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ISSN 1479-2621

Plant Genetic Resources 3(3); 360–372
DOI: 10.1079/PGR200589

Associations between geographical origin and morphological characters in bread wheat (*Triticum aestivum* L.)

Andreas Börner*, Marina Schäfer, Andrea Schmidt, Michael Grau and Jörn Vorwald

Institut für Pflanzengenetik und Kulturpflanzenforschung, Corrensstrasse 3, D-06466 Gatersleben, Germany

Received 15 March 2005; Accepted 1 June 2005

Abstract

We report the morphological typing of 13,337 accessions of bread wheat. The individual characters assessed were: awnedness, awn colour, glume colour, presence/absence of glume hairs, spike type, spike density, spike branching, grain colour, stem type (hollow/solid) and presence/absence of ligules. We have associated these morphological data with accession provenance, to analyse global patterns of the traits. Whereas some of the traits (awnedness, awn colour, glume colour, presence/absence of hairs on glumes, stem type) are concentrated in distinct geographical regions, others (spike type, spike density, grain colour, presence/absence of ligules) appear to be randomly distributed. Spike branching was not observed. Possible reasons for the geographical distributions of the characters, in the light of their inheritance, are discussed.

Keywords: genebank collections; geographical origin; morphology; *Triticum aestivum*

Introduction

Bread wheat (*Triticum aestivum* L.) emerged about 10,000 years ago, in north-western Iran or north-eastern Turkey, following natural hybridization and chromosome doubling of the cross tetraploid wheat × diploid *Aegilops tauschii* (McFadden and Sears, 1946). Today, it is a widely adapted crop grown from the tropics to the edges of the Arctic circle, and from sea level to well over 3000 m asl on the Andean Plateau. Adaptation to specific environments is associated with the selection of particular genotypes. From the physiological point of view, the adjustment of the life cycle to suit local seasonal climatic conditions is critical, and has been largely achieved by the specification of ear emergence time via genes involved in the determination of the vernalization response, the photoperiodic response and in earliness *per se*. A further source of genetic variation to allow adaptation may be in the genes responsible for plant architecture, and in particular in genes determining the morphology of the spike (spike density, awnedness, awn and glume colour, etc.) or stem (hollow or solid).

In the present study, we describe about 13,000 bread wheat accessions of worldwide origin held in the Gatersleben genebank using a number of key morphological characters. We have used Mansfeld's (1951) classification system, which types accessions on the basis of presence/absence of single morphological traits (10 characters in all), and have analysed associations between these morphotypes and geographical provenance.

Materials and methods

Plant materials

A total of 28,188 wheat accessions are maintained at the German *ex situ* genebank in Gatersleben, following its recent fusion with the collection formerly held at the Federal Centre for Breeding Research on Cultivated Plants in

* Corresponding author. E-mail: boerner@ipk-gatersleben.de

https://doi.org/10.1079/PGR200589 Published online by Cambridge University Press

Braunschweig (Anonymous, 2004). About two-thirds (18,939) of the accessions are represented by the hexaploid species *Triticum aestivum* L. For the purposes of the present study, we have excluded accessions for which either no provenance information was available, or where the morphological description was incomplete. Geographical regions represented by less than 20 accessions were also excluded, so that finally 13,337 accessions were included in the analysis. The countries of origin and the number of accessions studied are given in Table 1.

Trait analysis

The botanical classification system of Mansfeld (1951) is based on 11 characters, of which 10 have been considered in this study. 'Presence of wax on stems' was omitted, because it has never been used to characterize the collection. The characters analysed and the classification used in the present study are given in Table 2, some of the traits are illustrated in Figs 1–3.

Statistical analyses

We have assumed an equal distribution of each trait among material originating from a single country. The hypothesis was tested by the χ^2 statistic, for each trait separately (Zöfel, 2001). Taking into account unequal sizes of the sub-collections, the test was based on percentage values, rather than on absolute numbers. Where a test result indicated a significant deviation from expectation, a level of significance was computed. Since the test algorithm uses standardized residuals, the level of significance may differ between the traits: for example, among the Belgian accessions, the presence of inflate awns is highly significantly distributed, while its absence does not differ significantly from expectation.

Results

Total numbers, percentages and significance levels of the characters are summarized in Table 3. Although part of Mansfeld's classification system, no accessions with branched spikes were detected in the collection and therefore this trait does not appear in the data. For the remaining characters, the statistical analysis indicates that while some are more common than expected in particular regions, others are equally distributed. Thus, awnless wheats are common in the cooler, temperate climatic regions of northern and central Europe as well as northern America, while the awned type predominates in the

Table 1. Countries of origin and number of accessions studied

Country of origin	No. of accessions
Europe	
Germany	1,391
Austria	976
Italy	904
France	514
Czech Republic and Slovakia	410
Greece	347
Poland	364
Portugal	282
Sweden	265
Bulgaria	189
Romania	183
UK	130
Hungary	118
Spain	106
Yugoslavia	106
Albania	99
Finland	76
Netherlands	72
Cyprus	58
Belgium	42
Ukraine	29
Total	6,661
Africa	
Libya	395
Ethiopia	228
Kenya	78
Tunisia	59
Morocco	28
Total	788
Asia	
Iran	1,098
India	985
China	710
Russia	591
Afghanistan	327
Nepal	249
Turkey	171
Pakistan	165
Japan	131
Georgia	97
Korea	63
Iraq	60
Uzbekistan	40
Israel	28
Mongolia	25
Total	4,740
Americas	
USA	628
Argentina	129
Mexico	114
Canada	80
Chile	50
Uruguay	33
Total	1,034
Australasia	
Australia	84
New Zealand	30
Total	114
Total	13,337

https://doi.org/10.1079/PGR200589 Published online by Cambridge University Press

Table 2. Characters studied and character classification used

Character	Classification
Presence of awns	Absent (0), Short awns present (1), Long awns present (2)
Awn colour	Uncoloured (0), Coloured (1)
Glume colour	Uncoloured (0), Coloured (1)
Presence of hairs on glumes	Absent (0), Present (1)
Presence of inflate spike type	Absent (0), Present (1)
Spike density	Loose (rachis segments >3.2 mm) (0) Dense (rachis segments between 2.5 and 3.2 mm) (1) Compact (rachis segments <2.5 mm) (2)
Spike branching[a]	Normal (0), Branched (1)
Grain colour	Uncoloured (0), Coloured (1)
Stem filling	Hollow (0), Filled (1)
Presence of ligules	Absent (0), Present (1)

[a] In the *T. aestivum* accessions investigated no branching was detected.

