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ORIGINAL PAPER

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Genetic diversity in European winter triticale determined with SSR markers and coancestry coefficient

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Abstract Knowledge of the genetic diversity of a species is important for the choice of crossing parents in line and hybrid breeding. Our objective was to investigate European winter triticale using simple sequence repeat (SSR) markers and the coancestry coefficient (*f*) with regard to genetic diversity and grouping of germplasm. Three to five primer pairs for each of the 42 chromosomes were selected to analyse 128 European winter triticale varieties and breeding lines. SSR analysis resulted in the identification of 657 alleles with an average of 6.8 alleles per primer pair. The average polymorphism information content (PIC) for polymorphic markers was 0.54. Correlation between *f* and genetic similarity (GS) estimates based on Rogers' Distance was low ($r_{f\times GS(ABDR)}$=0.33). The analysis of molecular variance (AMOVA) revealed that 84.7% of the total variation was found within breeding companies, and 15.3% among them. In conclusion, SSR markers from wheat and rye provide a powerful tool for assessing genetic diversity in triticale. Even though no distinct groups within the European winter triticale pool could be detected by principal co-ordinate analysis, this study provides basic information about the genetic relationships for breeding purposes.

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Introduction

Triticale (×*Triticosecale* Wittm.), the intergeneric hybrid between wheat and rye, has gained considerable importance in recent years in Europe as a feed grain, due to its favourable amino acid composition and performance in less productive environments. Triticale is a partially allogamous crop, but for cultivar development it is treated as a self-pollinator and line breeding is practised. The rye genome portion in triticale nurtures the expectation that the crop has a potential for the commercial use of heterosis in hybrids. First experiments with spring and winter triticale showed on average a nearly 10% mid-parent heterosis for grain yield with a wide range among hybrids (Pfeiffer et al. 1998; Oettler et al. 2003). A basic aspect to fully exploit heterosis is the characterisation of crossing parents with regard to the development of heterotic groups.

The search for and establishment of heterotic groups can be based on geographical origin, agronomical traits, pedigree data or on molecular marker data (Melchinger 1999). Up to now, only two studies have investigated the diversity of genetic resources in triticale. Furman et al. (1997) assessed more than 3,000 genotypes from the United States, Canada and Mexico for agronomical traits, but found only differences between 'complete' and 'substituted' types. A study of American and European triticale based on morphological traits revealed the existence of two main groups, winter and spring types, but no grouping according to geographical origin was possible (Royo et al. 1995).

The coancestry coefficient (*f*) is based on pedigree information and provides an indirect measure for the relative genetic similarity of related individuals. If pedigrees are well documented and reliable, as for example in maize, the establishment of groups is possible (Smith et al. 1985). In triticale, however, primary types were synthesised using tetraploid or hexaploid wheat and rye populations. Secondary types were frequently backcrossed to wheat and rye and pedigree data are not well documented or not reliable. Finally, calculation of *f* has

often failed for estimating genetic diversity in breeding material, because assumptions do not always apply (Messmer et al. 1991; Graner et al. 1994). In self-pollinating crops, selection often takes place towards the elite parent. As a consequence, the assumption that the descendants inherit half the parental genome is incorrect.

Molecular markers are the latest and most reliable tools to characterise germplasm and to estimate the relationship between genotypes at the DNA level. A variety of molecular techniques are available for genome analysis in cereals (Graner et al. 1994; Plaschke et al. 1995; Schut et al. 1997). SSRs in particular have been reported to be useful to analyse the structure of germplasm collections, because they are codominant, multiallelic and chromosome-specific (Ahmad 2002; Huang et al. 2002; Parker et al. 2002). Big efforts have been made by several groups to develop SSR markers for wheat and rye (Röder et al. 1995, 1998; Saal et al. 1999; Prasad et al. 2000; Korzun, personal communication). The presumption that genome-specific wheat SSR markers rarely amplify fragments in rye (Röder et al. 1995) gives the opportunity to assess the diversity of the wheat and rye genomes in triticale separately.

The objectives of this study were to investigate the suitability of SSR markers developed from wheat and rye for application in the composite genome of triticale, to estimate the level of diversity of winter triticale using SSR markers and to determine the correlation between the coancestry coefficient and genetic similarities estimated from SSR markers.

