.00	23.00	3.00
SY87	IG 45500	Syria, Sweida, 40 km from Sweida between Sale and Malah	32 31 26	36 47 13	Not specified	Deleted	IV		90.00	7.50	9.50	+		9.00	24.57	1.00
SY89	IG 45502	Syria, Idlib	35 55 47	36 37 54	440	V	IV		90.00	8.75	12.00		±	13.25	21.29	3.00
SY90	IG 46397	Syria, Sweida	32 42 00	36 34 00	1,089	V	IV		70.00	9.00	15.25		+	15.00	27.86	1.00
SY98	IG 46439	Syria, Sweida	32 42 00	36 34 00	1,089	V	IV		60.00	7.25	11.25		+	12.50	26.00	1.00
SY99	IG 46457	Syria, Sweida	32 42 00	36 34 00	1,089	V	IV		70.00	7.00	9.00		+	8.00	18.40	1.00

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
SY100[e]	IG 46420	Syria, Hama	35 07 60	36 45 00	300	V	IV		55.00	6.50	10.75		+	8.50	20.60	1.00
SY137	TA 122	Israel, Gamla	32 54 21	35 44 41	369	V	IV		–	–	–			–	–	–
SY139[e]	TA 1058	Syria, Al Qunavtirah (Al Qunaytirah?)	35 58 60	36 30 30	364	V	IV		–	–	–			–	–	–
SY144	108-2	Syria, NW of Suweida	32 43 54	36 32 30	900	V	IV		–	–	–			–	–	–
SY145	108-3	Syria, NW of Suweida	32 43 54	36 32 30	900	V	IV		–	–	–			–	–	–
Group IV									**69.86**	**7.75**	**11.47**			**11.32**	**21.43**	**1.38**
Western Group									**69.87**	**7.75**	**11.47**			**11.32**	**21.40**	**1.38**
IS35	PI 466949	Israel, Central, Yahudiyya	32 02 06	34 53 10	48	IV	IV	i	65.00	7.25	11.25	+		13.75	35.14	1.00
IS42	PI 471016	Israel, Jerusalem, Sanhedriyya	31 48 00	35 13 00	665	IV	IV	i	80.00	9.50	14.75	+		13.00	24.85	3.00
IS54	PI 538684	Israel, Northern, ca. 3 km south of Rosh Pinna	32 58 00	35 32 00	713	IV	IV	i	60.00	8.75	13.50		+	9.50	30.14	3.00
Group IVi									**68.33**	**8.50**	**13.17**			**12.08**	**30.04**	**2.33**
IS1[c]	17902	Israel, Rosh-Pinnar	32 58 00	35 31 60	369	IV	V		75.00	7.75	17.25		±	12.75	30.43	1.00
IS2[c]	17901	Israel, Korazim	32 54 00	35 33 00	−122	IV	V		90.00	7.25	16.50	+		12.75	34.10	3.00
IS9[c]	PI 414721	Israel, Northern, Mountian of Beatitudes, Korazim Sill	32 54 00	35 32 00	36	IV	V		70.00	7.75	15.25	+		11.00	36.57	3.00
IS23[c]	PI 428093	Israel, Northern, Afula-Tiberias	32 36 40	35 17 30	300	IV	V		70.00	–	–		+	10.50	21.43	1.00