Mediterranean area, including northern Africa, and in the Middle East (Fig. 4).

A contrasting situation applies for both awn and glume coloration, which often occur together. Non-coloured spikes dominate in most regions, but more than 40% of all accessions with coloured awns and/or glumes are from Albania, Austria, Finland, Greece, Portugal, Spain, Afghanistan, India, Iran, Iraq, Japan, Mongolia, Turkey, Uzbekistan, Argentina and Chile. For glume colour alone, the frequency is over 50% in Austrian, Mongolian, Argentinian and Chilean materials.



Fig. 1. Loose (left), dense (middle) and compact (right) spikes.

Hairy glumes are randomly distributed at a low frequency (<10%). However, over 20% of all hairy-glumed accessions originate from northern Europe (Finland, Sweden), Asia (Afghanistan, India, Iran, Nepal, Pakistan, Turkey) and northern Africa (Libya) (Table 3; Fig. 5), with maximum frequencies of 65% and 41% in Libya and Nepal, respectively. Interestingly, these two countries also contribute the highest proportions of inflate spikes (38% and 20%, respectively). The inflate ear type was detected at low frequencies in only 10 countries, with a global occurrence of 2.7%.

With respect to spike density, loose spikes dominate over the dense or compact types. The percentage of accessions with loose spikes is above 90% for all countries of origin, except for Germany (89%), Israel (89%), the Netherlands (86%), Cyprus (79%), Turkey (77%) and Austria (70%). (For Israel only 28 accessions are available.) The highest percentage of compact spikes occurred in accessions from Turkey (16%), Israel (11%), Libya (9%) and Afghanistan (7%).

The majority of wheats across most regions had coloured grain, although white-grained accessions represented about 50% of the collection from Ethiopia, Libya, India, Iran, Iraq, Pakistan, Australia and New Zealand. (Note that the representation of accessions was only 84, 60 and 30 in Australia, Iraq and New Zealand, respectively.)

Two traits unrelated to the spike or grain were included. Most wheats have hollow stems—only 0.7% of accessions have solid stems, and these are restricted to southern European, Asian, African and South American origin. Notably high frequencies were observed among the Moroccan (64%) and Tunisian (20%) materials,

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Fig. 2. The inflate spike type. (A) Complete spike (left: normal; right: inflate); (B) glumes (left: normal; right: inflate).

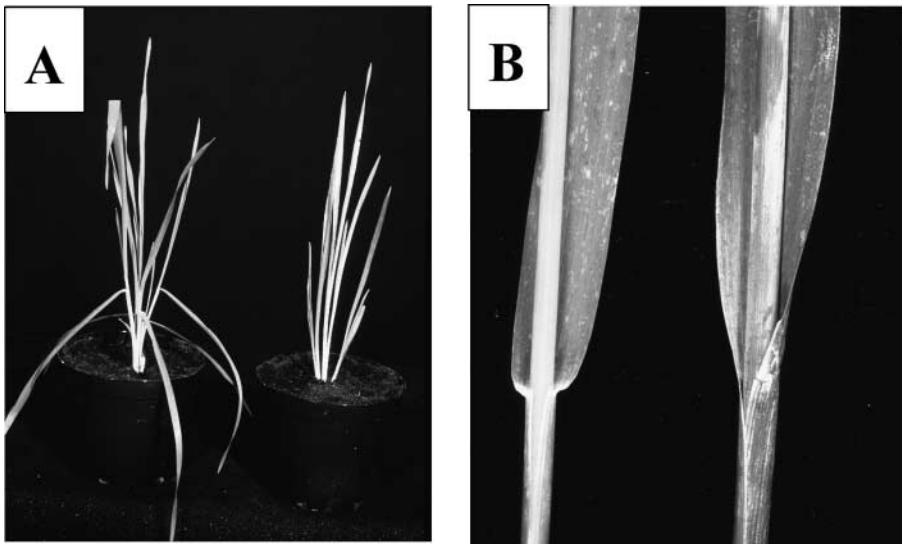


Fig. 3. The liguleless mutation. (A) At the tillering stage (left: wild type; right: mutant); (B) leaves of adult plants (left: wild type; right: mutant).

https://doi.org/10.1079/PGR200589 Published online by Cambridge University Press

Table 3a. Global distribution of the morphological characters studied: presence of awn and awn colour (for character classification see Table 2)