Materials and methods

Plant material and pedigree data

A total of 128 winter triticale varieties and breeding lines of middle and east European origin were made available for this study by 13 breeding companies and institutes from seven countries (Table 1). Pedigree information of the genotypes was submitted confidentially. Furthermore, 18 winter wheat (*Triticum aestivum* L.), 2 durum wheat (*T. durum* Desf.) and 8 winter rye genotypes (*Secale cereale* L.) of German origin were also included in this study as references for marker analysis. The Malécot (1948) coancestry coefficient (*f*) was calculated for triticale from pedigree data using the rules of Cox et al. (1985) with the KIN program (Tinker et al. 1993). If available, pedigree information up to the fourth generation was used for calculating *f* values.

SSR marker analysis

From each genotype, DNA was extracted from 40 mg vacuum-dried leaf tissue of a bulk sample of 15–20 individual plants using the sodium bisulfite method (Schweizer et al. 1995). One hundred and ninety-seven publicly available or proprietary primer pairs (Röder et al. 1995; Saal et al. 1999; Prasad et al. 2000; Hackauf et al. 2002; Korzun, personal communication; Röder, personal communication) were screened to characterise loci containing microsatellite sequences among triticale, winter wheat, durum wheat, and rye genotypes. (The list of the SSR markers is included in the electronic supplementary material.) Polymerase chain reaction (PCR) was performed in 10 μl reaction volumes containing the following reagents: 25 ng of template DNA, 0.2 mM of each of the four dNTPs, *Taq* DNA polymerase buffer, 0.3 U *Taq* DNA polymerase (Amersham Pharmacia Biotech, Freiburg), 150 nM of each of the two primers (one was fluorescence-tagged with Cy5). The PCR program consisted of a 3 min initial denaturation step at 96°C, followed by 30–40 cycles with 1 min denaturation at 96°C, 2 min primer annealing at primer-specific temperature (for details see electronic supplementary material) and 1 min primer extension at 72°C. The resulting amplification products were resolved by electrophoresis in polyacrylamide gels. Signals were scored by an ALF Express (Amersham Pharmacia Biotech) automated sequencer and transferred to a 1/0 matrix. For the final analysis, three to five primers were selected for each chromosome according to the quality of banding pattern and location in the genome.

Data analysis

For each SSR marker, the PIC (polymorphic information content) value was calculated according to Powell et al. (1996) including null-alleles. Genetic similarity (GS) between two triticale cultivars was determined as 1−Rogers' Distance (Rogers 1972) using the statistical software R (Ithaka et al. 1996). As a basis for calculating GS values three different sets of selected markers were used: the whole marker set of 96 loci (GS_{ABDR}), the 68 wheat markers (GS_{ABD}), and the 28 rye markers (GS_R). Genetic distances between groups, defined as breeding companies represented by six or more

Table 1 Country of origin of breeding companies and institutes, their symbol and number of genotypes submitted for the set of triticale varieties

Country of origin	Breeding company/institute	Symbol	No. of genotypes
France	INRA (Institute Nationale de la Recherche Agronomique)	◇	16
Germany	Nordsaat Saatzucht	★	25
Germany	Lochow-Petkus	△	15
Germany	Saatzucht Dr. Hege	✜	16
Germany	SaKa-Ragis Pflanzenzucht	●	10
Germany	W. von Borries-Eckendorf	▲	1
Germany	IG Saatzucht	▼	1
Poland	Danko Breeding	☆	9
Poland	IHAR (Plant Breeding and Acclimatization Institute)	❑	6
Romania	Research Institute for Cereals & Industrial Crops (RICIC)	✚	9
Russia	Agricultural Research Institute of Non-Chernozem Zone (ARINCZ)	■	1
Sweden	Svalöf Weibull	▽	13
Switzerland	RAC (Swiss Federal Research Station for Plant Production)	◆	6

genotypes, were calculated based on Rogers' Distance using the whole marker set (RD_{ABDR}). Correlations of the three estimates based on GS and *f* values were calculated with the computer package PLABSTAT (Utz 2001). Associations among genotypes and companies were revealed by principal co-ordinate analysis (PCoA) based on marker data using the computer package NTSYS-pc-2.11h (Rohlf 1989). To divide the genetic variation into components attributable to the variance within and among triticale genotypes of different breeding companies, an analysis of molecular variance (AMOVA) was performed with the program ARLEQUIN according to Michalakis et al. (1996).

