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Wheat genetic diversity trends during domestication and breeding

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Abstract It has been claimed that plant breeding reduces genetic diversity in elite germplasm which could seriously jeopardize the continued ability to improve crops. The main objective of this study was to examine the loss of genetic diversity in spring bread wheat during (1) its domestication, (2) the change from traditional landrace cultivars (LCs) to modern breeding varieties, and (3) 50 years of international breeding. We studied 253 CIMMYT or CIMMYT-related modern wheat cultivars, LCs, and *Triticum tauschii* accessions, the D-genome donor of wheat, with 90 simple sequence repeat (SSR) markers dispersed across the wheat genome. A loss of genetic diversity was observed from *T. tauschii* to the LCs, and from the LCs to the elite breeding germplasm. Wheat's genetic diversity was narrowed from 1950 to 1989, but was enhanced from 1990 to 1997. Our results indicate that breeders averted the narrowing of the wheat germplasm base and subsequently increased the genetic diversity through the introgression of novel materials. The LCs and *T. tauschii* contain numerous unique alleles that were absent in modern spring bread wheat cultivars. Consequently, both the LCs and *T. tauschii* represent useful sources for broadening the genetic base of elite wheat breeding germplasm.

Introduction

Domestication and modern plant breeding have presumably narrowed the genetic base of bread wheat (*Triticum aestivum*), which could jeopardize future crop improvement. Tetraploid varieties of domesticated wheat were derived from a single tetraploid progenitor, *Triticum dicoccoides*, the donor of the A and B genomes (Kimber and Feldman 2001). Soon after the domestication of *T. dicoccoides*, free-threshing forms evolved from less amenable hulled genotypes, known as *Triticum turgidum*. Wheat species with tetraploid genomes were subsequently involved in a fateful experiment: accidental crosses with the wild diploid species *T. tauschii*, the donor of the D genome. This gave rise to the hexaploid wheat *T. aestivum*, also known as bread wheat (Kihara 1944; McFadden and Sears 1946; Salamini et al. 2002). The number of independent crosses between the progenitors of *T. aestivum* is considered limited (Dvorák et al. 1998; Talbert et al. 1998), resulting presumably in a loss of diversity.

Through the centuries, mutation generated new alleles, while recombination created novel allele combinations. The genetic variation was subsequently reduced by genetic drift and selection, both natural and that of early farmers, which eventually resulted in landrace cultivars (LCs) adapted to specific conditions of their habitats. During the past century so many of the traditional LCs were continually replaced by modern wheat cultivars (MWCs) that currently only about 3% of the wheat-growing area is sown with LCs (Smale et al. 2002). The MWCs were bred with a limited number of LCs in their pedigree, and it is postulated that MWCs contain less genetic diversity than LCs (Frankel 1970).

A popular hypothesis is that an extended period of plant breeding and intensive selection have further reduced genetic diversity among cultivars, narrowing the germplasm base available for future breeding advances (Tanksley and McCouch 1997). Cultivation of germplasm with a narrow genetic base entails a risk due to genetic vulnerability. This risk is that mutations in pest

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populations or changes in environmental conditions may bring about stresses that the cultivar could not cope with and, therefore, could lead to severe crop losses. This risk was brought sharply into focus in 1970 with the outbreak of the southern corn leaf blight (Anonymous 1972). The first signs that germplasm with a narrow genetic base might also lead to disasters in wheat came from several severe epidemics of shoot fly (*Atherigona* spp.) and karnal bunt (*Tilletia indica*) in India in the 1970s (Dalrymple 1986). Nevertheless, plant breeding does not inevitably lead to a loss of genetic diversity. Reduction in diversity caused by intensive selection can be counterbalanced by introgression of novel germplasm.

During the last 40 years, the International Maize and Wheat Improvement Center (CIMMYT) has had a tremendous impact on spring wheat. In all developing countries, excluding China, approximately 86% of the spring bread wheat area in 1997 was sown with CIMMYT or CIMMYT-related germplasm involving at least one CIMMYT ancestor (Smale et al. 2002). CIMMYT's wheat germplasm is therefore exceptionally suitable for investigation whether breeding has reduced genetic diversity in wheat in a detrimental manner.