	Character				
	Presence of awn			Awn colour	
Country	0	1	2	0	1
Europe					
Albania	27 (27%**)	2 (2%)	70 (71%**)	63 (64%)	36 (36%**)
Austria	665 (68%**)	– (0%)	311 (32%**)	783 (80%)	193 (20%)
Belgium	40 (95%***)	1 (2%)	1 (2%***)	41 (98%*)	1 (2%***)
Bulgaria	39 (21%***)	– (0%)	150 (79%***)	130 (69%)	59 (31%*)
Czech Republic and Slovakia	265 (65%**)	– (0%)	145 (35%*)	364 (89%)	46 (11%*)
Cyprus	8 (14%***)	– (0%)	50 (86%***)	44 (76%)	14 (24%)
Finland	69 (91%***)	– (0%)	7 (9%***)	72 (95%)	4 (5%***)
France	468 (91%***)	– (0%)	46 (9%***)	494 (96%*)	20 (4%***)
Germany	1266 (91%***)	– (0%)	125 (9%***)	1319 (95%)	72 (5%***)
Greece	83 (24%**)	1 (0%)	263 (76%***)	245 (71%)	102 (29%)
Hungary	21 (18%***)	– (0%)	97 (82%***)	106 (90%)	12 (10%*)
Italy	501 (55%)	15 (2%)	388 (43%)	736 (81%)	168 (19%)
Netherlands	68 (94%***)	– (0%)	4 (6%***)	70 (97%*)	2 (3%***)
Poland	229 (63%*)	1 (0%)	134 (37%*)	292 (80%)	72 (20%)
Portugal	117 (41%)	1 (0%)	164 (58%)	200 (71%)	82 (29%)
Romania	39 (21%***)	– (0%)	144 (79%***)	153 (84%)	30 (16%)
Spain	30 (28%**)	1 (1%)	75 (71%**)	78 (74%)	28 (26%)
Sweden	253 (95%***)	– (0%)	12 (5%***)	259 (98%*)	6 (2%***)
Ukraine	13 (45%)	– (0%)	16 (55%)	25 (86%)	4 (14%)
UK	111 (85%***)	– (0%)	19 (15%***)	119 (92%)	11 (8%**)
Yugoslavia	72 (68%**)	2 (2%)	32 (30%**)	100 (94%)	6 (6%***)
Africa					
Ethiopia	95 (42%)	9 (4%)	124 (54%)	174 (76%)	54 (24%)
Kenya	49 (63%*)	– (0%)	29 (37%*)	71 (91%)	7 (9%**)
Libya	197 (50%)	73 (18%***)	125 (32%**)	329 (83%)	66 (17%)
Morocco	1 (4%***)	– (0%)	27 (96%***)	18 (64%)	10 (36%**)
Tunisia	22 (37%)	1 (2%)	36 (61%)	48 (81%)	11 (19%)
Asia					
Afghanistan	67 (20%**)	22 (7%**)	238 (73%**)	194 (59%*)	133 (41%***)
China	297 (42%)	142 (20%***)	271 (38%)	531 (75%)	179 (25%)
DPR of Korea	4 (6%***)	– (0%)	59 (94%***)	55 (87%)	8 (13%)
Georgia	48 (49%)	1 (1%)	48 (49%)	72 (74%)	25 (26%)
India	391 (40%)	57 (6%*)	537 (55%)	708 (72%)	277 (28%)
Iran	113 (10%***)	143 (13%***)	842 (77%***)	640 (58%*)	458 (42%***)
Iraq	15 (25%**)	– (0%)	45 (75%***)	34 (57%*)	26 (43%***)
Israel	3 (11%***)	– (0%)	25 (89%***)	19 (68%)	9 (32%*)
Japan	37 (28%**)	17 (13%***)	77 (59%)	77 (59%*)	54 (41%***)
Mongolia	16 (64%**)	–	9 (36%*)	18 (72%)	7 (28%)
Nepal	143 (57%)	54 (22%***)	52 (21%***)	192 (77%)	57 (23%)
Pakistan	32 (19%***)	13 (8%***)	120 (73%**)	120 (73%)	45 (27%)
Russia	304 (51%)	2 (0%)	285 (48%)	454 (77%)	137 (23%)
Turkey	50 (29%*)	1 (1%)	120 (70%**)	104 (61%*)	67 (39%***)
Uzbekistan	– (0%***)	– (0%)	40 (100%***)	22 (55%**)	18 (45%***)
Americas					
Argentina	18 (14%***)	1 (1%)	110 (85%***)	66 (51%**)	63 (49%***)
Canada	57 (71%***)	– (0%)	23 (29%**)	68 (85%)	12 (15%)
Chile	22 (44%)	– (0%)	28 (56%)	35 (70%)	15 (30%)
Mexico	18 (16%***)	– (0%)	96 (84%***)	94 (82%)	20 (18%)
USA	306 (49%)	4 (1%)	318 (51%)	539 (86%)	89 (14%)
Uruguay	18 (55%)	– (0%)	15 (45%)	26 (79%)	7 (21%)
Australasia					
Australia	69 (82%***)	– (0%)	15 (18%***)	81 (96%*)	3 (4%***)
New Zealand	28 (93%***)	– (0%)	2 (7%***)	29 (97%*)	1 (3%***)
Total	6,804 (51%)	564 (4%)	5,969 (45%)	10,511 (79%)	2,826 (21%)

*, **, *** Significant at 5%, 1% and 0.1% level, respectively.

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Table 3b. Global distribution of the morphological characters studied: glume colour and presence of hair on glumes (for character classification see Table 2)