Results

SSR markers which were developed in wheat and rye proved to be suitable for analysing the composite genome of triticale. Altogether, SSR markers for 197 loci were tested. To ensure an even distribution of the markers over the entire triticale genome, we selected 3–5 primers with a clear banding pattern for each chromosome. This set consisted of 93 markers detecting 96 loci (the complete list of the SSR markers is given in the Electronic Supplementary Material). A total of 657 fragments were obtained. In the bulk DNA samples of the triticale genotypes, 10.9% of all loci showed more than one band per SSR marker.

Out of the 39 D-genome-specific markers tested, only three, on chromosomes 2D and 7D, amplified products in some triticale genotypes (Table 2). A D-genome specific primer pair for a repetitive sequence (*Dgas44*, McNeil et al. 1994; data not shown) produced an intense signal in 19 of 128 genotypes and weak signals in further 11 genotypes, but the location of these repetitive sequences is unknown. The number of alleles and PIC values varied in a wide range within the set of 128 triticale genotypes (Table 2). Ten of the 28 rye markers were derived from expressed sequences (ESTs), while the others were from genomic libraries. The average number of alleles for the genomic rye markers was 7.8 with a mean PIC of 0.54, in comparison with an average of 2.7 alleles and a mean PIC of 0.29 for the EST-derived markers.

The number of known ancestors in the pedigree information provided for the 128 triticale genotypes was inconsistent. For several lines only one parent was submitted, but for others the complete pedigree up to the fourth generation was available. For all 128 pairwise comparisons of triticale genotypes the coancestry coefficient varied from 0 to 1, with an average of 0.059 (Fig. 1A). Of all possible pairwise triticale comparisons, 42% were not related according to the pedigree data. More than 85% had an *f* value smaller than 0.1. Six pairs of genotypes with *f*=1.0 consisted of one genotype and its three mutations. Thus, these four genotypes were regarded as being identical by descent.

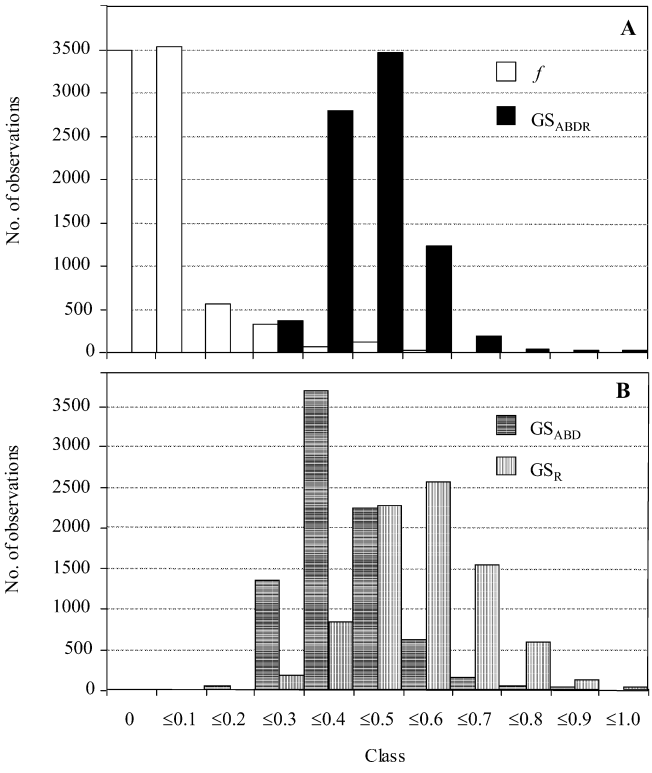

Fig. 1 Distribution of similarity estimates for all pairwise comparisons of 128 triticale genotypes, based on **A** the coancestry coefficient (*f*) and GS_{ABDR}, and **B** GS_{ABD} and GS_R

For all pairwise comparisons of GS estimates, where the comparison of a genotype with itself was excluded, the GS_{ABDR} was on average 0.43 with a range from 0.16 to 0.94 (Fig. 1A). By comparison, GS_{ABD} averaged 0.38 and ranged from 0.12 to 0.95 and the mean GS_R was 0.54 and ranged from 0.17 to 1.00 (Fig. 1B). Correlations between the coancestry coefficient *f* with GS_{ABDR}, GS_{ABD}, GS_R were low even between related (f>0.1) genotypes (Table 3). The moderate correlation between GS_{ABD} and GS_R increased from 0.43 to 0.57 after discarding all unrelated genotypes.

