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## Comparative analyses of RFLP diversity in landraces of *Triticum aestivum* and collections of *T. tauschii* from China and Southwest Asia

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**Abstract** Chinese accessions of *Triticum tauschii* and *T. aestivum* L. from the Sichuan white (SW), Yunnan hulled (YH), Tibetan weedrace (TW), and Xinjiang rice (XR) wheat groups were subjected to RFLP analysis. *T. tauschii* and landraces of *T. aestivum* from countries in Southwest Asia were also evaluated. For *T. tauschii*, a west to east gradient was apparent where the Chinese accessions exhibited less diversity than those from Southwest Asia. Compared to the Southwest Asian gene pool, the Chinese *T. tauschii* was highly homogeneous giving a low frequency of polymorphic bands (16%) and banding patterns (1.33 per probe) with 75 RFLP probe-*Hind*III combinations. Accessions of *T. tauschii* from Afghanistan and Pakistan were genetically more similar to the Chinese *T. tauschii* than those from Iran. Of 368 bands found for 39 Chinese hexaploid wheat accessions with 63 RFLP probe-*Hind*III combinations, 28.3% were polymorphic with an average of 2.6 banding patterns per probe and 5.0 bands per genotype. The individual Chinese landrace wheat groups revealed less variation than those from Afghanistan, Iran, and Turkey. When classified into country based groups, however, the diversity level over all Chinese landraces was greater than that of some Southwest Asian landraces, especially those from Afghanistan and Iran. The XR wheat group was genetically distinct from the other three Chinese landrace groups and was more related to the Southwest Asian

landraces. The TW group was genetically similar to, but more diverse than, the SW and YH groups. The Chinese landraces had a higher degree of genetic relatedness to the Southwest Asian *T. tauschii*, particularly to accessions from Iran, rather than to the Chinese *T. tauschii*. ‘Chinese Spring’ was most related to ‘Chengdu-guang-tou’, a cultivar from the SW wheat group.

**Key words** Genetic diversity · *Triticum tauschii* · *Triticum aestivum* · RFLP · Landrace wheat

### Introduction

Wheat (*Triticum aestivum* L. em. Thell.) has been cultivated in China for several thousands of years and China has been proposed as a center of diversity for wheat (Yen et al. 1988). China is also home to many other species in the *Triticeae* tribe, including *T. tauschii*. Recent efforts in the comparative characterization of genetic diversity among Chinese accessions of *T. aestivum* and *T. tauschii* may encourage the optimal management of genetic resources both within China and internationally (Kim 1995; Yang and Smale 1996).

At least four groups of exotic landraces of *T. aestivum* are found in China (Yang et al. 1992). The Yunnan hulled wheat (YH) group (*T. aestivum* ssp. *yunnanense* King) is found in the valleys of the Nujiang and the Lanchangjiang Rivers in Yunnan province and is locally referred to as ‘Tiekemai’ or iron glume wheat because of its hard glumes. Although they exhibit a brittle rachis, like *T. spelta*, YH wheat accessions have the wedge type of disarticulation, whereas *T. spelta* has the barrel type (Shao et al. 1983; Tsunewaki et al. 1990). The Tibetan weedrace wheat (TW) group (*T. aestivum* ssp. *tibetanum* Shao) is known as ‘Duansuimai’ or fragile spike wheat. Accessions of

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this group have a naturally broken rachis with wedge-type disarticulation and consequently exhibit spontaneous disarticulation of the rachis in the field (Shao et al. 1983; Tsunewaki et al. 1990). This group is found as a weed in fields of wheat and barley mixtures in Tibet. The Xinjiang rice wheat (XR) group (*T. petropavlovskyi* Udats et Migusch), known as 'Daosuimai' or rice-head wheat, has spikes similar to those of tetraploid Polish wheat (*T. turgidum* L. var. *polonicum*) and is found in the Xinjiang province of western China. The Sichuan white (SW) wheat group, the likely origin of the cultivar 'Chinese Spring', is composed of cultivated common wheats characterized by multifloret spikelets and rounded glumes (Yen et al. 1988).