Examining the loss of genetic diversity in spring bread wheat during (1) its domestication, (2) the change from traditional LCs to modern breeding varieties, and (3) 50 years of international breeding requires molecular analyses that incorporate comprehensive samples of MWCs, LCs, and their progenitors. In this article, we report the first such extensive molecular diversity analysis of wheat, which used a sample of 253 MWCs, LCs, and *T. tauschii* accessions, the D-genome progenitor of wheat, and 90 simple sequence repeat markers (SSR) that provide a broad coverage of the wheat genome.

Materials and methods

Plant materials

We chose 123 CIMMYT, CIMMYT-related, and other MWCs on the basis of information obtained from an impact study (Smale et al. 2002) on their total area sown, year of release, contribution to the development of new important lines (key parents), and geographic distribution. The MWCs were divided into five time periods according to the year of release: period 1: 1950–1965; period 2: 1966–1973; period 3: 1974–1981; period 4: 1982–1989; period 5: 1990–1997. Each period included a minimum of 20 MWCs. Detailed information on the 123 MWCs is available as supporting information at <http://www.uni-hohenheim.de/~jochreif/TAG/TableA.pdf>. Five Mexican and four Turkish spring wheat LCs composed of 3–25 sub-lines were added to our study, resulting in a total of 119 LC genotypes. Detailed information about the LCs is published elsewhere (Dreisigacker et al. 2004a). Additionally, 11 *Triticum tauschii* accessions were chosen for analysis, six collected

in Iran, two in China, and three of an unknown origin [see Zhang et al. (2005) for more details].

SSR genotyping

The plants were genotyped at the Applied Biotechnology Center at CIMMYT. Details of the protocol can be found in Dreisigacker et al. (2004b). Briefly, DNA was extracted by the cetyltrimethylammonium bromide (CTAB) method, and the SSR regions were amplified by PCR with fluorescent-labeled primers. PCR products were size-separated on an ABI Prism 377 DNA Sequencer (Perkin Elmer Biotechnologies, Foster City, Calif.) and classified to specific alleles by GENESCAN and GENOTYPER software programs (Dreisigacker et al. 2004b). MWCs were genotyped with a set of 90 SSRs [51 expressed sequence tags (ESTs) and 39 genomic-derived markers] covering the entire wheat genome. The LCs were fingerprinted with a subset of SSRs consisting of 41 markers (Dreisigacker et al. 2004a). SSR information was obtained from the Institute of Plant Genetics and Crop Plant Research (IPK; Gatersleben, Germany) and DuPont (Wilmington, Del.). In addition, we used SSR markers Taglgap, Taglut (Devos et al. 1995), and WMC56 developed by the Wheat Microsatellite Consortium (Agrogene, France). The *T. tauschii* SSR genotypes were obtained with 28 SSRs mapping to the D genome, as described elsewhere (Zhang et al. 2004). Detailed information for all SSRs is available as supporting information at <http://www.uni-hohenheim.de/~jochreif/TAG/TableB.pdf>.

Statistics

Rogers' genetic distance (RD) (Rogers 1972) was estimated among pairs of genotypes, considering the absence of an SSR marker band as a missing value. We used the FITCH program in the PHYLIP package (Felsenstein 1993) with the RD estimates to construct a phylogenetic tree based on the Fitch-Margoliash least-squares algorithm. In FITCH, the *J* option was used to randomize the input orders of samples. Standardized numbers of alleles per locus (N_a) were estimated by re-sampling nine plants per group (MWCs, LCs, and *T. tauschii*) (Reif et al. 2004). Gene diversity (H) was calculated for the MWCs, LCs, and *T. tauschii* for polymorphic loci (Nei 1987). Standard errors of N_a and H were determined by a bootstrap procedure over SSRs. The relative loss of gene diversity between two germplasm groups was calculated as $\Delta H = 1 - (H_1/H_2)$, where H_1 and H_2 denote the gene diversities of the two germplasm groups. Furthermore, the average number of unique alleles per SSR was determined for comparison between *T. tauschii* and the LCs, as well as between the LCs and MWCs. The coefficient of parentage (COP) (Malecot 1948) was estimated among pairs of MWCs as described by St. Martin (1982).