Table 2 Mean and range of number of alleles and the PIC values of SSR markers within triticale, according to their location in the genome

	Location	No. of loci	No. of alleles		PIC	
			Mean	Range	Mean	Range
Wheat genome	A-genome	33	8.9	4–18	0.63	0.28–0.82
	B-genome	32	7.7	3–21	0.57	0.08–0.88
	D-genome	3	2.3	2–3	n.d.[b]	n.d.
Rye genome	R-genome[a]	28	6.0	2–13	0.45	0.03–0.79
Total		96	7.5	2–21	0.54	0.03–0.88

[a] SSR markers from EST and genomic libraries
[b] n.d.: not determined

Table 3 Correlation among estimates of coancestry (*f*) and genetic similarity (GS) based on different marker sets calculated across all triticale combinations (8,128 entries, above diagonal) and across combinations of related genotypes (*f*>0.1, 1,090 entries, below diagonal)

	f	GS_{ABDR}[a]	GS_{ABD}[b]	GS_R[c]
f	–	0.33**	0.34**	0.17**
GS_{ABDR}	0.39**	–	0.93**	0.74**
GS_{ABD}	0.43**	0.96**	–	0.43**
GS_R	0.17**	0.77**	0.57**	–

** Significant at 0.05 level
[a] All markers
[b] Markers from wheat genome
[c] Markers from rye genome

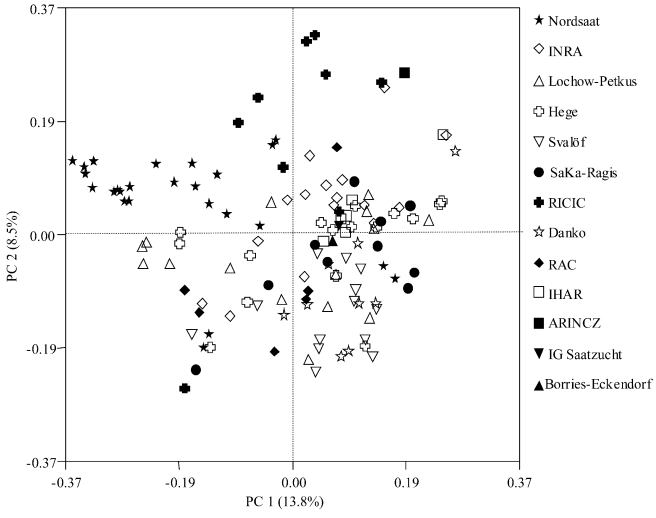

Fig. 2 Two-dimensional principal co-ordinate analysis based on GS_{ABDR} for 128 triticale genotypes. PC1 and PC2 are the first and second principal co-ordinate

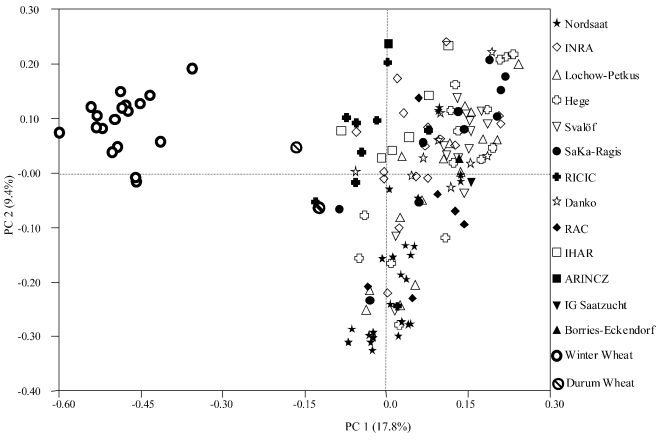

Fig. 3 Two-dimensional principal co-ordinate analysis based on GS_{ABD} with similarity data for 128 triticale, 18 winter wheat and 2 durum wheat genotypes. PC1 and PC2 are the first and second principal co-ordinate