Several morphological and cytogenetic studies have been conducted with these four landrace groups (Shao et al. 1983; Chen et al. 1985, 1988; Yen et al. 1988; Yang et al. 1992). Riley et al. (1967) reported that the chromosome structure of 'Chinese Spring' is not different from that of the putative ancestral wheat species, *T. turgidum* L. ssp. *dicoccoides* ( $2n = 28$ , AABB) and *T. tauschii* ( $2n = 14$ , DD). The YH, TW, and XR wheat groups also appear to have a primitive chromosomal constitution for the D genome (Yen et al. 1988; Yang et al. 1992). One or two chromosomes (especially in the B genome) distinguish 'Chinese Spring' from members of the YH, TW and XR wheat groups (Chen et al. 1988; Yang et al. 1992). Chen et al. (1988) reported that chromosomes of the YH wheat group were less differentiated from 'Chinese Spring' than those of the TW and XR wheat groups. The Polish wheat-like spike morphology of XR wheat and its relatively greater chromosomal differentiation led Yang et al. (1992) to suggest that it may have originated through an independent hexaploidization event. Chen et al. (1988) and Chen et al. (1985) also suggested introgression from *T. polonicum* or some other wild emmer wheat as the mechanism leading to XR wheat's unusual characteristics. The discovery of *T. tauschii* in China, along with the cytogenetic fact of complete bivalent chromosome pairing of the D genome in interspecific hybrids, has also led to the hypothesis that some Chinese hexaploid landraces might have originated from natural hybridization between cultivated emmer wheats and Chinese *T. tauschii* (Yen et al. 1983; Yang et al. 1992).

In an effort to broaden the available diversity in wheat, we explored levels of RFLP diversity among the exotic Chinese wheat genetic resources described above. RFLP data of the present study were used to assess the possibility of independent hexaploidization in which *T. tauschii* from China was the donor of the D genome of Chinese landraces. We also traced the origin of Chinese *T. tauschii* by comparison with the genetic variation present in the fertile crescent and near regions.

## Materials and methods

### Germplasm

Ten accessions of *T. tauschii* collected from Henan (HN), Shaanxi (SX), and Xinjiang (XJ) in China were employed in the RFLP analysis (Fig. 1). Ten accessions of *T. tauschii* collected from the five regions of Southwest Asia were also used (Fig. 1). Thirty eight accessions of Chinese landraces of *T. aestivum* were used as representatives of the four exotic groups described above (Fig. 1). *T. aestivum* ssp. *typicum* cv Hongmangmai was also included in this study as one of the common wheat cultivars currently grown in China. For studies concerning genetic relationships with other groups, 55 accessions of landraces of *T. aestivum* from Turkey (TUR), Iran (IRN), and Afghanistan (AFG) were used. Details regarding these landraces, not provided here, are available upon request.

### RFLP analysis

Southern-blot analysis for RFLPs was performed as described by Kim and Ward (1997). For DNA digestion, one restriction enzyme, *Hind*III, was employed in the present study. Seventy five probes were used for analysis of the *T. tauschii* accessions. Thirty of these clones were from genomic DNA of *T. tauschii* and were provided by Dr. B. S. Gill at Kansas State University (Gill et al. 1991). Dr. M. E. Sorrells at Cornell University provided the other 45 probes [see Kim and Ward (1997) for a description of these clones]. All of the Cornell probes and 18 of the KSU probes were used for the analysis of the Chinese landraces of *T. aestivum*. RFLP data with 30 Cornell probes, commonly used for both the Southwest Asian and the Chinese landraces of *T. aestivum*, were applied to estimate the genetic variation and relationships of all sets of landraces in this study.