	Character			
	Glume colour		Presence of hair on glumes	
Country	0	1	0	1
Europe				
Albania	54 (55%)	45 (45%)	96 (97%)	3 (3%*)
Austria	396 (41%**)	580 (59%***)	969 (99%)	7 (1%**)
Belgium	38 (90%**)	4 (10%***)	38 (90%)	4 (10%)
Bulgaria	128 (68%)	61 (32%)	188 (99%)	1 (1%**)
Czech Republic and Slovakia	286 (70%)	124 (30%)	403 (98%)	7 (2%*)
Cyprus	40 (69%)	18 (31%)	44 (76%)	14 (24%***)
Finland	44 (58%)	32 (42%)	52 (68%*)	24 (32%***)
France	429 (83%*)	85 (17%**)	505 (98%)	9 (2%*)
Germany	971 (70%)	420 (30%)	1355 (97%)	36 (3%*)
Greece	205 (59%)	142 (41%)	337 (97%)	10 (3%*)
Hungary	99 (84%*)	19 (16%**)	114 (97%)	4 (3%*)
Italy	594 (66%)	310 (34%)	860 (95%)	44 (5%)
Netherlands	65 (90%**)	7 (10%***)	71 (99%)	1 (1%**)
Poland	239 (66%)	125 (34%)	364 (100%)	– (0%**)
Portugal	147 (52%)	135 (48%*)	276 (98%)	6 (2%*)
Romania	146 (80%)	37 (20%*)	182 (99%)	1 (1%**)
Spain	60 (57%)	46 (43%)	98 (92%)	8 (8%)
Sweden	225 (85%*)	40 (15%**)	212 (80%)	53 (20%**)
Ukraine	22 (76%)	7 (24%)	28 (97%)	1 (3%*)
UK	95 (73%)	35 (27%)	116 (89%)	14 (11%)
Yugoslavia	85 (80%)	21 (20%*)	104 (98%)	2 (2%*)
Africa				
Ethiopia	150 (66%)	78 (34%)	221 (97%)	7 (3%*)
Kenya	57 (73%)	21 (27%)	78 (100%)	– (0%**)
Libya	290 (73%)	105 (27%)	140 (35%***)	255 (65%***)
Morocco	18 (64%)	10 (36%)	28 (100%)	– (0%**)
Tunisia	44 (75%)	15 (25%)	59 (100%)	– (0%**)
Asia				
Afghanistan	169 (52%)	158 (48%**)	249 (76%)	78 (24%***)
China	437 (62%)	273 (38%)	595 (84%)	115 (16%)
DPR of Korea	56 (89%**)	7 (11%***)	60 (95%)	3 (5%)
Georgia	73 (75%)	24 (25%)	95 (98%)	2 (2%*)
India	583 (59%)	402 (41%)	696 (71%*)	289 (29%***)
Iran	597 (54%)	501 (46%*)	717 (65%**)	381 (35%***)
Iraq	30 (50%*)	30 (50%**)	54 (90%)	6 (10%)
Israel	19 (68%)	9 (32%)	26 (93%)	2 (7%)
Japan	53 (40%**)	78 (60%***)	131 (100%)	– (0%**)
Mongolia	10 (40%**)	15 (60%***)	24 (96%)	1 (4%)
Nepal	142 (57%)	107 (43%)	136 (55%**)	113 (45%***)
Pakistan	117 (71%)	48 (29%)	130 (79%)	35 (21%***)
Russia	395 (67%)	196 (33%)	534 (90%)	57 (10%)
Turkey	85 (50%*)	86 (50%**)	104 (61%**)	67 (39%***)
Uzbekistan	24 (60%)	16 (40%)	39 (98%)	1 (2%*)
Americas				
Argentina	63 (49%*)	66 (51%**)	129 (100%)	– (0%**)
Canada	53 (66%)	27 (34%)	73 (91%)	7 (9%)
Chile	24 (48%*)	26 (52%**)	47 (94%)	3 (6%)
Mexico	92 (81%)	22 (19%*)	112 (98%)	2 (2%*)
USA	467 (74%)	161 (26%)	603 (96%)	25 (4%)
Uruguay	23 (70%)	10 (30%)	33 (100%)	– (0%**)
Australasia				
Australia	58 (69%)	26 (31%)	78 (93%)	6 (7%)
New Zealand	19 (63%)	11 (37%)	28 (93%)	2 (7%)
Total	8,516 (64%)	4,821 (36%)	11,631 (87%)	1,706 (13%)

*, **, *** Significant at 5%, 1% and 0.1% level, respectively.

https://doi.org/10.1079/PGR200589 Published online by Cambridge University Press

Table 3c. Global distribution of the morphological characters studied: presence of inflate spikes and spike density (for character classification see Table 2)

	Character				
	Presence of inflate spikes		Spike density		
Country	0	1	0	1	2
Europe					
Albania	99 (100%)	– (0%)	99 (100%)	– (0%)	– (0%)
Austria	976 (100%)	– (0%)	684 (70%)	243 (25%***)	49 (5%*)
Belgium	35 (83%)	7 (17%***)	40 (95%)	2 (5%)	– (0%)
Bulgaria	189 (100%)	– (0%)	189 (100%)	– (0%)	– (0%)
Czech Republic and Slovakia	410 (100%)	– (0%)	404 (99%)	5 (1%)	1 (0%)
Cyprus	58 (100%)	– (0%)	46 (79%)	11 (19%***)	1 (2%)
Finland	76 (100%)	– (0%)	76 (100%)	– (0%)	– (0%)
France	512 (100%)	2 (0%)	506 (98%)	3 (1%)	5 (1%)
Germany	1391 (100%)	– (0%)	1233 (89%)	141 (10%***)	17 (1%)
Greece	347 (100%)	– (0%)	339 (98%)	5 (1%)	3 (1%)
Hungary	118 (100%)	– (0%)	116 (98%)	– (0%)	2 (2%)
Italy	904 (100%)	– (0%)	868 (96%)	28 (3%)	8 (1%)
Netherlands	72 (100%)	– (0%)	62 (86%)	10 (14%***)	– (0%)
Poland	364 (100%)	– (0%)	346 (95%)	18 (5%)	– (0%)
Portugal	282 (100%)	– (0%)	269 (95%)	2 (1%)	11 (4%)
Romania	183 (100%)	– (0%)	181 (99%)	– (0%)	2 (1%)
Spain	106 (100%)	– (0%)	103 (97%)	2 (2%)	1 (1%)
Sweden	265 (100%)	– (0%)	243 (92%)	11 (4%)	11 (4%)
Ukraine	29 (100%)	– (0%)	29 (100%)	– (0%)	– (0%)
UK	130 (100%)	– (0%)	120 (92%)	7 (5%)	3 (2%)
Yugoslavia	106 (100%)	– (0%)	105 (99%)	1 (1%)	– (0%)
Africa					
Ethiopia	222 (97%)	6 (3%)	225 (99%)	1 (0%)	2 (1%)
Kenya	78 (100%)	– (0%)	78 (100%)	– (0%)	– (0%)
Libya	244 (62%)	151 (38%***)	355 (90%)	4 (1%)	36 (9%***)
Morocco	28 (100%)	– (0%)	28 (100%)	– (0%)	– (0%)
Tunisia	59 (100%)	– (0%)	58 (98%)	– (0%)	1 (2%)
Asia					
Afghanistan	318 (97%)	9 (3%)	293 (90%)	11 (3%)	23 (7%***)
China	677 (95%)	33 (5%*)	680 (96%)	21 (3%)	9 (1%)
DPR of Korea	63 (100%)	– (0%)	63 (100%)	– (0%)	– (0%)
Georgia	97 (100%)	– (0%)	93 (96%)	2 (2%)	2 (2%)
India	933 (95%)	52 (5%*)	958 (97%)	15 (2%)	12 (1%)
Iran	1068 (97%)	30 (3%)	1077 (98%)	12 (1%)	9 (1%)
Iraq	60 (100%)	– (0%)	60 (100%)	– (0%)	– (0%)
Israel	28 (100%)	– (0%)	25 (89%)	– (0%)	3 (11%***)
Japan	130 (99%)	1 (1%)	125 (95%)	5 (4%)	1 (1%)
Mongolia	25 (100%)	– (0%)	24 (96%)	– (0%)	1 (4%)
Nepal	199 (80%)	50 (20%***)	249 (100%)	– (0%)	– (0%)
Pakistan	154 (93%)	11 (7%***)	162 (98%)	– (0%)	3 (2%)
Russia	591 (100%)	– (0%)	580 (98%)	5 (1%)	6 (1%)
Turkey	170 (99%)	1 (1%)	131 (77%)	13 (8%***)	27 (16%***)
Uzbekistan	40 (100%)	– (0%)	39 (98%)	1 (2%)	– (0%)
Americas					
Argentina	129 (100%)	– (0%)	129 (100%)	– (0%)	– (0%)
Canada	80 (100%)	– (0%)	80 (100%)	– (0%)	– (0%)
Chile	50 (100%)	– (0%)	49 (98%)	– (0%)	1 (2%)
Mexico	114 (100%)	– (0%)	110 (96%)	1 (1%)	3 (3%)
USA	627 (100%)	1 (0%)	610 (97%)	8 (1%)	10 (2%)
Uruguay	33 (100%)	– (0%)	33 (100%)	– (0%)	– (0%)
Australasia					
Australia	84 (100%)	– (0%)	84 (100%)	– (0%)	– (0%)
New Zealand	30 (100%)	– (0%)	30 (100%)	– (0%)	– (0%)
Total	12,983 (97%)	354 (3%)	12,486 (94%)	588 (4%)	263 (2%)

