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Genetic diversity in cultivated plants—loss or stability?

Received: 12 August 2003 / Accepted: 3 December 2003 / Published online: 23 January 2004
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Abstract Human activities like urbanisation, the replacement of traditional agriculture systems by modern industrial methods or the introduction of modern high-yielding varieties may pose a danger to the biological diversity. Using microsatellite markers, we analysed samples of cultivated wheat (*Triticum aestivum* L.) collected over an interval of 40–50 years in four comparable geographical regions of Europe and Asia. No significant differences in both the total number of alleles per locus and in the PIC values were detected when the material collected in the repeated collection missions in all four regions were compared. About two-thirds of the alleles were common to both collection periods, while one-third represented collection mission-specific alleles. These findings demonstrate that an allele flow took place during the adaptation of traditional agriculture to modern systems, whereas the level of genetic diversity was not significantly influenced.

Introduction

Concern has been expressed that human activities like urbanisation, the replacement of traditional agriculture systems by modern industrial methods or the introduction

Communicated by G. Wenzel

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of modern high-yielding varieties may decrease the existing biological diversity. In the early 1920s, plant specialists of several countries initiated collection missions in order to accumulate and store genetic resources ex situ. N.I. Vavilov of the former Soviet Union started to collect material systematically in all of the climatic zones within the country and abroad. Based on those missions, he postulated the law of homologous series in variation and the theory of centres of origin of cultivated plants (Vavilov 1922, 1926). In the Austrian Alps, E. Mayr was collecting landraces of cereals in the period 1922–1932 (Mayr 1924, 1928, 1935, 1937). In Germany, K.O. Müller and his group initiated collection missions to Anatolia between 1928 and 1932, A. Scheibe and his group sent missions to Hindukusch in 1935, A. Herrlich and his collaborators collected in the Himalayas (India, Nepal) in 1937/1938, E. Schäfer and associates went to Tibet in 1938/1939, C. Troll and his group went to Ethiopia and Eritrea between 1937 and 1939 and H. Stubbe and his associates collected in the Balkans (Albania, Greece) in 1941/1942. The material collected during the these German and Austrian missions was incorporated into the Gatersleben genebank collection by Hans Stubbe, the founder of the Gatersleben Institute, and Christian Lehmann, the former Head of the genebank, after the Second World War (Gäde 1998).

In certain areas collection trips were repeated after several years, although not always exactly the same areas were covered. Recurrent missions were made, for example, in Nepal in 1971, northern India in 1976, Austria in 1982, 1983 and 1986 and Albania in 1993 and 1994. With respect to Albania, Hammer et al. (1996) compared the number of accessions collected in 1941 and 1993. Based on these numbers the authors concluded that a genetic erosion of 72% had occurred.

In the investigation reported here, we used a set of wheat microsatellite (WMS) markers to analyse the genetic diversity within randomly selected wheat (*Triticum aestivum* L.) accessions of the Gatersleben genebank originating from different collection missions. We selected samples from four different geographical areas (Aus-

tria, Albania, northern India, Nepal) in which material had been collected between the 1920s and the 1940s and again between the 1970s and the 1990s.

Materials and methods

Plant materials

In the Gatersleben genebank about 70% of all accessions are landraces which were not influenced by 'modern' plant breeding. They originated from about 140 collection missions world-wide (Gäde 1998). In four selected areas recurrent missions were initiated. Eighteen accessions per area and collection mission were selected for Albania, northern India and Nepal. With respect to the Austrian material, 87 accessions originating from the first mission and 58 originating from a recurrent mission were studied (Table 1). The distribution of the collection sites within the countries was highly comparable. As an example, Fig. 1 shows the sites within Albania where the investigated accessions were collected.