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
IS34[c]	PI 466926	Israel, Al Qunaytirah, Kazrin (Golan Heights)	32 59 24	35 41 24	388	IV	V		80.00	8.00	13.50		±	12.50	33.90	3.00
IS39[c]	PI 466995	Israel, Central, Taiba	32 15 36	35 00 36	100	IV	V		60.00	8.25	12.50		+	12.50	25.00	1.00
IS53[c]	PI 538680	Israel, Korazin, 1 km E of junction to Almagor, below sealevel	32 53 00	35 34 00	100	Deleted	V		60.00	7.00	16.75		+	13.25	22.30	1.00
IS133[c]	14417	Israel, Yehudiya	32 02 06	34 53 10	45	IV′	V		–	–	–			–	–	–
IS134[c]	14419	Israel, Yehudiya	32 02 06	34 53 10	45	IV′	V		–	–	–			–	–	–
IS138[c]	TA 1030	Israel, Rosh Pinna	32 58 00	35 31 60	369	IV	V		–	–	–			–	–	–
IS174[c]	14474	Israel, Tabigha	32 52 26	35 32 57	0?	IV′	V		–	–	–			–	–	–
IS175[c]	14476	Israel, Tabigha	32 52 26	35 32 57	0?	IV′	V		–	–	–			–	–	–
Group V									**72.14**	**7.67**	**15.29**			**12.18**	**29.10**	**1.86**
TR69[d]	PI 503310	Turkey, 36.2 km west of Diyarbakir in the Karacadag	37 53 00	39 52 00	1,200	II	Hybrid?		85.00	8.25	9.25	+		12.25	11.75	1.00
SY46	PI 487253	Syria, Darà, Nawa, 10 km after Sheikh Muskein to Nawa, Der'a Province	32 51 37	36 04 38	490	V	Deleted		80.00	8.50	13.50		+	11.00	24.71	3.00
TR22	PI 428092	Turkey, 51 km west of Diyarbakir in the Karacadag	37 48 00	39 46 00	1,400	II	Deleted		65.00	8.75	–		+	12.00	13.40	1.00

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
IQ117	8814	Iraq, North slope of Jabal Sinjar N of Kursi	36 23 23	41 41 44	850	Deleted	Deleted		–	–	–			–	–	–
IS62	PI 538719	Israel, 10 km NW of Majdal Shams near sea level	32 50 00	35 30 00	Not specified	Deleted	Deleted		70.00	8.00	9.25		+	9.00	15.86	1.00
TR101	IG 46434	Turkey, Adiyaman, 4 km N of Yarpuzlu	38 03 31	38 31 16	Not specified	Deleted	Deleted		–	–	–			–	–	–
TR21	PI 428086	Turkey, 20.2 km E Siverek (Karacadag)	37 43 00	39 30 00	1,200	Deleted	Deleted		–	–	–			–	–	–
TR67	PI 554584	Turkey, Izmir, Menemen	38 36 00	27 04 00	30	Deleted	Deleted		–	–	–			–	–	–
IQ104	8541	Iraq, 20.3 km S from Sulaymaniyah to Qara Dagh	35 29 31	45 19 31	1,000	Deleted	Deleted		–	–	–			–	–	–
HW1	DIC 148	*T. dicoccon*, Italy					Dicoccon	II								
HW2	DIC 149	*T. dicoccon*, Italy					Dicoccon	II	120.00	9.50	18.00	+		11.00	53.10	5.00
HW3	DIC 150	*T. dicoccon*, Italy					Dicoccon	II	100.00	10.50	21.75	+		11.50	60.10	5.00
HW4	DIC 151	*T. dicoccon*, Italy					Dicoccon	I	95.00	6.50	17.50	+		9.50	49.00	5.00
HW5	DIC 152	*T. dicoccon*, Italy					Dicoccon	I	95.00	7.25	21.75	+		10.50	50.60	5.00
HW6	DIC 153	*T. dicoccon*, Italy					Dicoccon	II								
HW7	DIC 154	*T. dicoccon*, Italy					Dicoccon	II								
HW8	DIC 155	*T. dicoccon*, Italy					Dicoccon	I	90.00	7.25	19.00	+		11.50	48.20	5.00
HW9	DIC 156	*T. dicoccon*, Italy					Dicoccon	I	95.00	6.75	20.00	+		10.50	50.70	5.00
HW10	DIC 157	*T. dicoccon*, Italy					Dicoccon	II								
HW11	DIC 158	*T. dicoccon*, Italy					Dicoccon	I	105.00	8.00	24.25	+		8.50	53.60	5.00