A linear relationship between COP and RD is expected under certain simplified assumptions (Melchinger

et al. 1991). Pearson's correlation coefficient (r) was calculated between RD estimates based on SSRs and COP values based on all pairs of MWCs with $COP \geq 0.05$. Trends of RD- or COP-based genetic diversity estimates of the MWCs during the last 50 years of wheat breeding were examined by performing multiple regression analyses of these measures on the time periods, following established procedures (Snedecor and Cochran 1980). All analyses were performed with version 2 of the PLABSIM software (Frisch et al. 2000), which is implemented as an extension to the statistical software R (Ihaka and Gentleman 1996).

Results and discussion

Relationships among MWCs, LCs, and *T. tauschii*

The Fitch-Margoliash phylogenetic tree of all 253 genotypes revealed a clear separation of *T. tauschii* accessions from LCs and MWCs with only one *T. tauschii* accession positioned in the group of MWCs (Fig. 1). This result reflects the long isolation of the two gene pools after domestication, as well as the divergence caused by selection, drift, and mutation. The LCs and MWCs also formed two separated main clusters. This outcome can be explained by: (1) the limited number of LCs used as the germplasm base for the development of MWCs and (2) selection and drift during the breeding of MWCs. The LCs and *T. tauschii* accessions are quite diverse from the MWCs, indicating their potential as a source of novel germplasm for wheat breeding.

Loss of diversity from *T. tauschii* to landraces

We observed a non-significant decrease in N_a and H from *T. tauschii* accessions to LCs (Fig. 2) but a significant ($P < 0.1$) relative diversity loss ($\Delta H = 0.19$). These results, together with the findings of 2.5 unique alleles per locus present in *T. tauschii* but not in the LCs, indicate a reduction in genetic variation during the process of wheat domestication. This is in agreement with previous studies reporting that the *T. tauschii* genome contains considerably more genetic variation than the D genome of hexaploid wheat (Lubbers et al. 1991; Lelley et al. 2000). The reduction in genetic diversity is probably the product of the relatively young history of the wheat crop, the presumably small founder population, and the intensive long-term selection for agronomic traits. Thus, the initial steps of crop domestication probably caused a severe population bottleneck.

Loss of diversity from landraces to MWCs

No change in H from the LC to the MWCs was observed for the D genome, but H decreased slightly from LCs to MWCs for the AB genomes (Fig. 2). Combining