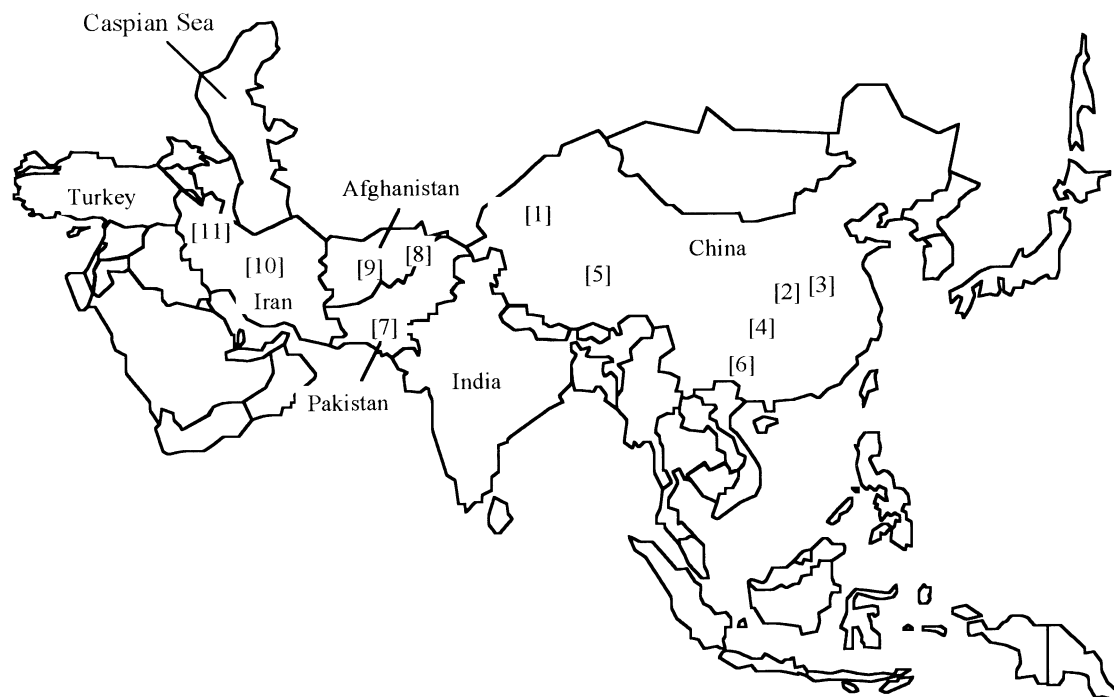
The collection and analysis of RFLP data were conducted as described by Kim and Ward (1997). Genetic similarity (GS) between lines was calculated with Nei and Li's coefficient (1979). Genetic relationships within and between groups were estimated by a UPGMA (unweighted pair group method arithmetic average) cluster analysis of GS matrices (Rohlf 1992).

## Results

### RFLP diversity in gene pools of *T. tauschii*

Analysis of the RFLP patterns generated with the 75 probes employed revealed a total of 309 bands, 46.9% of which were monomorphic across the entire set of *T. tauschii* accessions. Seventy six percent of the probes were polymorphic when considering the entire set of *T. tauschii* accessions. There were on average 2.7 RFLP banding patterns per probe and 2.9 bands per probe/accession combination. Probe polymorphic information content (PIC) values (Anderson et al. 1993) had a maximum of 0.80 and a mean of 0.34.

Within the Chinese *T. tauschii* accessions, 84% of the 233 bands scored were monomorphic, and only nine bands were unique. Only 28% of the probes detected polymorphism and the number of RFLP banding patterns per probe was low (mean = 1.33). Probe PIC values had a maximum of 0.59 and a mean of 0.11.