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
HW12	DIC 159	*T. dicoccon*, unknown					Dicoccon	I	90.00	6.50	19.75	+		11.00	50.40	5.00
HW14	DIC 161	*T. dicoccon*, India					Dicoccon	I	90.00	7.50	17.75	+		11.25	44.50	5.00
HW15	DIC 162	*T. dicoccon*, unknown					Dicoccon	I	115.00	11.25	24.50	+		13.00	36.40	5.00
HW16	DIC 163	*T. dicoccon*, Iran					Dicoccon	II								
HW17	DIC 164	*T. dicoccon*, unknown					Dicoccon	II	85.00	9.25	15.00	+		9.25	35.40	5.00
HW19	DIC 167	*T. dicoccon*, Lebanon					Dicoccon	I	95.00	11.00	18.50	+		7.75	32.00	5.00
HW20	DIC 168	*T. dicoccon*, Italy					Dicoccon	II								
HW21	TUR 03558	*T. dicoccon*, Turkey					Dicoccon	I								
HW22	TUR 02440	*T. dicoccon*, Turkey					Dicoccon	I								
HW23	TUR 03560	*T. dicoccon*, Turkey					Dicoccon	I								
HW24	TUR 03562	*T. dicoccon*, Turkey					Dicoccon	I								
HW25	TUR 02456	*T. dicoccon*, Turkey					Dicoccon	I								
Group *Dicoccon*									**97.92**	**8.44**	**19.81**			**10.44**	**47.00**	**5.00**
DW1	DIC 169	*T. durum*, France					Durum		55.00	6.00	17.50	+		11.25	30.20	5.00
DW2	DIC 170	*T. durum*, Italy					Durum		70.00	5.00	20.75	+		9.00	49.70	5.00
DW3	DIC 171	*T. durum*, Italy					Durum		70.00	6.00	17.50	+		11.00	40.80	5.00
DW4	DIC 172	*T. durum*, Italy					Durum		75.00	6.00	20.75	+		11.00	48.00	5.00
DW5	DIC 173	*T. durum*, Italy					Durum		105.00	6.00	22.25	+		17.25	51.70	5.00
DW6	DIC 174	*T. durum*, Italy					Durum		60.00	5.50	15.00	+		10.50	52.70	5.00

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
DW7	DIC 175	*T. durum*, Jordan					Durum		75.00	4.50	17.75	+		8.25	40.80	5.00
DW8	DIC 176	*T. durum*, Cyprus					Durum		70.00	5.75	26.00	+		14.50	40.90	5.00
DW9	DIC 177	*T. durum*, Italy					Durum		65.00	5.75	19.50	+		12.25	51.40	5.00
DW10	DIC 178	*T. durum*, Tunisia					Durum		70.00	5.75	21.25	+		12.25	62.40	5.00
DW11	DIC 179	*T. durum*, Spain					Deleted		70.00	5.75	21.75	+		12.25	47.40	5.00
DW12	DIC 180	*T. durum*, Syria					Durum		70.00	6.00	23.50	+		12.75	58.80	5.00
DW13	DIC 181	*T. durum*, Greece					Durum		65.00	5.50	20.75	+		11.75	42.80	5.00
DW14	DIC 182	*T. durum*, Italy					Durum		65.00	5.25	22.50	+		11.00	33.10	5.00
DW15	DIC 184	*T. durum*, Ukraine					Durum		90.00	6.00	24.50	+		14.25	53.30	5.00
DW16	DIC 185	*T. durum*, Italy					Durum		95.00	8.25	28.75	+		13.75	37.80	5.00
DW17	DIC 186	*T. durum*, Italy					Durum		80.00	6.00	20.50	+		12.75	38.10	5.00
DW18	DIC 187	*T. durum*, Tajikistan					Durum		100.00	7.75	21.50	+		11.75	39.10	5.00
DW19	DIC 188	*T. durum*, France					Durum		65.00	6.50	20.50	+		10.50	44.80	5.00
DW20	DIC 189	*T. durum*, Mexico					Durum		65.00	5.75	24.00	+		14.00	44.40	5.00
DW21	DIC 191	*T. durum*, Italy					Durum		100.00	7.25	24.25	+		14.75	46.30	5.00
DW22	DIC 192	*T. durum*, Italy					Durum		100.00	6.00	24.75	+		13.50	52.80	5.00
DW23	DIC 193	*T. durum*, Italy					Durum		125.00	7.50	24.75	+		–	61.90	5.00
DW24	DIC 194	*T. durum*, Italy					Durum		105.00	6.25	22.50	+		17.50	53.50	5.00