Marker analysis

Total genomic DNA was extracted from pools of five grains of each accession according to the procedure described by Plaschke et al. (1995). Between 21 and 24 primer pairs representing wheat microsatellites (GWM) were used for the analyses (Table 2). Detailed sequence information on the microsatellites is given in Röder et al. (1998) or can be obtained from Dr. M. Röder, IPK, Gatersleben. The primer sequence of TAGLGA was described by Devos et al. (1995). PCR analyses and fragment detection were performed according to Röder et al. (1998), Plaschke et al. (1995)

and Devos et al. (1995). In order to ensure size accuracy, we used vars. *Chinese Spring*, *Soisson* and *Aztec* as controls in each run.

Data analysis

The numbers of both collection mission-specific and shared alleles were counted for each microsatellite locus. Allelic polymorphic information content (PIC) was calculated according to the formula of Anderson et al. (1993)— $PIC = 1 - \sum (P_i)^2$ —where P_i is the proportion of the population carrying the i^{th} allele, calculated for each locus. Collection mission means were compared using the parameter free test (U -test) of Mann and Whitney (1947). Dendrograms for each area were constructed using the UPGMA (unweighted pair-group method with arithmetic average) algorithm on NTSYS-PC, version 2.0 (Rohlf 1998).

Results

Information on the numbers of collection mission-specific and shared alleles is given in Table 2. For the total number of year-specific alleles, there was no clear tendency. Whereas this number was slightly higher for the early missions in the material collected in Albania and Nepal, the opposite trend was detected for Austria and India. At the single-locus level, however, contrasting tendencies were observed. Analogous results were obtained for the PIC values (Table 3). Applying the U -test, we detected no significant differences either in the number of alleles per locus or in the mean PIC values

Table 1 Wheat accessions included in this investigation that originated from recurrent collection missions carried out in Austria, Albania, northwest India and Nepal

Country of origin	Collection mission	Accessions investigated
Austria	1922–1932	TRI 6562, TRI 7772, TRI 8480, TRI 8481, TRI 8483, TRI 8487, TRI 8496, TRI 8504, TRI 8520, TRI 8525, TRI 8526, TRI 8532, TRI 8541, TRI 8545, TRI 8556, TRI 8578, TRI 8590, TRI 8609, TRI 8610, TRI 8616, TRI 8618, TRI 8637, TRI 8650, TRI 8656, TRI 8664, TRI 8668, TRI 8669, TRI 8671, TRI 8673, TRI 8693, TRI 8711, TRI 8715, TRI 8716, TRI 8717, TRI 8718, TRI 8723, TRI 8734, TRI 8755, TRI 8758, TRI 8775, TRI 8776, TRI 8778, TRI 8807, TRI 8808, TRI 8817, TRI 8832, TRI 8858, TRI 8863, TRI 8871, TRI 8872, TRI 8884, TRI 8923, TRI 8930, TRI 8931, TRI 8933, TRI 8941, TRI 8948, TRI 8950, TRI 8952, TRI 8955, TRI 8970, TRI 8985, TRI 8989, TRI 9000, TRI 9015, TRI 9053, TRI 9055, TRI 9062, TRI 9068, TRI 9087, TRI 9092, TRI 9105, TRI 9108, TRI 9120, TRI 9124, TRI 9129, TRI 9150, TRI 9156, TRI 9166, TRI 9192, TRI 9194, TRI 9277, TRI 9291, TRI 9292, TRI 9299, TRI 9307, TRI 9318
	1982	TRI 13620, TRI 13621, TRI 13623, TRI 13624, TRI 13626, TRI 13628, TRI 13630, TRI 13631, TRI 13632, TRI 13633, TRI 13635, TRI 13636, TRI 13638, TRI 13640, TRI 13641, TRI 13643, TRI 13645, TRI 13646, TRI 13649, TRI 13652, TRI 13655, TRI 13656, TRI 13657, TRI 13659, TRI 13660, TRI 13662, TRI 13664, TRI 13666, TRI 13667, TRI 13668, TRI 13669, TRI 13671, TRI 13672, TRI 13675, TRI 13676, TRI 13677, TRI 13679, TRI 13680, TRI 13681, TRI 13682, TRI 13685, TRI 13686, TRI 13687, TRI 13690, TRI 13694, TRI 13697, TRI 13698, TRI 13701, TRI 13702, TRI 13704, TRI 13707, TRI 14280, TRI 16044, TRI 16649, TRI 16651, TRI 16865, TRI 16870, TRI 17392
Albania	1941	TRI 1458, TRI 1462, TRI 1520, TRI 1637, TRI 1638, TRI 1640, TRI 1644, TRI 1648, TRI 1650, TRI 1667, TRI 1671, TRI 1706, TRI 1708, TRI 1766, TRI 1767, TRI 2302, TRI 2303, TRI 2320
	1994	TRI 17956, TRI 17957, TRI 17959, TRI 17299, TRI 17300, TRI 17630, TRI 17631, TRI 17632, TRI 17635, TRI 17637, TRI 17638, TRI 17639, TRI 17640, TRI 17672, TRI 17673, TRI 17674, TRI 17871, TRI 17874
India	1937	TRI 2459, TRI 2468, TRI 2471, TRI 2548, TRI 2576, TRI 2655, TRI 2744, TRI 2770, TRI 2772, TRI 2782, TRI 2790, TRI 2796, TRI 2904, TRI 3185, TRI 3540, TRI 3542, TRI 3957, TRI 4019,
	1976	TRI 12412, TRI 12413, TRI 12414, TRI 12417, TRI 12420, TRI 12432, TRI 12440, TRI 12457, TRI 12464, TRI 12465, TRI 12473, TRI 12494, TRI 12507, TRI 12509, TRI 12514, TRI 12525, TRI 12558, TRI 12567
Nepal	1937	TRI 2436, TRI 2437, TRI 2442, TRI 2445, TRI 2448, TRI 2450, TRI 2453, TRI 2455, TRI 2677, TRI 2733, TRI 2750, TRI 2758, TRI 2760, TRI 2816, TRI 3232, TRI 3255, TRI 3301
	1971	TRI 10891, TRI 10896, TRI 10898, TRI 10903, TRI 10907, TRI 10908, TRI 10920, TRI 10921, TRI 10927, TRI 10928, TRI 10929, TRI 10931, TRI 10933, TRI 10935, TRI 10937, TRI 10942, TRI 10943, TRI 11150