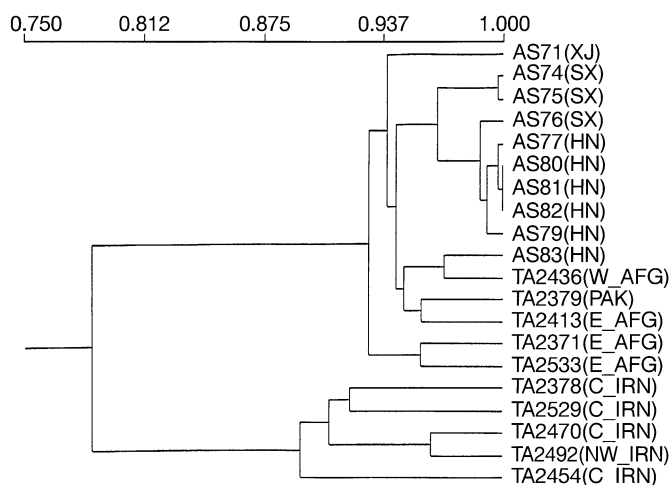
**Fig. 1** Accessions of *Triticum tauschii* and *T. aestivum* and their geographical origins. I. *Triticum tauschii* (DD) – 20 accessions. [1] Xinjiang (XJ): AS<sup>a</sup> 71; [2] Shaanxi (SX): AS 74, 75, and 76; [3] Henan (HN): AS 77, 79, 80, 81, 82, and 83; [7] Pakistan (PAK): TA<sup>b</sup> 2379; [8] E. Afghanistan (E\_AFG): TA 2371, 2413, and 2533; [9] W. Afghanistan (W\_AFG): TA 2436; [10] Caspian Iran (C\_IRN): TA 2378, 2454, 2470, and 2529; [11] NW. Iran (NW\_IRN): TA 2492. II. *T. aestivum* (AABBDD) – 39 accessions from China. [1] Xinjiang rice wheat (XR): AS 356, 357, 358, 360, 361, 362, 363, and 364; [4] Sichuan white wheat (SW): AS 489 ('Chengdu-guang-tou'), 742, 743, 745, 746, 749, 750, 751, 754, 755, 764, 2228 ('S-1'), and 'Chinese Spring'; [5] Tibetan weedrace (TW): AS 329, 330, 907, 908, 1025, 1026, and 1027; [6] Yunnan hulled wheat (YH): AS 331, 332, 333, 334, 335, 336, 337, 338, 339, and 340; Chinese common wheat cultivar (ssp. *typicum*): AS 1727 ('Hongmangmai'). <sup>a</sup>AS # = Identification number of accessions in the Triticeae Research Institute, Sichuan Agricultural University, China. <sup>b</sup>TA # = Identification number of accessions in the Wheat Genetics Resource Center, Kansas State University, USA. III. The Chinese accessions of *T. tauschii* and *T. aestivum* except Chinese Spring were provided by Professor C. Yen at Sichuan Agricultural University. Ten accessions of *T. tauschii* from Southwest Asia were provided by Dr. B.S. Gill at Kansas State University. Fifty-five accessions of Southwest Asian landraces of *T. aestivum*, not shown here, were provided by Dr. H. Bockelman at the United States Department of Agriculture's World Small Grains Collection

RFLP variation was greater among the Southwest Asian *T. tauschii* accessions. A total of 300 bands were scored with 50% of them being monomorphic. Seventy bands were unique to the Southwest Asian *T. tauschii* pool. Seventy two percent of the probes detected polymorphism among the Southwest Asian accessions. The mean number of RFLP banding patterns per probe was 2.5. Probe PIC values had a maximum of 0.80 and a mean of 0.4.

The accessions from Iran exhibited more RFLP diversity compared to the other *T. tauschii* groups employed in this study. There were 1.68 RFLP banding patterns per probe in the Iranian accessions, compared to 1.39 for accessions from Afghanistan, and 1.33 for the Chinese accessions. In spite of the small number of accessions, about 60% of banding patterns in the Iranian accessions did not appear in other groups, including the Chinese *T. tauschii*. About 16.3% and 16% of the RFLP patterns were unique to the Afghanistan and Chinese groups, respectively.

#### Genetic relationships among gene pools of *T. tauschii*

UPGMA cluster analysis based on the GS matrix generated two large sub-clusters: one for the accessions from Iran and the other for those from China, Afghanistan and Pakistan (Fig. 2). Chinese accessions were closely related to each other with a mean GS within a pool of 0.969, which was greater than that of Afghanistan (0.947) and Iran (0.848). Six HN accessions from China were generally homogeneous as a group, with a relatively high mean GS within a group. Genetic relatedness between the Chinese gene pool and the gene pools of Afghanistan and Pakistan was prominent as expected from their geographical proximity. The estimated mean GS of Chinese accessions with accessions from Afghanistan and Pakistan was 0.937 and 0.945, respectively. The mean GS between the Chinese and Iranian gene pools was relatively low (0.787).



**Fig. 2** Dendrogram resulting from cluster analysis of the RFLP-based genetic similarity matrix among 20 accessions of *T. tauschii*

#### RFLP diversity in Chinese landrace groups of *T. aestivum*

Sixty three probes and the *Hind*III restriction enzyme were employed in the RFLP analysis of the 39 accessions of Chinese *T. aestivum*. In total, 368 bands were scored, 71.7% of which were monomorphic across the entire set of Chinese accessions. On average, there were 2.6 RFLP banding patterns per probe and 5.0 bands per accession. More than 60% of the probes revealed polymorphism across all accessions.