Table 2 continued

No[a]	Accession number[b]	Origin	Lat (north)	Long (east)	Alt (m)	Grouping based on Ozkan et al. 2005	Grouping based on new analysis, main group (M), sub-group (S) based on Fig. 2		Plant height (cm)	Ear length (cm)	Flag leaf (cm)	Growth type errect (e) vs. prostrate (p)		Awn length (cm)	Seed weight (g)	Fragility
							M	S	1	2	3	e	p	5	6	7
Group *Durum*									**79.58**	**6.08**	**21.78**			**12.51**	**46.78**	**5.00**

Morphological characters scored and compared for different groups are based on accessions considered in Ozkan et al. (2002). Traits: (1) Plant heigt (cm); (2) ear length (cm); (3) flag leaf length (cm); (4) growth type; (5) awn length; (6) seed weight (g) and (7) ear fragility

Based on available mean values (five plants per accession in 2002) the following conclusions can be made: Plant height: Eastern wild emmer individuals are taller than western wild individuals; *Judaicum* plants are taller than the western wild plants. Ear length: Eastern wild emmer individuals have larger ears than western wild individuals. Flag leaf length: Eastern wild emmer individuals have longer flag leaves than western wild individuals; *Judaicum* plants have longer flag leaves than the western wild plants. Awn length: Eastern wild emmer individuals have shorter awns than western wild individuals; *Judaicum* plants have longer awns than the western wild plants. Seed weight: Eastern wild emmer individuals have a smaller seed weight than western wild individuals; *Judaicum* plants have heavier seeds than the western wild plants. Fragility: Eastern wild emmer individuals are less fragile than western wild individuals (0-brittle, 5-non brittle); *Judaicum* plants are less fragile than other western wild plants on average. The traits 1, 2, 3, 5 and 7 support that the eastern wild group is morphologically closer related to domesticated emmer. The same traits provide evidence that *T. dicoccon* was probably domesticated from the eastern wild race and that *T. durum* probably has been selected in the west. The same traits provide also evidence that the *judaicum* race is probably of hybrid origin: wild western emmer × *T. durum*. Comparing only the eastern wild groups individually with *T. dicoccon*: there is only one trait (flag leaf length) were group Id (that is genetically closest related to domesticated tetraploids) is also morphologically the closest wild eastern group to *T. dicoccon*

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[a] Accession number in our collection as described in Ozkan et al. (2005)

[b] See Ozkan et al. (2005) for sources

[c] *Judaicum* race = group V in Fig. 2

[d] Possible hybrid

[e] Closest collection site to the region where wild western and wild central/eastern emmer races are expected to meet

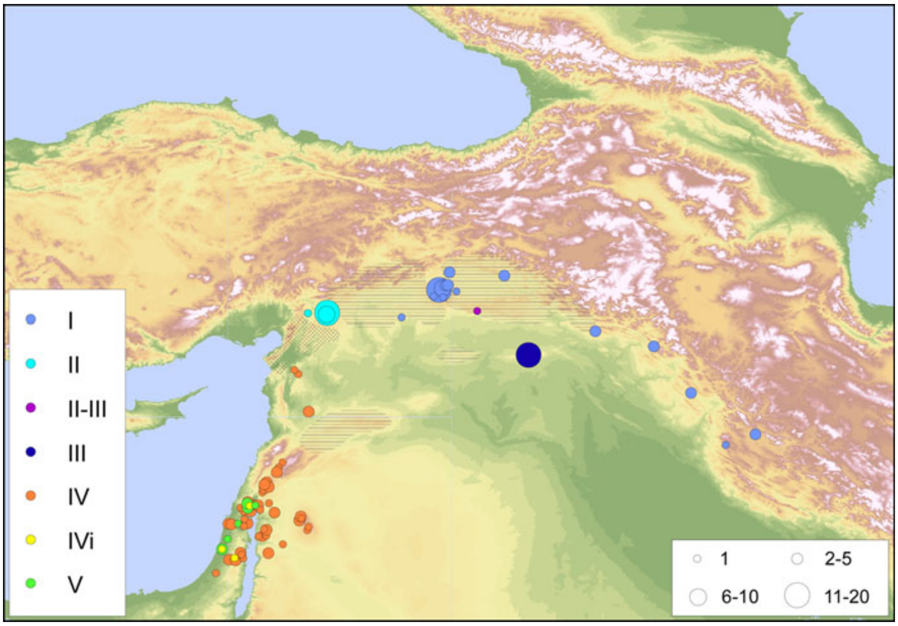

Fig. 4 GIS based distribution map of wild emmer lines considered by Ozkan et al. (2005) as in Fig. 1 and Table 2. Race assignments are based on our new genetic analyses (Fig. 2) and named as in Table 2. The western race consists of subgroups IV, IVi and V. The central-eastern one comprises subgroups I, II and III. Group IVi consists of three wild emmer lines from Israel. Group V includes the wild emmer hybrid race "*judaicum*". The expected contact zone of wild western and wild central-eastern emmer races is indicated with *crossed lines*. Important regions for future expeditions and collection trips for wild emmer are presented with *parallel lines*