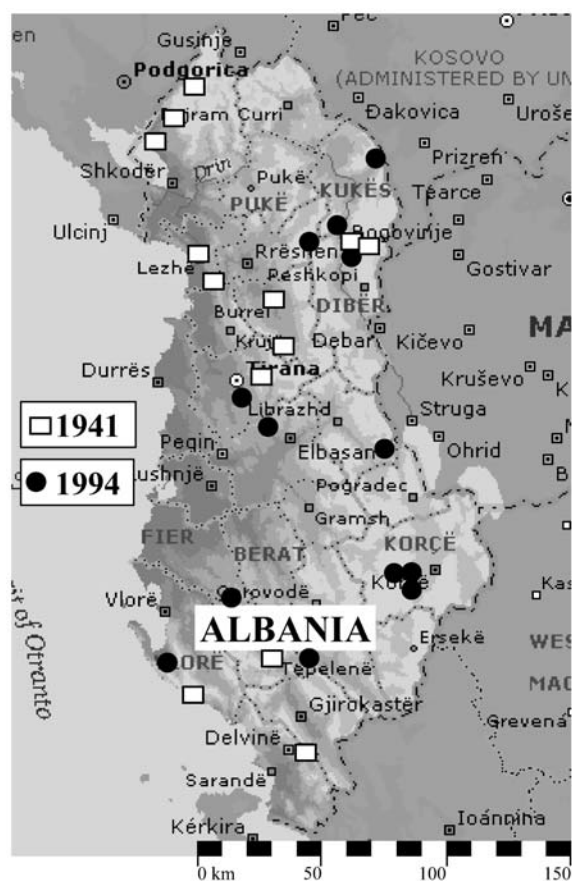


Fig. 1 Collection sites of recurrent missions carried out in Albania in 1941 (boxes) and 1994 (circles)