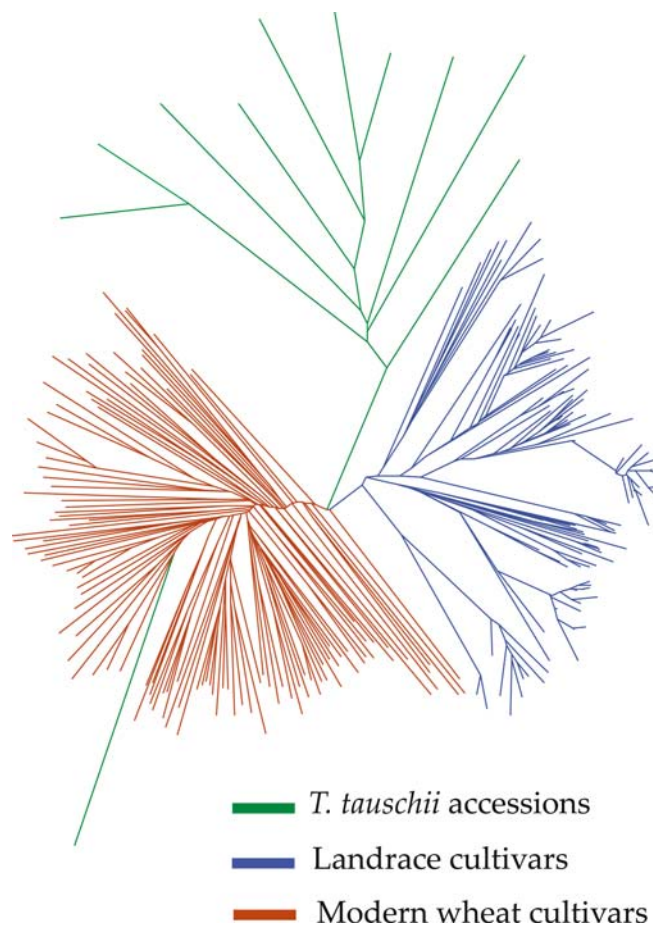


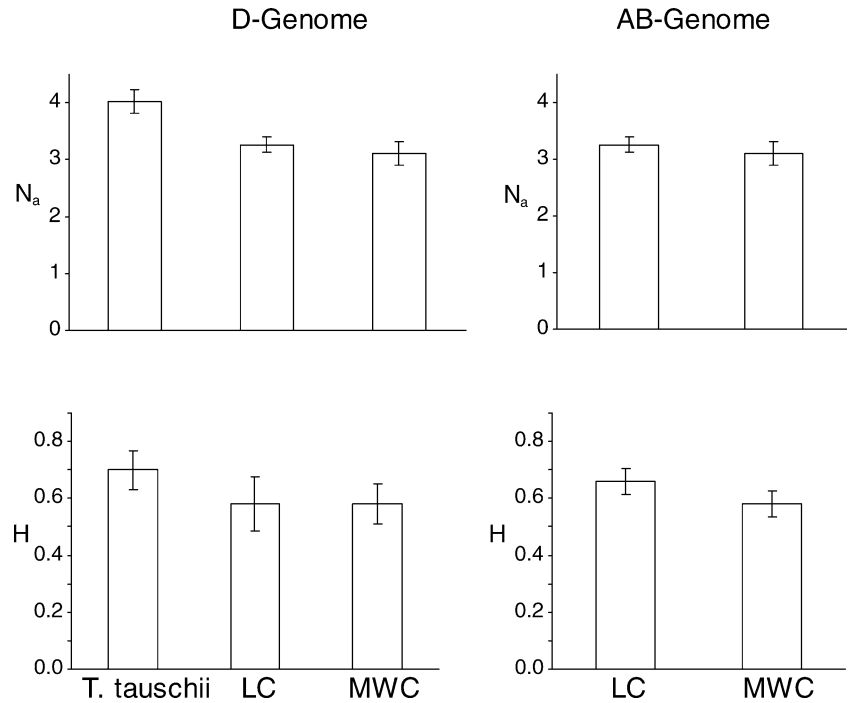
Fig. 1 Fitch-Margoliash tree for the 11 *Triticum tauschii* accessions, 119 wheat landrace cultivars (LCs), and 123 modern wheat cultivars (MWCs) based on Rogers' genetic distance (RD) between individual plants

all SSRs, a relative loss of gene diversity ΔH of 0.05 was revealed from LCs to MWCs. Together with the observation that 1.9 unique alleles per locus were present in the LCs but absent in the MWCs, this indicated a substantial genetic diversity loss from the LCs to the MWCs. Possible explanations are those already stated in discussing the clustering pattern of the material in our study. The loss of genetic diversity may indicate an elimination of undesired or even deleterious alleles, but may also reflect an erosion of alleles valuable for plant improvement and future demands of producers and consumers. The latter hypothesis was supported by various surveys reporting the potential of LCs as a source of novel useful allelic variation (Cox et al. 1992; Villareal et al. 1995).

Diversity trends during 50 years of international breeding

The global impact of the spring bread wheat breeding program of CIMMYT has been significant and well-documented (Rajaram 1994). The main objectives of this

Fig. 2 Standardized number of alleles per locus (N_a) and gene diversity (H) of 11 *T. tauschii* accessions, 119 LC, and 123 MWC genotypes. Values for the D genome are based on 14 SSRs, and for the AB genomes on 27 SSRs



breeding program were high and stable yields across mega-environments combined with widely effective disease resistances. An average annual increase in yield of 0.88% was reported from 1960 to 1990 (Sayre et al. 1997). Nevertheless, there has been growing public concern that the tremendous enhancements of yield by modern breeding would go hand in hand with a large decrease in diversity (Harlan 1972), which could threaten future selection progress.