*, **, *** Significant at 5%, 1% and 0.1% level, respectively.

https://doi.org/10.1079/PGR200589 Published online by Cambridge University Press

Table 3d. Global distribution of the morphological characters studied: grain colour, presence of ligules and stem filling (for character classification see Table 2)

	Character					
	Grain colour		Presence of ligules		Stem filling	
Country	0	1	0	1	0	1
Europe						
Albania	25 (25%)	74 (75%)	− (0%)	99 (100%)	97 (98%)	2 (2%)
Austria	18 (2%***)	958 (98%*)	− (0%)	976 (100%)	976 (100%)	− (0%)
Belgium	5 (12%)	37 (88%)	− (0%)	42 (100%)	42 (100%)	− (0%)
Bulgaria	3 (2%***)	186 (98%*)	− (0%)	189 (100%)	188 (99%)	1 (1%)
Czech Republic and Slovakia	22 (5%***)	388 (95%)	− (0%)	410 (100%)	410 (100%)	− (0%)
Cyprus	6 (10%*)	52 (90%)	− (0%)	58 (100%)	58 (100%)	− (0%)
Finland	19 (25%)	57 (75%)	− (0%)	76 (100%)	76 (100%)	− (0%)
France	45 (9%**)	469 (91%)	− (0%)	514 (100%)	514 (100%)	− (0%)
Germany	91 (7%**)	1300 (93%)	− (0%)	1391 (100%)	1391 (100%)	− (0%)
Greece	106 (31%*)	241 (69%)	− (0%)	347 (100%)	331 (95%)	16 (5%)
Hungary	2 (2%***)	116 (98%*)	− (0%)	118 (100%)	118 (100%)	− (0%)
Italy	131 (14%)	773 (86%)	− (0%)	904 (100%)	899 (99%)	5 (1%)
Netherlands	23 (32%*)	49 (68%)	− (0%)	72 (100%)	72 (100%)	− (0%)
Poland	36 (10%*)	328 (90%)	− (0%)	364 (100%)	364 (100%)	− (0%)
Portugal	41 (15%)	241 (85%)	− (0%)	282 (100%)	263 (93%)	19 (7%**)
Romania	5 (3%***)	178 (97%*)	− (0%)	183 (100%)	182 (99%)	1 (1%)
Spain	23 (22%)	83 (78%)	− (0%)	106 (100%)	105 (99%)	1 (1%)
Sweden	47 (18%)	218 (82%)	− (0%)	265 (100%)	265 (100%)	− (0%)
Ukraine	− (0%***)	29 (100%*)	− (0%)	29 (100%)	29 (100%)	− (0%)
UK	16 (12%)	114 (88%)	− (0%)	130 (100%)	130 (100%)	− (0%)
Yugoslavia	7 (7%**)	99 (93%)	− (0%)	106 (100%)	106 (100%)	− (0%)
Africa						
Ethiopia	101 (44%***)	127 (56%**)	2 (1%)	226 (99%)	225 (99%)	3 (1%)
Kenya	10 (13%)	68 (87%)	− (0%)	78 (100%)	78 (100%)	− (0%)
Libya	204 (52%***)	191 (48%***)	1 (0%)	394 (100%)	395 (100%)	− (0%)
Morocco	3 (11%*)	25 (89%)	1 (4%***)	27 (96%)	10 (36%)	18 (64%***)
Tunisia	14 (24%)	45 (76%)	− (0%)	59 (100%)	47 (80%)	12 (20%***)
Asia						
Afghanistan	100 (31%*)	227 (69%)	1 (0%)	326 (100%)	327 (100%)	− (0%)
China	138 (19%)	572 (81%)	4 (1%)	706 (99%)	710 (100%)	− (0%)
DPR of Korea	4 (6%**)	59 (94%)	− (0%)	63 (100%)	61 (97%)	2 (3%)
Georgia	8 (8%**)	89 (92%)	− (0%)	97 (100%)	97 (100%)	− (0%)
India	489 (50%***)	496 (50%**)	5 (1%)	980 (99%)	983 (100%)	2 (0%)
Iran	575 (52%***)	523 (48%***)	2 (0%)	1096 (100%)	1098 (100%)	− (0%)
Iraq	31 (52%***)	29 (48%***)	− (0%)	60 (100%)	60 (100%)	− (0%)
Israel	7 (25%)	21 (75%)	− (0%)	28 (100%)	28 (100%)	− (0%)
Japan	8 (6%**)	123 (94%)	− (0%)	131 (100%)	131 (100%)	− (0%)
Mongolia	2 (8%**)	23 (92%)	− (0%)	25 (100%)	25 (100%)	− (0%)
Nepal	61 (24%)	188 (76%)	6 (2%**)	243 (98%)	247 (99%)	2 (1%)
Pakistan	83 (50%***)	82 (50%**)	− (0%)	165 (100%)	164 (99%)	1 (1%)
Russia	94 (16%)	497 (84%)	− (0%)	591 (100%)	590 (100%)	1 (0%)
Turkey	62 (36%***)	109 (64%)	− (0%)	171 (100%)	171 (100%)	− (0%)
Uzbekistan	3 (8%**)	37 (92%)	− (0%)	40 (100%)	40 (100%)	− (0%)
Americas						
Argentina	10 (8%**)	119 (92%)	− (0%)	129 (100%)	128 (99%)	1 (1%)
Canada	14 (18%)	66 (82%)	− (0%)	80 (100%)	80 (100%)	− (0%)
Chile	17 (34%**)	33 (66%)	− (0%)	50 (100%)	50 (100%)	− (0%)
Mexico	26 (23%)	88 (77%)	− (0%)	114 (100%)	112 (98%)	2 (2%)
USA	95 (15%)	533 (85%)	− (0%)	628 (100%)	628 (100%)	− (0%)
Uruguay	− (0%***)	33 (100%*)	− (0%)	33 (100%)	32 (97%)	1 (3%)
Australasia						
Australia	50 (60%***)	34 (40%***)	− (0%)	84 (100%)	84 (100%)	− (0%)
New Zealand	20 (67%***)	10 (33%***)	− (0%)	30 (100%)	30 (100%)	− (0%)
Total	2,900 (22%)	10,437 (78%)	22 (0%)	13,315 (100%)	13,337 (99%)	90 (1%)