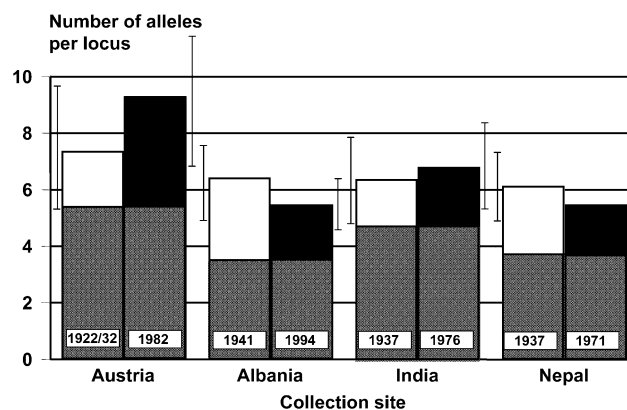
when the material of the repeated collection missions in all four regions was compared (Fig. 2). In two of the investigated regions the number of alleles per locus was even slightly higher in the material originating from the recurrent collection missions. About two-thirds of the alleles were common to both collection periods, while one-third represented collection mission-specific alleles. These findings demonstrate that an allele flow occurred, whereas the genetic diversity was not significantly influenced.

Two types of dendrograms were obtained. Type I was observed for Austria only. Here the two collection missions clustered separately (Fig. 3A). For the other three regions, however, a type-II dendrogram was detected, showing no such division. Figure 3B is an example of a type-II dendrogram, which was obtained for Albania.

Discussion

Detailed studies on genetic diversity within certain gene pools can be performed by studying morphological traits or by employing molecular marker systems such as isozymes, RFLPs, RAPDs or AFLPs. Examples are known

A



B

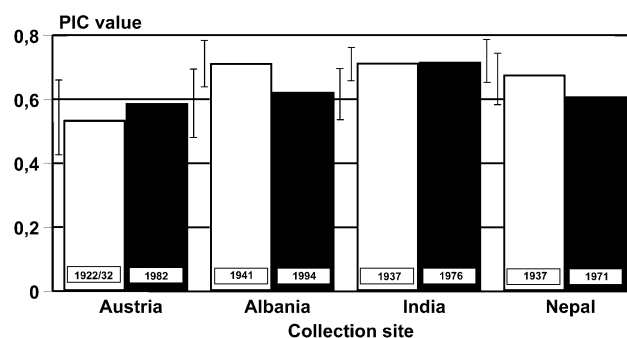


Fig. 2 Average number of alleles per locus (A) and average PIC values (B) detected in wheat accessions collected during repeated expeditions in Austria (1922/32 and 1982), Albania (1941 and 1994), India (1937 and 1976) and Nepal (1937 and 1971). Collection mission-specific alleles are shown as white (first expedition) or black (recurrent expedition) columns; common alleles are indicated in grey

for many species, including cereals. For wheat, simple sequence repeats (SSRs; synonym: microsatellites) have recently been shown to be more variable than most of the other molecular markers (Röder et al. 1995; Huang et al. 2002). In addition, it has been found that microsatellites are preferentially associated with low-copy regions of plant genomes (Morgante et al. 2002). Consequently, they provide a powerful methodology for discriminating genotypes and studying genetic diversity of germplasm as demonstrated by Plaschke et al. (1995), Donini et al. (1998), Fahima et al. (1998), Ben Amer et al. (2001), Chebotar et al. (2001), Huang et al. (2002), Alamerew et al. (2004) and Khlestkina et al. (2004).

The influence of human activities on the biological diversity of crop plants is of general interest. In particular, the activities of modern plant breeding have been postulated to narrow the diversity of currently released varieties compared to older ones. However, objective assessments have become possible only recently with the introduction of biochemical or molecular marker tech-

Table 2 Chromosomal location and numbers of collection mission-specific and shared alleles detected for microsatellite loci analysed