The average RD and COP between MWCs of different time periods (Table 1) showed that the relatedness of the germplasm increased with decreasing differences in time periods, indicating the presence of drift and/or selection. The average RD and COP between MWCs of adjacent time periods revealed that the relatedness of the germplasm decreased with increasing time periods. This reflects the effects of second-cycle breeding, where the next breeding cycle is generated by intermating the best genotypes of the previous cycle.

Pairwise RD within a period regressed on the period number corroborated a significant ($P < 0.05$) quadratic trend. This indicates a narrowing of the genetic diversity among major CIMMYT MWCs from period 1 to period 4, but an enhancement from period 4 to period 5 (Fig. 3a).

COP determines the similarity between two individuals using the concept of identity by descent. Pairwise 1-COP values between individuals within time periods present therefore an alternative measure of genetic diversity. Although the correlation (r) between RD and 1-COP across all 7,503 data points was only 0.48 ($P < 0.01$), we also observed a significant ($P < 0.05$) quadratic trend between SSR-based RDs and time periods, with an increase in diversity for the last time period

studied (Fig. 3b). The low correlation between RD and 1-COP can be explained by several simplifying assumptions underlying the COP estimation, including (1) unrelated founder individuals, (2) equal parental genome distribution, and (3) the absence of selection, mutation or drift (Cox et al. 1986).

Owing to the length of a breeding cycle and the low multiplication rate of wheat after the initial cross is made, it takes approximately 10–12 years for a newly developed cultivar to reach the market and influence genetic diversity on a large scale. Therefore, the decreasing pairwise 1-COP values and pairwise RDs from periods 1 to 4 reflect the reduction in genetic diversity until the late 1970s. This reduction in diversity levels might be explained by the “Early Green Revolution” (Evenson and Gollin 2003), which was characterized by breeding semi-dwarf varieties possessing a higher yielding potential due to an increased harvest index and better lodging tolerance, especially under high fertilizer and water inputs. These high-yielding new semi-dwarf MWCs were based on a limited number of key parents and rapidly dominated the wheat germplasm base (Dalrymple 1986). Roussel et al. (2004) studied 559 French bread wheat accessions and also reported a reduction in genetic diversity probably linked to the “Early Green Revolution”. Thus, their results support our findings.

The increase in genetic diversity (1-COP values and RD) from periods 4 to 5 can be explained by a change in the breeding strategy of CIMMYT in the late 1970s. CIMMYT’s wheat breeding program aimed at increasing genetic diversity on a large scale by taking into account the need for biological diversification, environmental sustainability, and durable resistance to

Table 1 Average Rogers' distance (above diagonal) and coefficient of parentage (below diagonal) for 123 CIMMYT and CIMMYT-related wheat cultivars grouped into five time periods: period 1: 1950–1965; period 2: 1966–1973; period 3: 1974–1981; period 4: 1982–1989; period 5: 1990–1997. The mean of the standard errors of Rogers' distances is 0.053

Period	1	2	3	4	5
1		0.477	0.487	0.481	0.487
2	0.109		0.463	0.462	0.474
3	0.103	0.144		0.443	0.465
4	0.089	0.122	0.141		0.445
5	0.094	0.136	0.150	0.155	