in Table 2 support this view. (5) Wild emmer line TR69 from the Karacadağ appears as of hybrid origin of wild eastern emmer and domesticated wheats (introgression in situ or *ex situ*; or mixture of DNAs). Line TR146 from Mardin, Turkey appears as a hybrid of wild emmer groups II and III (highlighted in purple in Fig. 4). (6) We identified two main groups of *T. dicoccon* and both groups are further subdivided. Our cultivated emmer sample is quite small because no accessions from Morocco, Ethiopia or Oman have been scored. Group I possibly consists of *T. dicoccon* ssp. *asiaticum*; group II possibly includes *T. dicoccon* ssp. *europaeum*. One split highlighted in green separates *T. dicoccon* group I to the exclusion of *T. dicoccon* group II and *T. durum*. This supports the view that *T. durum* has been selected from European emmer in the Mediterranean region. Furthermore, *T. polonicum* is placed within the *T. durum* group.

In the second step (Fig. 2) we described genetic diversity among 219 wheat individuals based on 175 polymorphic AFLP chromosome markers and Dice distances between individuals. The wild emmer race "*judaicum*" (hybrid between wild emmer and durum wheat, convar *judaicum* vav. Dorofeev et al. 1979) was excluded from the analysis (Table 2). The split in red clearly separates the western and the central-eastern wild emmer groups. One split highlighted in blue further separates the wild eastern group I from group II and III. This provides further evidence that the wild eastern group I was probably domesticated by humans. In this analysis, eight Karacadağ lines (TR16, TR17, TR19, TR20, TR51, TR52, TR66, TR190) and one line from Iraq (Sulaymaniyah region, IQ167) are the closest wild relatives to the domesticated tetraploid wheats investigated. The split highlighted in green separates *T. dicoccon* group I from *T. dicoccon* group II and *T. durum*.

In step three (Fig. 4) we plotted the distribution of wild emmer lines in a GIS (Geographical Information System) based distribution map. The race assignments are based on our recent genetic analyses and the expected contact zone of wild western and wild central-eastern emmer races is indicated. We also suggest important regions for future expeditions and collection trips for wild emmer.

The transition from wild emmer to modern tetraploid wheats involved several changes in morphological traits and genome structure. The genome size has been reduced during cultivation and domestication from about 12.91 pg in wild *T. dicoccoides* to about 12.87 pg (mean 1C DNA amount in pg) in domesticated emmer (Eilam et al. 2008). Older data from Rees and Walters (1965) support these findings, however larger collection have to be studied in order to consolidate the data. Furthermore, genes have been silenced or changed their function (Ayal et al. 2005; Shaked et al. 2001; Kashkush et al. 2002; Ozkan et al. 2001).