Locus	Chromosomal location	Geographical region									
		Austria					Albania				
		Number of specific alleles in:					Number of specific alleles in:				
		1922–1932	1982	Number of shared alleles	Number of shared alleles	1941	1944	Number of shared alleles	Number of specific alleles in:	1937	1971
<i>Xgwm357</i>	1A(C)	1	0	4	3	0	1	3	1	1	3
<i>Xgwm95</i>	2AS	1	4	2	4	1	1	4	1	5	0
<i>Xgwm155</i>	3AL	0	1	7	4	3	1	4	3	0	1
<i>Xgwm160</i>	4AL	0	3	9	-	-	-	-	-	-	-
<i>Xgwm192c</i>	4AS	0	1	2	-	-	-	-	-	-	-
<i>Xgwm186</i>	5AL	0	3	8	7	2	3	7	3	2	4
<i>Xgwm459</i>	6AS	10	12	12	-	-	-	-	-	-	-
<i>Xgwm631</i>	7AS	1	1	1	2	3	1	2	2	1	0
<i>Xgwm18</i>	1BS	1	1	7	4	2	2	4	0	1	2
<i>Taglgap</i>	1BS	3	4	8	4	5	1	4	1	1	3
<i>Xgwm619</i>	2BL	1	5	5	5	5	1	5	4	5	3
<i>Xgwm389</i>	3BS	1	2	6	4	5	4	4	2	5	3
<i>Xgwm513</i>	4BL	1	1	4	3	1	2	3	1	5	1
<i>Xgwm192a</i>	4BL	3	1	5	-	-	-	-	1	1	0
<i>Xgwm408</i>	5BL	1	6	5	6	1	0	6	1	3	0
<i>Xgwm680</i>	6BS	0	4	3	4	3	0	4	2	3	1
<i>Xgwm46</i>	7B(C)	4	2	10	3	4	4	3	5	6	1
<i>Xgwm577</i>	7BL	2	10	7	3	6	5	3	1	3	2
<i>Xgwm337</i>	1DS	2	6	6	-	-	-	-	-	-	-
<i>Xgwm458</i>	1D(C)	1	1	2	3	1	1	3	0	0	1
<i>Xgwm261</i>	2DS	0	7	4	3	1	1	3	0	2	5
<i>Xgwm3</i>	3DL	3	1	5	2	1	1	2	0	3	2
<i>Xgwm165b</i>	4DL	-	-	-	1	2	3	1	0	0	0
<i>Xgwm192b</i>	4DL	1	0	4	-	-	-	-	-	-	-
<i>Xgwm190</i>	5DS	1	2	8	3	2	2	3	2	4	3
<i>Xgwm325</i>	6DS	4	3	5	5	1	2	5	1	0	0
<i>Xgwm437</i>	7DL	1	4	10	3	10	3	3	2	3	2
Total		43	93	149	76	59	39	41	32	49	35
					102					80	