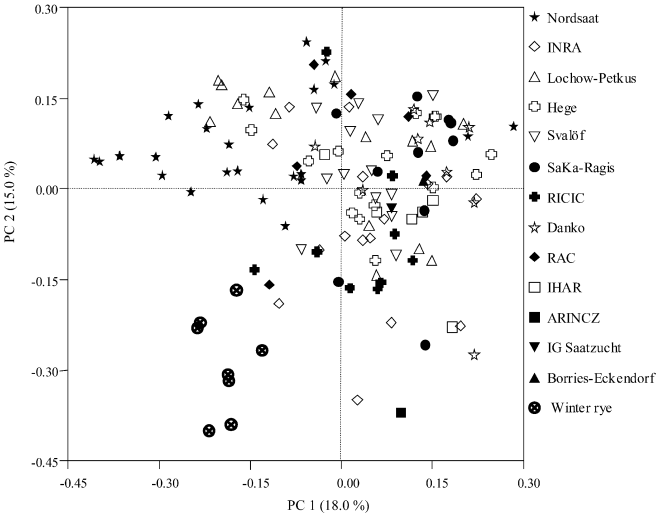

Fig. 4 Two-dimensional principal co-ordinate analysis based on GS_R with similarity data for 128 triticale genotypes and 8 rye genotypes. PC1 and PC2 are the first and second principal co-ordinate

PCoA based on 128 triticale genotypes revealed no distinct groups (Fig. 2). Apart from most of the lines from the breeding company 'Nordsaat' and several genotypes from 'RICIC', there is no clear grouping obvious in the triticale germplasm. The first two principal co-ordinates (PC) together explained 22.3% of the total variation.

To assess the diversity of the wheat genome (ABD) component of triticale, PCoA based on GS_{ABD} was performed and included all triticale and wheat genotypes (Fig. 3). Here, the first two principal co-ordinates together explained 27.2% of the total variation. The two durum wheat genotypes were grouped close to the triticales. The German winter wheat cultivars formed a distinct group. The variation of the wheat genome within triticale was relatively narrow in the first principal co-ordinate (-0.13 to 0.24) in comparison with the second principal co-ordinate (-0.33 to 0.24).

In a separate analysis, PCoA was performed with GS_R values, including triticale and the eight rye genotypes. (Fig. 4). The first two principal co-ordinates explained 33.0% of the total variation. Most of the 'Nordsaat' germplasm formed a distinct group as was also observed for the wheat genome portion (Fig. 3). The genotypes of 'RICIC' were scattered among the other genotypes with regard to the rye genome component.

In the PCoA based on RD_{ABDR} for 10 breeding companies represented by six or more genotypes, the first three principal co-ordinates explained 59.5% of the total variation (Fig. 5). The following groups were clearly separated from other breeding companies by one PC: 'RICIC' (PC1), 'Nordsaat' (PC2), and 'Danko', 'Svalöf', and 'RAC' (PC3). GS_{ABDR} between pairs of companies averaged 0.23 and ranged between 0.18 and 0.40 for those breeding companies represented by six or more genotypes (Table 4). AMOVA based on the whole marker set revealed significant variation of 15.3% among companies

Table 4 Genetic distance based on RD_{ABDR} between companies/institutes (below diagonal) and their standard error (above diagonal)