Conclusions

Taking all published molecular data together, including the findings of our recent analysis, we propose that the accessions of extant domesticated emmer that we analyzed were derived from populations of the central-eastern wild emmer race. The wild emmer lines from the Karacadağ region in southeast Turkey (group I in Figs. 2, 3, 4) are the closest to present-day domesticated emmer. On the other hand the cpDNA data point more to the Kartal-Karadağ mountains (280 km west of the Karacadağ mountains). Archaeobotanical studies strongly suggest that wild emmer was possibly twice and independently taken into cultivation: (1) in the southern Levant and (2) in the northern Levant. This is not incompatible with the molecular data which demonstrates that the domestic populations which survive today whether from Asia or Europe may have originated in southeast Turkey. So why these particular wild lines southeast Turkey and not those from the southern Levant? We propose five possible reasons why cultivated emmer originated from eastern wild emmer lines has survived. First, the late ripening lines from the high regions of southeast Turkey would have been better adapted to the climatic conditions of Central Anatolia, the Caucuses, Central Asia and Europe than the heat and drought tolerant early ripening lines from the south. Secondly, most wild emmer from the southern Levant has the disadvantage of having extremely thick robust glumes which are difficult to remove. Thirdly, if emmer was domesticated in the southern Levant it may not have had much of a chance to diffuse out of this area which was a geographical cul-de-sac. The Syrian desert being a barrier to the east while to the north emmer was blocked by better adapted populations where natural routes for diffusion led west, east and north. The only possibility of expansion from the southern Levant was to Egypt and the Nile Valley. But in this area Near Eastern crops arrived only about 7,000 years ago by which time cultivated domestic emmer had become widespread in the Eastern Mediterranean region. Fourthly, we are not sure that cultivation in the southern Levant led to domestication. Fifthly, the introduction of einkorn into the southern Levant, around 10,000 years ago, could be because it probably accompanied new crops including northern emmer populations that came from the north.

The spread of domestic emmer would have been extremely complex and would not represent a simple linear progression. Seed stocks may have been exchanged. Southern expansion of domesticated emmer may have generated sympathy with the southern populations of *T. dicoccoides* and the rise of a secondary diversity center (Schiemann 1939; Luo et al. 2007). This was followed by the subdivision of domesticated emmer into northern and southern subpopulations. Northeast expansion provided contact with the distribution of *Ae. tauschii* Coss. and, consequently the possibility for the emergence of hexaploid bread wheat (Zohary 1969). In fact, genetic evidence indicates that hexaploid wheat originated within the corridor from Armenia to the southwestern coast of the Caspian Sea (Dvorak et al. 1998), indeed this area has produced early naked wheats but at present we cannot be sure that these are hexaploids (Hovsepyan and Willcox 2008). The D genome diversity indicates that hexaploid wheat may have arisen at least twice (Dvorak et al. 1998; Giles and Brown 2006).

Lev-Yadun et al. (2000) proposed a “core area” for the origins of agriculture within the Fertile Crescent. This was based on the proposition that wild einkorn and wild emmer from this area are genetically more closely related to the domesticated crop plants than elsewhere; and that chickpea, one of the founder crops is restricted to this region of southeast Turkey which includes the Karacadağ mountain range (Ladizinsky 1985; Lev-Yadun et al. 2000; Gopher et al. 2001; Salamini et al. 2002; Ozkan et al. 2002, 2005; Abbo et al. 2006; Lichter 2007; Kilian et al. 2007b). However, there are objections and several scientists disagree with the idea of a core area in south east

Turkey for the following reasons: (1) with regard to barley several studies point to domestication having taken place in the Israel-Jordan region and possibly farther east (Morrell and Clegg 2007; summarized in Kilian et al. 2009), (2) Present-day chickpea distribution may be reduced as suggested by chickpeas being found at early PPNB sites outside the area (Tanno and Willcox 2006b), (3) No other molecular studies on crops other than einkorn and emmer support the existence of a core area (admittedly, studies are lacking), (4) During the PPNA pre-domestic cultivation was occurring over a wide area at sites south and possible east of the core area and these sites pre-date key sites in the core area such as Göbekli Tepe and Cayonü. Perhaps the apparent disagreements are related to choice of terms: no one would deny the importance of southeast Turkey as a key region for the origins of agriculture. Interpretative problems arise because archaeobotany and DNA fingerprinting provide an incomplete picture. On the one hand fossil finds are scarce and do not present the whole chronological sequence, or the whole geographical area, and sometimes they are poorly identified; on the other hand, traditional landraces have become extinct with the decline of emmer cultivation so extant modern specimens used for molecular studies represent a small relic of what was from the tenth to the fifth millennia (or more) the most commonly cultivated wheat.