Table 3 PIC values calculated for the microsatellite loci analysed

Locus	Geographical region							
	Austria		Albania		India		Nepal	
	1922–32	1982	1941	1994	1937	1976	1937	1971
<i>Xgwm357</i>	0.39	0.61	0.61	0.63	0.74	0.73	0.62	0.63
<i>Xgwm95</i>	0.18	0.44	0.76	0.52	0.58	0.50	0.70	0.10
<i>Xgwm155</i>	0.66	0.70	0.79	0.60	0.67	0.64	0.73	0.80
<i>Xgwm160</i>	0.36	0.69	-	-	-	-	-	-
<i>Xgwm192c</i>	0.47	0.42	-	-	-	-	-	-
<i>Xgwm186</i>	0.75	0.66	0.86	0.86	0.80	0.87	0.82	0.89
<i>Xgwm459</i>	0.66	0.81	-	-	-	-	-	-
<i>Xgwm631</i>	0.02	0.69	0.68	0.52	0.65	0.52	0.70	0.63
<i>Xgwm18</i>	0.61	0.60	0.74	0.74	0.75	0.70	0.76	0.73
<i>Taglgap</i>	0.70	0.68	0.83	0.62	0.74	0.78	0.63	0.73
<i>Xgwm619</i>	0.47	0.76	0.86	0.75	0.86	0.81	0.82	0.68
<i>Xgwm389</i>	0.43	0.64	0.82	0.78	0.78	0.81	0.80	0.60
<i>Xgwm513</i>	0.36	0.43	0.62	0.73	0.56	0.57	0.64	0.51
<i>Xgwm192a</i>	0.63	0.71	-	-	-	-	-	-
<i>Xgwm408</i>	0.68	0.65	0.81	0.70	0.77	0.74	0.73	0.52
<i>Xgwm680</i>	0.47	0.54	0.78	0.51	0.67	0.74	0.35	0.10
<i>Xgwm46</i>	0.79	0.78	0.66	0.82	0.91	0.86	0.86	0.77
<i>Xgwm577</i>	0.62	0.75	0.84	0.82	0.69	0.85	0.70	0.62
<i>Xgwm337</i>	0.74	0.69	-	-	-	-	-	-
<i>Xgwm458</i>	0.09	0.03	0.65	0.57	0.61	0.65	0.28	0.61
<i>Xgwm261</i>	0.14	0.10	0.48	0.58	0.70	0.79	0.77	0.80
<i>Xgwm3</i>	0.81	0.37	0.65	0.42	0.53	0.59	0.36	0.19
<i>Xgwm165b</i>	-	-	0.20	0.28	0.62	0.64	0.71	0.64
<i>Xgwm192b</i>	0.50	0.56	-	-	-	-	-	-
<i>Xgwm190</i>	0.80	0.74	0.68	0.37	0.89	0.87	0.87	0.83
<i>Xgwm325</i>	0.59	0.47	0.76	0.81	0.65	0.49	0.53	0.66
<i>Xgwm437</i>	0.84	0.79	0.89	0.43	0.85	0.90	0.81	0.72
Means	0.53	0.59	0.71	0.62	0.72	0.72	0.68	0.61

nologies. A number of research groups have applied these techniques in their investigations on wheat varieties (Gregova et al. 1997, Donini et al. 2000, Manifesto et al. 2000, Khlestkina et al. 2004). Surprisingly, it was shown, that wheat breeding over time has resulted in a qualitative, rather than a quantitative shift in the genetic diversity. Comparable studies performed in barley have confirmed that differences in genetic diversity between landraces and cultivars appear not to be as dramatic as has often been assumed (Petersen et al. 1994; Struss and Plieske 1998; Backes et al. 2003).

In the present paper the diversity of genebank accessions collected up to 80 years ago in four divergent geographical regions was compared with material that entered the genebank about 50 years later but originating from the same areas. The results obtained with the genebank material were highly comparable to those found when investigating wheat varieties. Genetic diversity has been maintained within hexaploid wheat in the period since genebank activities commenced in the first half of the last century. However, there was clear evidence of qualitative changes in the observed diversity. About one-third of the alleles detected were unique for the period of collection, indicating that an allele flow took place during the adaptation of traditional agriculture to modern systems.

In assembling the dendrograms, it became clear to us that the qualitative changes were more pronounced in the material originating from Austria than in the other three

regions. This may be due to the fact that modern wheat breeding did influence the Austrian germplasm significantly. The cereals collected and described in detail by Mayr (1924, 1928, 1935, 1937) were characterised as mainly autochthonous landraces, cultivated for many human generations under the isolated conditions of the Alps. This situation changed dramatically during the last century by the introduction of 'new' germplasm.

The successful utilisation of genebank accessions for improving modern varieties depends not only on the genetic diversity per se available in the material. The presence of specific—in many cases rare—alleles is often much more important. The data presented here clearly demonstrate that in a certain period of cultivation a certain number of unique alleles is present. This may have consequences for the conservation of plant genetic resources. The exploitation of the whole range of allelic variation makes it necessary both to maintain the already existing ex situ collections and to collect new material. One can only preserve the allelic composition of the present situation, which will change after a certain period of time in nature. Maintained ex situ accessions of self-pollinating species show a high degree of identity, as demonstrated for wheat multiplied up to 25-fold in the Gatersleben genebank (Börner et al. 2000). In addition, the data presented here enable the quantification of the evolution occurring in cultivated plants. It was a surprising discovery that after about 50 years of cultivating a