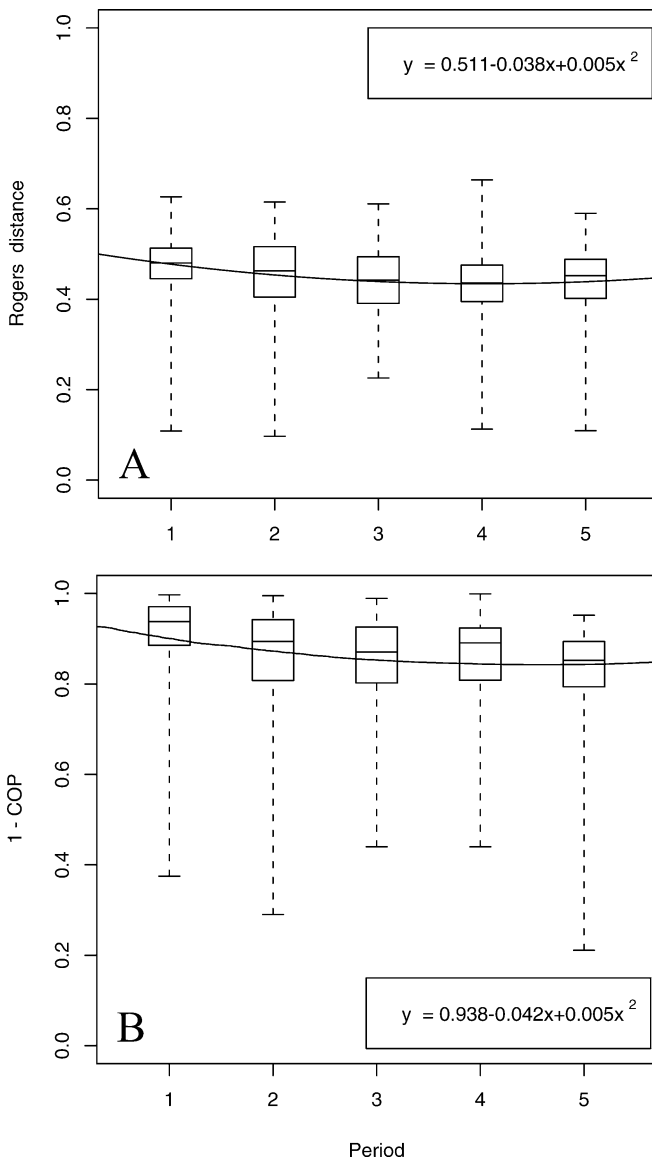


Fig. 3 Boxplot of pairwise Rogers' distances (a) and 1-COP (b) values for 123 CIMMYT and CIMMYT-related wheat cultivars grouped into five time periods. The closed boxes comprise values between the 25% and 75% quantiles

combat ever-evolving pathogens. In parallel, the wide geographic adaptation of the germplasm remained as an important breeding goal (Reeves et al. 1999; Rajaram and van Ginkel 2001). The spring bread wheat breeding germplasm was broadened with (1) spring and winter wheat from different regions, (2) exotic germplasm such as Chinese or Brazilian wheat cultivars, (3) LCs from many regions, and (4) wild relatives such as *Agropyrum* derivatives (Rajaram 1994; Reeves et al. 1999).

Our results indicate that CIMMYT breeders successfully increased the genetic diversity through the introgression of various novel wheat materials once they realized the danger of narrowing down their germplasm base. Grain yield of spring bread wheat has been systematically increased through genetic improvement from periods 4 to 5 (Sayre et al. 1997) without reducing the genetic diversity (Fig. 3b). Thus, the enhancement of yield in plant breeding does not necessarily cause a loss of genetic diversity.

Sources of novel genetic variation for wheat breeding

Over the last 100 years, the development and successful application of wheat breeding has produced high-yielding MWCs on which present-day agriculture is based. Yet, ironically, it is the plant breeding process itself that threatens the genetic base upon which breeding depends. A report commissioned by the National Academy of Sciences, in response to the 1970 southern corn leaf blight disaster, recommended placing more emphasis on collecting and preserving genetic diversity in crop species (Anonymous 1972). One result of that report was the foundation of germplasm banks such as the one at CIMMYT, where approximately 150,000 accessions of wheat and its wild relatives are conserved.

A classical way experienced scientists and research staff use to identify useful novel genes and alleles in genetic resources is to look for potentially useful traits. This may happen during the routine maintenance and systematic screening of collections or as a spin-off of pre-breeding and breeding programs carried out for other purposes. Once a desired trait has been identified, backcrossing can be used to introduce it into elite breeding germplasm. This approach works well when the trait of interest is controlled by one or only a few genes but many traits important to agriculture, such as yield, show polygenic inheritance. The identification of genes of agronomic importance therefore requires more sophisticated methods (Vigouroux et al. 2002). After their localization in the genome, a systematic search of novel alleles can be conducted in genetic resources via new approaches such as association mapping (Lynch and Walsh 1997). New valuable genetic variants can then be introgressed systematically, applying marker-assisted backcrossing or genetic transformation. Consequently, the genetic potential present in genetic resources can be unlocked, facilitating a sustainable future selection gain in plant breeding.

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