*, **, *** Significant at 5%, 1% and 0.1% level, respectively.

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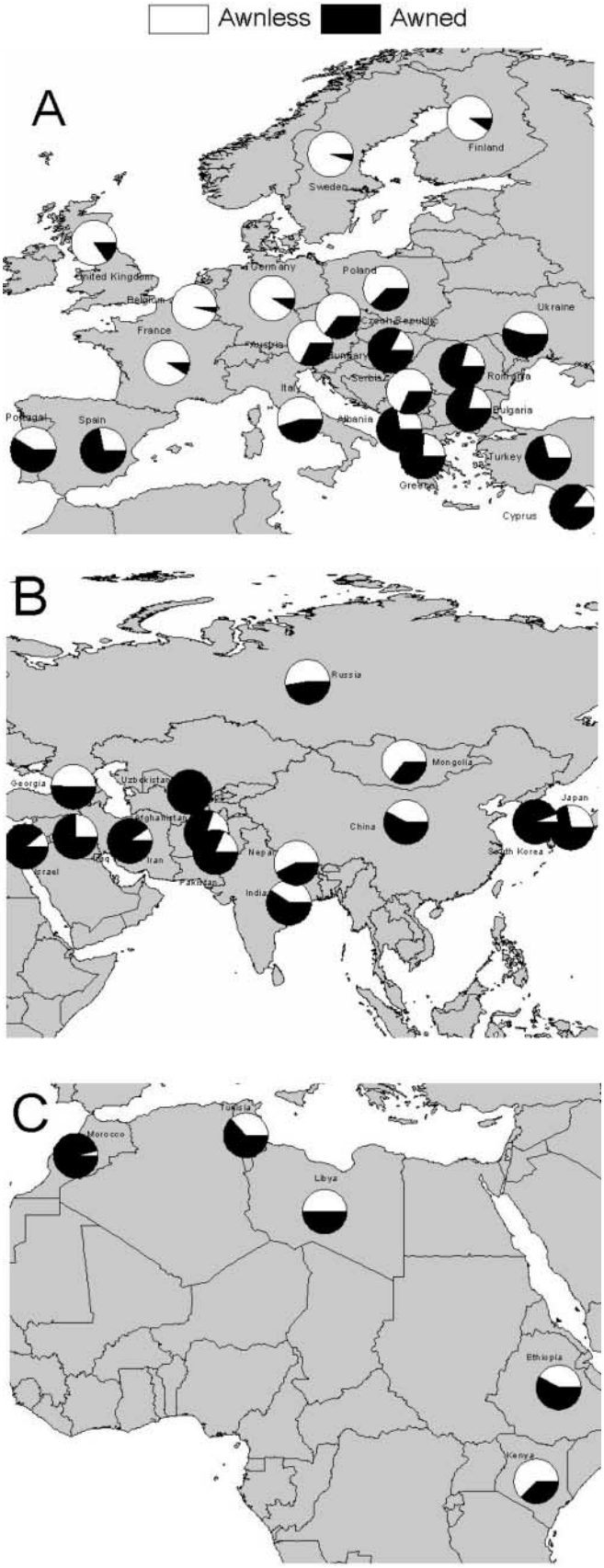


Fig. 4. Geographical distribution of awnless (white) and awned (black) spikes. (A) Europe; (B) Asia; (C) Africa.