	Nord-saat	INRA	Lochow-Petkus	Hege	Svalöf	SaKa-Ragis	RICIC	Danko	RAC	IHAR	ARINCZ[a]	IG Saat-zucht[a]	Borries-Eckendorf[a]
Nordsaat	–	0.012	0.015	0.018	0.021	0.018	0.020	0.019	0.019	0.020	0.025	0.028	0.027
INRA	0.30	–	0.014	0.011	0.018	0.012	0.019	0.018	0.014	0.018	0.025	0.026	0.025
Lochow-Petkus	0.27	0.23	–	0.013	0.019	0.014	0.018	0.017	0.017	0.018	0.026	0.026	0.024
Hege	0.29	0.19	0.22	–	0.016	0.010	0.021	0.015	0.016	0.019	0.029	0.029	0.028
Svalöf	0.31	0.27	0.28	0.23	–	0.018	0.023	0.013	0.022	0.022	0.030	0.030	0.029
SaKa-Ragis	0.32	0.21	0.22	0.18	0.27	–	0.020	0.017	0.017	0.020	0.027	0.027	0.026
RICIC	0.38	0.33	0.37	0.35	0.40	0.37	–	0.022	0.023	0.022	0.029	0.032	0.031
Danko	0.33	0.26	0.28	0.23	0.21	0.27	0.38	–	0.020	0.021	0.028	0.030	0.029
RAC	0.30	0.26	0.27	0.25	0.29	0.28	0.39	0.32	–	0.023	0.029	0.032	0.031
IHAR	0.39	0.29	0.33	0.29	0.35	0.30	0.39	0.34	0.36	–	0.030	0.033	0.033
ARINCZ[a]	0.41	0.46	0.43	0.44	0.49	0.45	0.53	0.50	0.42	0.52	–	0.045	0.045
IG Saatzucht[a]	0.51	0.47	0.50	0.45	0.45	0.48	0.55	0.46	0.51	0.53	0.59	–	0.036
Borries-Eckendorf[a]	0.49	0.45	0.47	0.42	0.44	0.45	0.54	0.44	0.47	0.51	0.56	0.13	–

[a] Three groups represented by only one genotype are separated by a dashed line

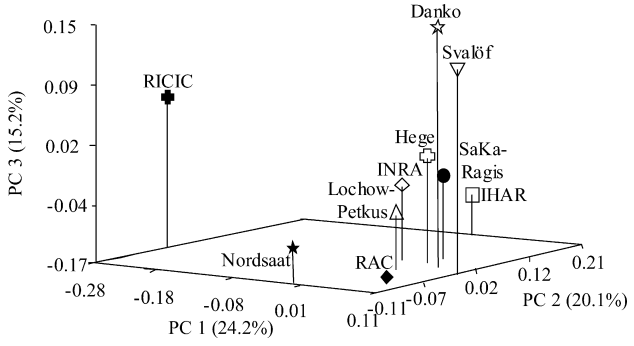

Fig. 5 Principal co-ordinate analysis based on RD_{ABDR} of 10 breeding companies with six or more genotypes. PC1, PC2, PC3 are the first, second and third principal co-ordinate, respectively

in comparison with 84.7% within. Separate computations for the wheat and rye genome portion resulted in similar findings (data not shown).

Discussion

With the objective of selecting and maintaining parental lines to exploit heterosis for a hybrid breeding program in winter triticale, germplasm groups have to be identified and developed. In triticale, the creation of gene pools has not yet received any attention, and pedigree information is scarce and incomplete. For some genotypes used in this study, only information on the female parent was available but for other genotypes the complete pedigree back to the initial wheat×rye cross was submitted by the breeding company. The distribution of *f* values differs clearly from the estimates based on GS_{ABDR} (Fig. 1A), because of the fundamental differences in the concepts underlying both measures (Bohn et al. 1999). Even with detailed and complete pedigree data this would be the case. Hence, the distribution of the *f* values demonstrates the low differentiation power compared with GS estimates. Furthermore, rye as an allogamous species might have transmitted a high degree of heterogeneity to triticale by using population varieties as crossing parents. As ancestor, heterozygous rye in contrast to the strictly autogamous wheat does not comply with the assumption for the calculation of *f* that all ancestors have to be homozygous and homogeneous.

Autogamy limits genetic recombination and allopolyploidy hinders the gene flow from the wild progenitors into the gene pool of the cultivated crop. Therefore, the genetic basis will become narrower during evolution (Spillane et al. 2001). Both mechanisms are absent in rye. Hence, GS_R in triticale should be smaller than GS_{ABD}. However, genetic similarity based on GS_{ABD} with a mean of 0.38 is smaller than that based on GS_R which averaged 0.54 (Fig. 1B). In our study this might be due to the application of 10 EST-derived rye SSR markers instead of genomic markers. The average PIC value of the latter (0.54) was much higher than that of the EST-derived rye SSR markers (0.29) in triticale. The variation of alleles within the expressed regions of DNA is lower but polymorphisms in coding regions might have direct impact on physiology and further on the phenotype. Several groups are working on the isolation of EST-derived SSRs in wheat and rye (Eujayl et al. 2002; Hackauf et al. 2002; Holton et al. 2002), which may improve marker-assisted selection, comparative genetic analysis and exploitation of genetic resources by providing a more direct estimate of functional diversity.