Recently, Kilian et al. (2007b) reasoned that extensive sampling of genetic diversity among wild and domesticated accessions should discriminate between different hypotheses of cereal domestication. The attempt to introduce a view of crop domestication unbiased by the green revolution type of breeding: the nucleotide variation at 18 loci from 92 domesticate einkorn lines (*T. monococcum*), compared to 321 lines from wild populations (*T. boeoticum*), was examined. The data indicate that wild einkorn underwent a natural genetic differentiation, prior to domestication, resulting in three distinct *T. boeoticum* races. Only one of these wild races, indicated as race β, was exploited by humans during domestication. Nucleotide and haplotype diversity in domesticate einkorn was found to be higher than in the β race; supporting the conclusion that domesticated einkorn did not undergo a reduction of nuclear diversity. This is in contrast to the conclusions of studies of domestication in moderately bred crop species like emmer (Haudry et al. 2007), and intensively crops from the Fertile Crescent like barley (Kilian et al. 2006), where claims for domestication bottlenecks are commonplace. In nature, race β has been sampled only in the "core area" of agricultural development in south-eastern Turkey (Lev-Yadun et al. 2000; Bar-Yosef 2002; Lichter 2007). Detailed archaeological reports by Hillman (2000), Willcox (2005), Weiss et al. (2006) and Willcox et al. (2008) demonstrated that pre-domestication cultivation of wild cereals probably lasted for centuries in the region. This pre-domestication cultivation was followed by gradual (Kislev 2002,) and multiple (Gebel 2004; Willcox 2005) appearances of domesticate phenotypes. The genetic and cultural mechanisms underlying the emergence of those phenotypes are remaining questions. If geographically distinct domestication events each entailed a random sampling from local genotypes, and if local populations can be identified based on molecular markers, domesticated lines should trace to different localities across the range of the wild progenitor (Jones 2004). This was not observed for einkorn: race β described in Kilian et al. (2007b) appeared to be the sister of domesticated einkorn which had no reduction in genetic variation. This can be explained by a new domestication model designated as "dispersed-specific". This model is to different from the monophyletic model suggested previously by Heun et al. (1997). In essence, in this new scenario a sedentary society (Bar-Yosef 2002) first harvested, and then cultivated wild β race population(s) of *T. boeoticum*, which was probably distributed near settlements in the "core area". At these settlements favourable traits would have been selected from the β race over the centuries and the β race became adapted to cultivation. It is still unclear how much intermixture from other wild einkorn races occurred. In a later phase of agricultural expansion, the β race was transferred to other locations outside the "core area", possibly already in a state of nascent domestication. Transport could have involved migrating farmers (Nadel 2002; Renfrew 2002) or exchange between sedentary groups; it resulted in crops arriving in areas where climatic and soil conditions did not allow them to grow naturally, but where man with his knowledge of plant husbandry could cultivate them (Willcox 2005).

We are still far from understanding the emmer domestication process in detail and we do not have an emmer domestication model at hand. This is due to smaller germplasm collections available, particularly from southeastern Turkey and mountain areas in eastern Iraq and western Iran, and perhaps the less extensive wild emmer stands compared to einkorn (Zohary and Hopf 2000). On the other hand, no comprehensive molecular studies have been conducted on emmer wheat. However, we could imagine that a domestication model could work for emmer domestication similar to the "dispersed-specific" model proposed for einkorn domestication (no loss of genetic diversity during domestication). Differences are expected due to more widespread emmer cultivation during the Neolithic and due to more intermixture and gene flow especially with cultivated taxa (Schiemann 1939; Zohary 1969; Luo et al. 2007; Allaby et al. 2008). Selection, breeding bottlenecks and genetic erosion could blanket a direct view back to emmer domestication as discussed in Kilian et al. (2007b) for einkorn. Ongoing and future archaeological excavations for example at Göbekli Tepe, Turkey (Schmidt 2001, 2006; Neef 2003) and elsewhere, and continued molecular studies will provide deeper insights into emmer domestication. At the molecular level the time has come to use, to genotype and to re-sequence larger emmer collections in order to compare many wild and many domesticated individuals and whole populations at many loci. Such studies will provide more detailed insights into the natural variation in wild and domesticated plants and will shed light upon emmer domestication process. This knowledge will, in turn, help us to understand human history and the origin of agriculture.

Currently very limited germplasm collections of wild emmer wheat are available. Larger collections are needed and the time is overdue to collect wild accessions as the landscape is changing. More and more land is used for farming in order to grow commercial crops to feed the increasing human population. Extensive herding has led to overgrazing and erosion. The last primary habitats of wild stands will soon be destroyed. We are close to losing a valuable source of genetic diversity that could help plant breeders to provide food for future generations.

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