https://doi.org/10.1079/PGR200589 Published online by Cambridge University Press

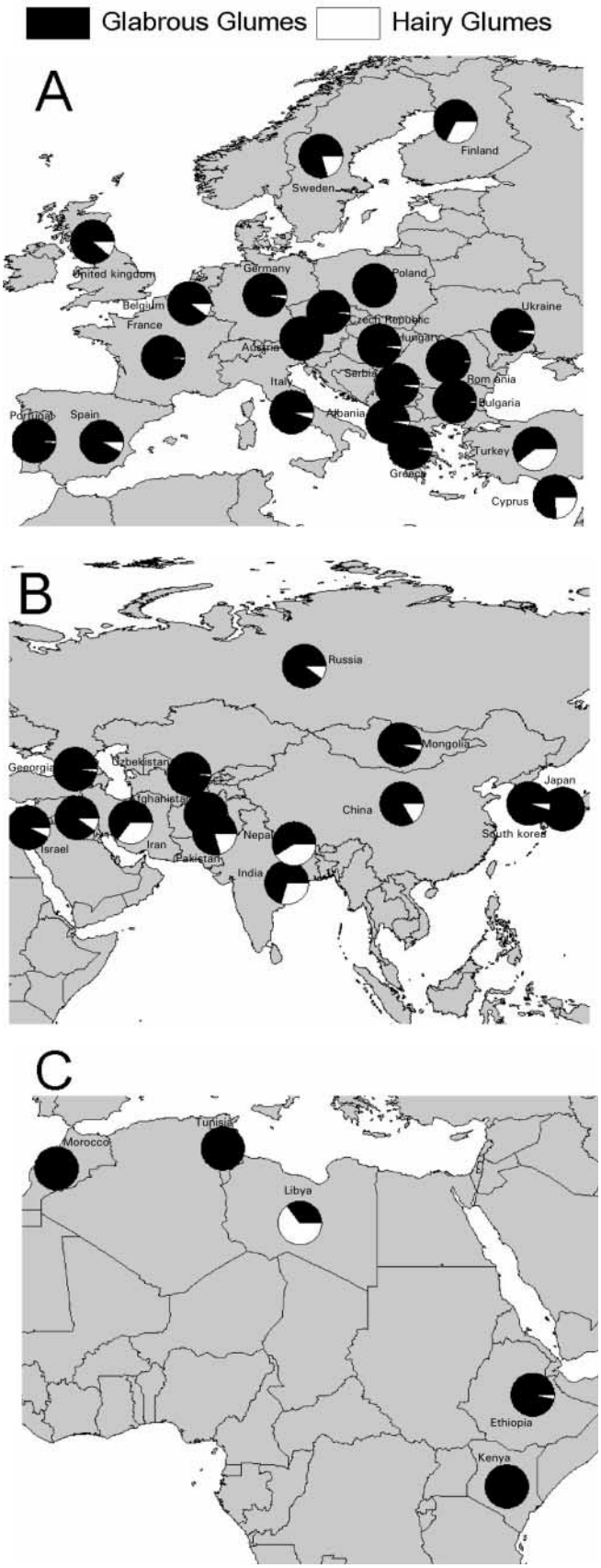


Fig. 5. Geographical distribution of hairy (white) and glabrous (black) glumes. (A) Europe; (B) Asia; (C) Africa.

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although these estimates are based on only 28 and 59 accessions, respectively. Just 22 of the accessions are liguleless—less than 0.2% of the collection—originating from Africa and Asia. This includes six (3%) accessions from Nepal.

Discussion

The regional distribution of morphological characters is informative for their importance to local adaptability. For the majority of the accessions, there are no precise descriptions of locality of origin, and, consequently, of the environment (e.g. climate, elevation, vegetation types) in which the varieties were selected. Therefore, in this paper we have only considered the primary step of classifying by country of origin supposing that the sampling was made randomly. However, some preliminary conclusions regarding the distribution of the traits and their relevance to adaptation are possible.

Characters used in keys or intraspecific classifications often have high heritability, since experience has shown that only such characters give consistent and correct groupings (Lehmann and Blixt, 1984). In many cases, a given character used in the botanical sense is in fact determined by a single gene and the character states by allelic differences. The present state of knowledge of the genetics of the characters used in the present study is discussed below.

Awnedness

Final grain yield is dependent on the amount of assimilate produced. Assimilate is generated mainly from the spike, the flag leaf and its sheath. Nonetheless, it has been long recognized that awns can substantially increase spike photosynthesis and yields under dry conditions (Atkins and Norris, 1955; Bremner and Rawson, 1972; Evans *et al.*, 1972; Olugbemi *et al.*, 1976). Our observations are consistent with this notion, since awnedness is much more prevalent in regions where severe drought stress is common (Fig. 4). The genetics of awnedness is rather complicated. Three dominant inhibitors have been described (McIntosh *et al.*, 2003), located on chromosomes 4AS (*Hd*), 5AL (*B1*) and 6BL (*B2*), with each inhibitor acting independently.