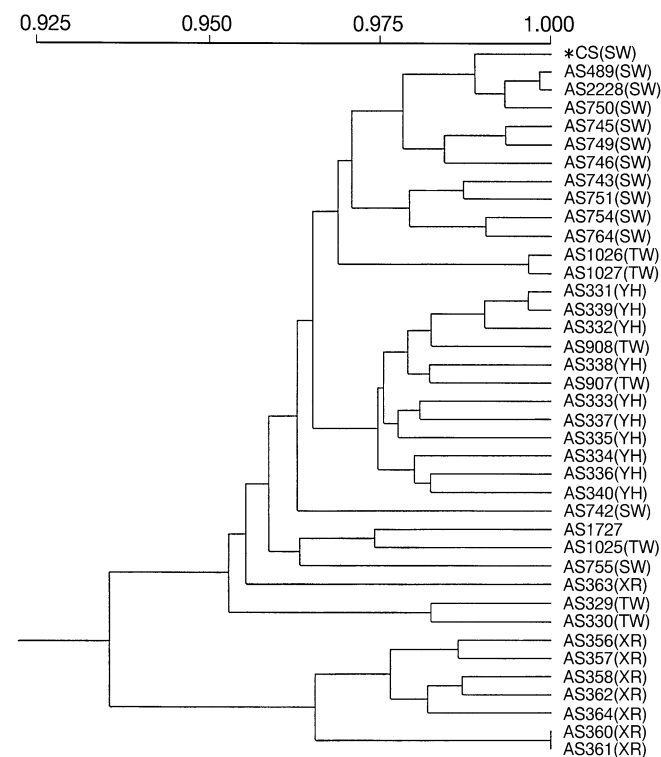
At least 83% of the bands were monomorphic within any of the Chinese landrace groups (Table 1). The YH wheat group showed the lowest genomic diversity with the highest percentage of monomorphic bands, the highest mean GS within a group, and the lowest mean PIC value (Table 1). There was also no group-specifically unique band in this group (Table 1). PIC values within a group ranged from 0 to 0.83, with higher values prevailing in the TW and XR wheat groups (Table 1).

#### Relationships among Chinese landrace groups of *T. aestivum*

The dendrogram derived from UPGMA cluster analysis based on the GS coefficient matrix for Chinese *T. aestivum* is presented in Fig. 3. Two distinct clusters are evident from this analysis. The first mainly consists of accessions from the SW, YH, and TW groups. The second cluster consists of XR wheat accessions. Within the first cluster, the SW and YH wheat accessions had a tendency to group together on the basis of common geographical origins. On the other hand, most of the TW accessions were distributed within this first cluster,

**Table 1** The level of DNA polymorphisms analyzed with 63 probes for the Chinese landrace groups of *T. aestivum*

Landrace group	SW	YH	TW	XR
No. of accessions	13	10	7	8
No. of total bands	344	332	342	348
No. of group-specific bands	9	0	4	9
Proportion of monomorphic bands	0.84	0.90	0.84	0.85
Mean PIC index	0.15	0.11	0.18	0.18
Mean GS within a group	0.972	0.978	0.960	0.969



**Fig. 3** Dendrogram resulting from cluster analysis of the RFLP-based genetic similarity matrix among 39 accessions of Chinese *T. aestivum* (Note: \*CS – Chinese Spring)

indicating that this group is more diverse than either the SW or YH wheat groups.

The XR wheat accessions were closely related to each other (mean GS within a group = 0.969), but distantly related to accessions from the other three Chinese landrace groups (mean GS between XR wheat and other three Chinese wheat landraces = 0.937).

#### Comparisons between landraces of Chinese *T. aestivum* and Southwest Asian *T. aestivum*

The thirty probes employed in the Chinese *T. aestivum* analysis were also used with 55 accessions of landraces from Southwest Asia (Table 2). Genomic diversity

**Table 2** Comparisons of RFLP characteristics using 30 probes for the Southwest Asian landraces and the Chinese landrace groups of *T. aestivum*