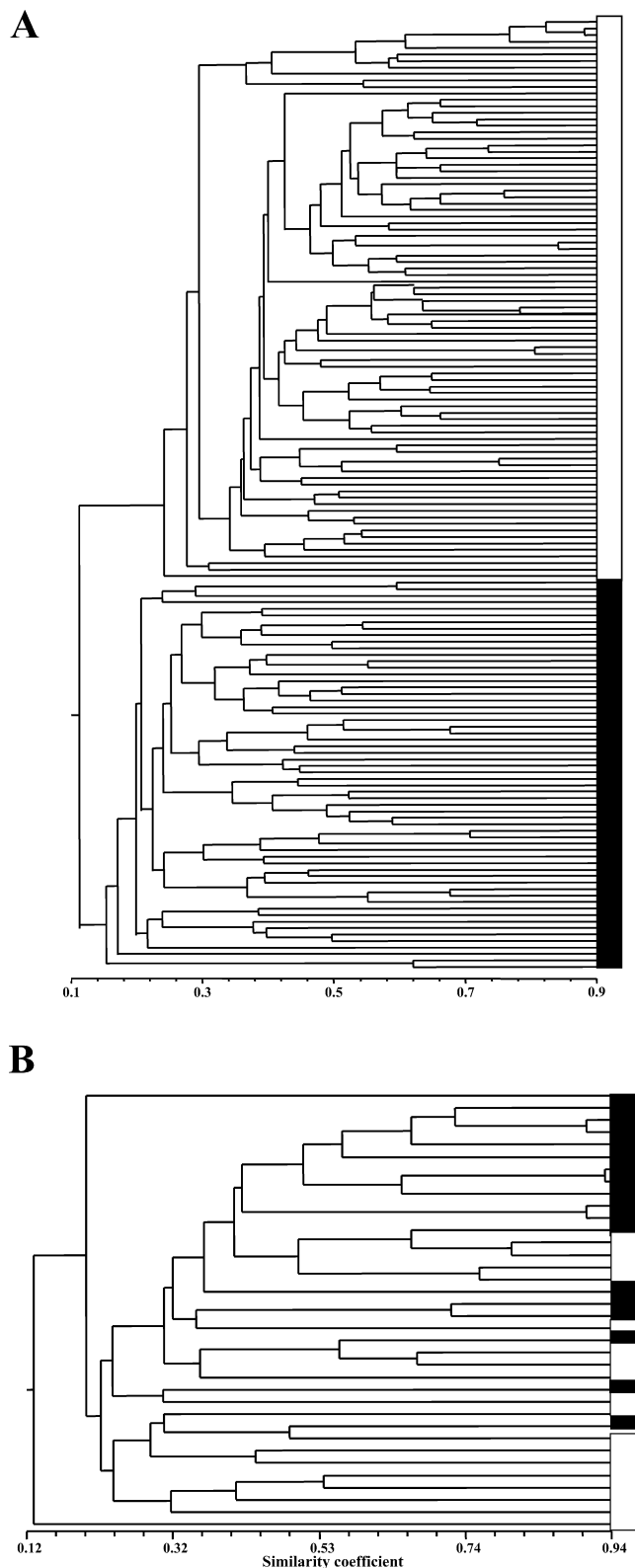


Fig. 3 UPGMA dendrogram describing the relationships among wheat accessions collected during repeated expeditions in Austria (**A**) and Albania (**B**) based on Dice's genetic similarity. Accessions are shown as white (first expedition) or black (recurrent expedition) boxes

self-pollinating species like wheat, 30% of the alleles were exchanged.

Acknowledgements Elena Khlestkina thanks the Deutsche Forschungsgemeinschaft for financial support (Project No. 436RUS 17/16/02), Florent J.-B. Quenum was supported by the Deutsche Stiftung für internationale Entwicklung (DSE) and Zentralstelle für Ernährung und Landwirtschaft (ZEL), Programme 72.3. We thank Michael Grau and Marina Schäfer for providing the seed samples.

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