Coloration of the spike

Brown coloration of the ripe ear (often referred to as red ear or red chaff) is common according to Zeven (1983), who assumed that brown-eared types are ubiquitous across the wheat-growing world, although with unknown frequency. Since brown-eared accessions are represented among recently bred materials, it is probable that this character is not under any negative selection pressure. On the other hand, a preference of coloured spikes for growing regions characterized by high light intensity was postulated early by Flacksberger (1935). Our results support this supposition, since the highest percentages of coloured glumes occur in areas of high irradiation intensity (e.g. the Alps (Austria), the Andes (Argentina and Chile), Iberia (Portugal and Spain) and the Balkans (Albania and Greece)). An alternative hypothesis is that coloration of spike is important in regions characterized by short vegetative growing periods. In Siberia, where the time between sowing and harvest is less than 4 months (T. Pshenichnikova, personal communication), most of the local varieties have coloured glumes (Efremova *et al.*, 1998). Note, in contrast, that the vegetative period in central Europe varies between 5 and 9 months for spring and winter types, respectively. A dark spike may help the plant to absorb the energy of the sun more effectively in order to dry the seeds and, therefore, shorten the time between grain filling and ripening. Genes controlling glume and awn colour are located on the short arms of the homoeologous group 1 chromosomes (McIntosh *et al.*, 2003), designated *Rg1* (1BS), *Rg2* (1DS) and *Rg3* (1AS). In addition, a gene *Brg* (brown glume) has been proposed, mapping to the distal end of 1DS (Koval, 1994), although it is possible that that *Brg* and *Rg2* are allelic. A further gene *Bg* (black glume) has been located to chromosome 1A, but the relationship between it and *Rg3* is not known. However, since both are linked to the gene hairy glume (*Hg*) the likelihood is that they are allelic. Awn colour is thought to be genetically associated with glume colour, in agreement with our results. According to Panin and Netsvetaev (1986), black awns are determined by the three complementary genes *Bla1*, *Bla2* and *Bla3*, and these were mapped to the distal region of the short arms of chromosomes 1A, 1B and 1D, respectively, by Börner *et al.* (2002).

Hairy glumes

The ecological significance of pubescence, as being associated with harsh moisture regimes, was proposed by Clausen *et al.* (1940), who noted a general tendency for desert, steppe and alpine tundra plants to show a high incidence of pubescence. On the other hand, Jain *et al.* (1975) suggested that the adaptive nature of glabrous/pubescent glumes is not clear. Recent studies by Reynolds *et al.* (1999) and Skovmand *et al.* (2003), however, do support the hypothesis that leaf pubescence increases drought tolerance. Its positive effect on cold tolerance has also been reported by Trethowan *et al.* (1998), following observations in the Mexican highlands that pubescent spikes suffered less damage than non-pubescent ones after severe frosting at anthesis. There is some support for a positive effect of pubescent glumes on drought and cold tolerance in our analysis, since we have noted similar high frequencies of pubescence both in Asia, northern Africa and also

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Scandinavia (Fig. 5). In addition to its possible importance for abiotic stress tolerance, a role of pubescence (especially of the leaves) in the control of seed diseases and insect pests has also been proposed (Ringlund and Everson, 1968; Roberts *et al.*, 1979; Wellso and Hoxie, 1982; Warham, 1988). Pubescence of glumes may influence the susceptibility to ear diseases. One major gene (*Hg*; *Hg1*) determining the trait hairy glume in wheat has been described (McIntosh *et al.*, 2003), mapping to chromosome 1AS, and closely linked to *Bg* (Khlestkina *et al.*, 2002).

Spike morphology

Spike morphology is determined by three distinct major genetic systems. In addition to the common wheat type, the three morphotypes *compactum*, *sphaerococcum* and *spelta* have been defined (McIntosh *et al.*, 2003). The relevant genes are located on chromosomes 2DL (*compactum*), 3AL, 3BL, 3DL (*sphaerococcum*) and 5AL (*spelta*). In the collection, the loose spike type predominates. It is possible that this has been driven by selection pressure for resistance to ear diseases, since a highly dense spike is typically more susceptible to such diseases. For the trait inflate ear type, the genetics of which is not known, we are unable to suggest a reasonable hypothesis for its relatively high frequency in certain geographical regions.

Grain colour

Since the work of Nilsson-Ehle (1909), it has been known that coloured grains are associated with a lower tendency to pre-harvest sprouting (germination in the ear). This association may be a pleiotropic effect, or may be due to genetic linkage (Groos *et al.*, 2002). The red pigmentation of the wheat testa is controlled by three genes, *R-A1*, *R-B1* and *R-D1*, present on chromosomes 3AL, 3BL and 3DL, respectively (Nelson *et al.*, 1995; Flintham and Gale, 1996). Due to the positive effect of colour genes on pre-harvest sprouting tolerance, it is not surprising that the majority of accessions investigated have coloured grains. However, since white-grained wheats also vary in their level of pre-harvest sprouting (Flintham *et al.*, 2002), the presence of effective genes other than *R* complicates the interpretation of the distribution of red-grained wheats. The relatively high frequencies of white-grained wheat in certain countries like India, Pakistan or Libya may also be because of the habit and preferences for the end-use product.

Stem filling

Little is known regarding the significance, if any, of stem filling. Solid stems tend to be found in accessions from regions where drought stress can occur. One mechanism to achieve grain yield under drought stress is an elevated capacity to accumulate and remobilize stem reserves, since it has been shown that stored fructans can contribute substantially to grain filling, especially when canopy photosynthesis is inhibited by drought (Rawson and Evans, 1971). In studies where crosses have been made between lines contrasting in stem filling, solid-stem derivatives contained more soluble carbohydrate per unit of stem length (Ford *et al.*, 1979). The inheritance of the trait has not yet been elucidated.

Absence of ligules

The extremely low frequency of liguleless accessions (0.2%) has led us to conclude that these are natural mutations without any selective advantage. The genes controlling the production of ligules are located on chromosomes 2B (*lg1*) and 2D (*lg2*) (McIntosh *et al.*, 2003).

General conclusions

The geographical mapping of certain morphological/colour traits has generated clear evidence that some are not distributed randomly and, therefore, probably play an important role in determining the adaptability of bread wheat. Awnedness, spike pubescence and coloration seem all to be important in the protection of plants from damage due to abiotic stress. The genetics of most of these characters is well known, and is generally simple. Thus only a small number of major genes may be needed to ensure good levels of adaptation to certain environments.

Of interest is that the most polymorphic region identified was northern Africa. Libyan accessions had the highest frequency of hairy glumes, while in Morocco inflate spikes were detected, and filled stems were frequent. Based on genotypic studies, Ben Amer *et al.* (2001) concluded that Libyan wheat germplasm is genetically isolated. Therefore, material from northern Africa in general, and from Libya in particular, may be of special value for broadening the diversity of wheats used in current breeding programmes.

Acknowledgements

We thank Tatyana Pshenishnikova and Ebrahim Kakman for the fruitful discussion.

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