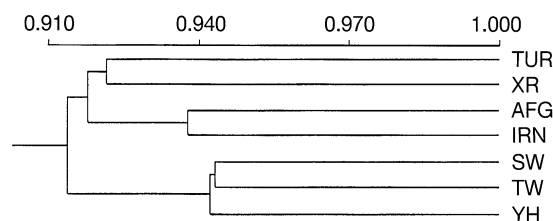
Landrace group	AFG	IRN	TUR	SW	YH	TW	XR
No. of accessions	19	20	16	13	10	7	8
No. of total bands	186	184	191	172	168	174	176
No. of group-specific bands	5	0	7	3	0	0	3
Proportion of monomorphic bands	0.67	0.67	0.62	0.78	0.83	0.77	0.80
Mean PIC index	0.25	0.29	0.38	0.23	0.18	0.26	0.26
Mean GS within a group	0.944	0.941	0.925	0.959	0.964	0.940	0.959

as measured by the proportion of monomorphic probes, mean PIC values, mean within-group GS, or the number of group-specific bands was generally, but not dramatically, higher in the Southwest Asian landrace groups (Table 2). The mean GS among all Chinese accessions of *T. aestivum* was 0.938 compared with values of 0.944, 0.941 and 0.925 for accessions from Afghanistan, Iran and Turkey, respectively.

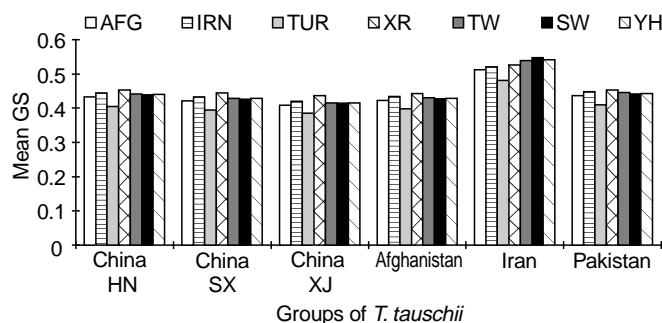
A dendrogram (data not shown, co-phenetic correlation = 0.72) based on the GS matrix of all 93 landraces of *T. aestivum* using the 30-probe set showed that accessions of the TUR, IRN, and AFG groups fell into three relatively distinct clusters according to the country of origin. These three clusters were distinct from the Chinese wheat clusters. A dendrogram (Fig. 4) based on a matrix of the mean GS between pairs of the seven landrace groups shows that the SW, YH and TW wheat groups are distinct from the TUR, IRN, and AFG wheat groups. This clustering was based on both the mutual similarities among groups and on the basis of their distinctiveness from the other four landrace groups, including the XR wheat group. The same trend of inter-group relationships was observed when dendrograms were based on Nei's genetic distance (Nei 1972) calculated using either band frequencies or banding-pattern frequencies (data not shown).

Genetic similarities between *T. tauschii* accessions and *T. aestivum* landraces

RFLP-based GS estimates revealed that there was no special relationships between the *T. tauschii* and *T. aestivum* accessions from China (Fig. 5). The Chinese landraces had a higher mean GS (=0.472) with the Southwest Asian *T. tauschii*, particularly with accessions from Iran (mean GS = 0.539), rather than with the Chinese *T. tauschii* (mean GS = 0.432). The other landraces from Southwest Asia also showed similar patterns of close relationships with *T. tauschii* from Iran (Fig. 5). The TUR wheat group exhibiting the greatest genetic diversity among landrace groups in our study had a relatively low mean GS with *T. tauschii* of different origins (Fig. 5).



**Fig. 4** Dendrogram resulting from cluster analysis of the RFLP-based mean genetic similarity estimates among 7 landrace groups of *T. aestivum*



**Fig. 5** Mean GS estimates between accessions in each of the *T. tauschii* groups and the seven landrace groups of *T. aestivum*

## Discussion

### Chinese *T. tauschii*

The Chinese accessions of *T. tauschii* appear to represent the far eastern end of a geographical gradient of declining diversity and uniqueness relative to the Iranian center of diversity. Lubbers et al. (1991) also showed that accessions from Iran showed greater variation than collections from other regions. The five accessions from Afghanistan and Pakistan clustered with the Chinese accessions in the dendrogram (Fig. 2). This grouping was also evident in the analysis of rDNA banding patterns conducted by Lagudah et al. (1991). They reported that there was a single rDNA banding pattern among accessions of *T. tauschii* from Afghanistan, Pakistan and China after surveying length variation of the rDNA spacer region at the *Nor* locus.

The trend of an eastward decline of genomic diversity in *T. tauschii* from the geographical center of origin, and the close genetic relatedness with adjacent gene pools, indicates that Chinese *T. tauschii* may originate from the Caspian Sea region following the “founder effect” model (Mayr 1942). According to this model, the development of populations at new habitats is initiated by a small number of individuals (i.e. founders) from the source population. New populations formed in this manner exhibit only a portion of the total genetic variation of their source populations.