Even though we tested only a limited number of D-genome specific SSR primers, the lack of amplification products in most triticale genotypes (Table 2) agrees with the presumption that winter triticale varieties are 'complete', i.e. without substitutions of D/R chromosomes (Mergoum et al. 1998). We suppose that the observed banding patterns of D-genome specific primers are the result of translocations instead of D/R substitutions, because of the lack of null alleles for the tested R-genome specific primers.

The low but significant correlation between coancestry and DNA-based similarity measures (Table 3) corresponds to findings in barley and wheat (Graner et al.

1994; Bohn et al. 1999; Corbellini et al. 2002). Tighter associations were found in maize (Lübberstedt et al. 2000; Lu and Bernardo 2001; Enoki et al. 2002), where pedigrees are more reliable and the simplifying assumptions more appropriate. In our study, the lowest correlation exists between *f* and GS_R, which corresponds with the uncertainties of calculating the coancestry coefficient for heterozygous ancestors.

PCoA showed no distinct groups within triticale (Fig. 2) except for two companies, i.e. most genotypes from 'Nordsaat' and 'RICIC' were situated apart from the remaining triticale varieties and breeding lines. In contrast, Sun et al. (2001) found a strong grouping according to breeding companies in maize when assessing the genetic diversity of commercial maize hybrids with SSR and RAPD markers. The finding in triticale corresponds with the free exchange of breeding material in self-pollinating crops. A further reason for the lack of distinct groups might be the exclusive use of triticale in Europe for one end-use purpose, namely grain feed. Hitherto, no management of germplasm with regard to hybrid breeding has taken place, which requires the division of the germplasm pool into several sections.

The limited number of wheat and rye genotypes included in the study as references for marker analysis gives a first impression on the relationship between the triticale AB(D)R genome portions and the winter wheat ABD and rye R genome. Clear clustering of the German wheat cultivars (Fig. 3) suggests a low influence on the wheat genome portion of European triticale. To illustrate the impact of *T. aestivum* or *T. durum* on triticale, a broader range of wheat genotypes has to be investigated. Our study, analysing only two durum wheats, might suggest that the AB genome portion of triticale may descend from durum wheat (Fig. 3). German wheat and rye genotypes differ clearly from German triticale with regard to the wheat and rye genome respectively (data not shown). To broaden the genetic diversity of triticale, information on the relationships between a wider range of winter wheat and triticale genotypes is required for the choice of crossing parents.

The AMOVA revealed lower but significant variation among breeding companies (15.3%) than within (84.7%) for RD_{ABDR}. The amount of molecular variance due to breeding programs in a comparable study for sugar beet (DeRiek et al. 2001) was much smaller (2.6%). Another study with seven tropical maize populations revealed only 10.2% between-population variation (Reif et al. 2003). Li et al. (2001) assessed soybean landraces from Korea, Japan and China and found 12.4% variation attributed to variation between countries of origin.

The widest genetic distance was 0.40 between 'Svalöf' and the 'RICIC' and may be attributed to the widest differences in our study for climatic and environmental conditions (Northern Europe vs Southeast Europe). It may also have historical reasons due to the initiation of the breeding programs in different parts of Europe. However, large RD values (0.39) were also found between companies from more similar regions ('IHAR'×'RICIC', 'IHAR'×'Nordsaat', 'RAC'×'RICIC').

Our study shows that wheat and rye SSR markers are suitable for triticale genome analysis. The application of these SSR markers leads to basic information for the development of germplasm pools. The genotypes of breeding companies with the widest differences may be a first basis for establishing heterotic pools in a hybrid breeding program. Parents from putative gene pools have to be selected for testcrosses to evaluate heterosis and hybrid performance. First results will be published in a companion study, where F_1 hybrids have been tested in field trials to assess hybrid performance and heterosis.

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