Yen et al. (1983) concluded from isozyme analysis that *T. tauschii*, growing as a weedrace in the habitat of the Yellow River region, originated from the natural vegetation of *T. tauschii* in Xinjiang. The results reported here are not inconsistent with this hypothesis, since the HN and SX accessions were generally more related to the single XJ accession than to accessions originating elsewhere.

#### Chinese landraces of *T. aestivum*

Relationships among the Chinese landraces studied here are comparable to previous taxonomic classifications based on morphological traits, chromosome-pairing behavior and eco-geographical origins. In the GS-based cluster analysis, the XR wheat group was distinct from the other three Chinese landrace groups.

Due to its semi-wild form, the TW group has been important for studies of the origin and evolution of Chinese common wheat (Shao et al. 1983; Chen et al. 1988; Yen et al. 1988; Tsunewaki et al. 1990; Yang et al. 1992). This group, with fragile spikes and tough glumes, has been presumed to be the ancestor for the SW and YH wheat groups based on their geographical distribution, morphological similarities, highly conserved genetic make-up, and high crossability with rye (Chen et al. 1988; Yen et al. 1988; Yang et al. 1992). Our results from RFLP analysis revealed that the TW group was genetically close to, but more diverse than, both the SW and YH wheat groups.

Variation within the individual Chinese landrace groups was only slightly lower than that observed in the landrace groups from Turkey, Afghanistan, and Iran. The non-Chinese landrace accessions are classified into groups on the basis of country of origin. On the other hand, the Chinese accessions are classified both on the basis of geographical origin and of morphology. It is reasonable to expect that a geography/morphology based classification scheme would lead to less within-group variation than one based solely on geography, unless there is more variation inherent in the former system. This suggests that the intrinsic diversity among Chinese landraces is actually higher than that for non-Chinese landraces, at least for the accessions studied here. In fact, when considered as a single Chinese landrace group, the mean GS among

pairs of Chinese accessions is lower than that for both Afghanistan and Iran, and slightly higher than that for Turkey.

Since the first discovery of *T. tauschii* in China in 1955, this taxon has been suggested as a D-genome donor to XR wheat and other Chinese landraces, presuming that these hexaploid landrace wheat groups originate from China (Yen et al. 1983). A sterile F<sub>1</sub> of Polish tetraploid wheat (*T. polonicum* from Xinjiang) and *T. tauschii* collected in Xinjiang resembled very much the XR wheat in terms of spike morphology (M. C. Luo, personal communication). In spite of some cytogenetic studies of these Chinese materials, none of them has presented a completely convincing case for independent hexaploidization in China.

We did not define the D-genome alleles in the hexaploid landraces in our study. Nonetheless, on the basis of the genetic similarity estimates from RFLPs, we noted that the Chinese landraces of *T. aestivum* were more closely related to the Iranian accessions of *T. tauschii* than to the Chinese accessions. About 49% of all scored bands in the Chinese landraces of *T. aestivum* were shared with the Southwest Asian accessions of *T. tauschii*, which was higher than the proportion (38%) with Chinese *T. tauschii*. The bands unique to the Southwest Asian *T. tauschii* were also present in the Chinese landraces. This indicates that these Chinese landraces do not represent a separate AB × D hybridization event, thus suggesting a possible monophyletic origin for *T. aestivum*. However, we cannot eliminate the contribution of Chinese *T. tauschii* to these Chinese landraces. In our studies, one band unique to the SX and XJ of Chinese *T. tauschii* was found in the XR wheat group only.

An interesting outcome of the work reported here concerns the origin of the cultivar ‘Chinese Spring’ which has been extensively used in cytogenetic and other studies of wheat. Yen et al. (1988) proposed that ‘Chinese Spring’ was a close relative of the Chinese cultivar ‘Chengdu-guang-tou’ (AS 489), which was also a member of the SW wheat group. On the basis of the RFLP-GS values reported here, ‘Chinese Spring’ was most highly related to ‘Chengdu-guang-tou’ and its derivative, ‘S-1’ (AS 2228) (GS ≥ 0.99), thus providing further support to the proposal that ‘Chinese Spring’ is a derivative of that cultivar and is a member of the SW wheat group.

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