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Genetic diversity in Eastern U.S. soft winter wheat (*Triticum aestivum* L. em. Thell.) based on RFLPs and coefficients of parentage

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Abstract Genetic diversity in a set of 11 red and 11 white wheat lines from the Eastern U.S. soft wheat germplasm pool was measured using restriction fragment length polymorphism (RFLP) assay and coefficients of parentage (COP) analysis. On average, 78% of all bands revealed by three enzymes with 48 RFLP clones were monomorphic. Average pairwise genetic similarity (GS) was 0.97 when data from all enzymes were pooled. Probe Polymorphic Information Content (PIC) indexes ranged from 0 to 0.73 with a mean of 0.2. Fewer than 55% of the probes revealed any polymorphism. The frequency of polymorphism in the Eastern U.S. soft white winter (SWW) wheat gene pool was much lower than that observed in the Eastern U.S. soft red winter (SRW) wheat gene pool. SWW lines formed a single group on a dendrogram based on cluster analysis of RFLP-derived GS estimates, while SRW lines did not form a single group.

COP values for all pairs of the Eastern U.S. soft wheat lines ranged from 0.02 to 0.9 with a mean of 0.21. SWW wheat lines traced to 53 ancestral lines and had an average COP of 0.51. The SRW wheat gene pool had more complex parentages (mean COP = 0.15 and a total of 65 ancestral lines). COPs were correlated with RFLP-based GS for all line pairs ($r = 0.73$, $P < 0.01$). However, correlations between the two similarity measures were substantially lower when the SRW and SWW wheat gene pools were considered individually (r values of 0.23 and 0.28, respectively). The actual GS among unrelated lines in the U.S. Eastern soft wheat gene pool appears to be higher than that observed for unrelated landraces from Southwest Asia (0.96 vs. 0.905), suggesting that the ancestral landrace parents of this gene pool were themselves drawn from a base population where inbreeding, i.e., F, was greater than zero.

Key words Genetic diversity · RFLP · Coefficient of parentage · *Triticum aestivum* · Gene pool

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Introduction

Restriction fragment length polymorphisms (RFLPs) and coefficients of parentage (COP) are used as indirect measures of genetic diversity. Marked differences have been observed in RFLP diversity in different species and at different loci within species. Relatively high levels of polymorphism were reported in maize, rice, and *Brassica* species as compared to soybean and common wheat (Helentjaris et al. 1985; McCouch et al. 1988; Song et al. 1988; Liu et al. 1990; Keim et al. 1992). The common wheats have low levels of RFLP diversity (Chao et al. 1989; Kam-Morgan et al. 1989; Kim 1995; Liu et al. 1990). Siedler et al. (1994) reported that the average pairwise genetic distance estimates were 0.083 for European winter wheat lines and 0.108 for European spring wheat lines.

COP analysis has been applied in several crop species including soybean (Delannay et al. 1983), common wheat (Cox et al. 1986; Murphy et al. 1986), and oat (Souza and Sorrells 1989). This approach has been used to identify important parental lines and trends in genetic diversity over time and space. In common wheat, the U.S. red winter wheat germplasm was grouped into soft red winter (SRW) and hard red winter (HRW) gene pools on the basis of cluster analysis of COPs (Murphy et al. 1986). Cox et al. (1986) monitored the change of genetic diversity of these two gene pools by using COP and its weighted values based on the acreage data of cultivars in a given year. The genetic relatedness of the U.S. SRW wheat gene pool has not

changed remarkably in this century when measured by acreage-weighted COP (i.e., from 0.30 in 1919 to 0.22 in 1984). On the other hand, mean acreage-weighted COP within the HRW wheat gene pool has significantly declined from 1.0 to 0.4 in the same period, which was due primarily to a reduction in the importance of the plant introduction 'Turkey' (Cox et al. 1986).

The relationship between MM (molecular marker)- and COP-based measures of genetic diversity has varied depending on the crop species studied and on the germplasm materials sampled. A low correlation ($r = 0.27$) between seed storage protein (gliadin)-based genetic similarity (GS) and COP was found among pairs of U.S. HRW wheat (Cox et al. 1985). Similarly, poor rank correlation between RFLP-based GS and COP was reported in related winter type cultivars ($r = 0.21$) and in related spring type cultivars ($r = 0.42$) of European barley germplasms (Graner et al. 1994). On the other hand, Messmer et al. (1993) found a good association between RFLP-based GS and COP among related pairs of flint corn lines ($r = 0.71$) and among related pairs of dent corn lines ($r = 0.86$). These previous reports postulated that the association of two different estimates of genetic diversity might be influenced by the level of selection and genetic drift, the type of molecular marker loci sampled in the genome, and the level of genetic identity among unrelated pairs of lines (i.e., the proportion of alleles alike *in state* but not *by descent* since the base populations).

Plant breeders working toward cultivar release need to know the RFLP and COP characteristics of their primary gene pools before they can determine the appropriate role of these analyses in breeding decisions. In this report, we present results of RFLP and COP characterization of 22 wheat lines representing the Eastern U.S. soft white winter wheat and the Eastern U.S. soft red winter wheat gene pools.

Materials and methods

Germplasm

Twenty-two lines of Eastern U.S. wheat were grouped into two subsets (SWW and SRW) on the basis of their breeding history. To a great extent, this classification system also grouped lines on the basis of grain color. Most SWW lines were developed from the breeding programs of New York ('Genesee' and 'Geneva') and Michigan ('Augusta', 'Chelsea', 'Frankenmuth', 'Hillsdale', 'Ionia', 'C4828', 'C5088', and 'C5107') in the U.S. and Ontario ('Harus') in Canada, which are also the main growing regions of this gene pool. Lines of this gene pool are generally characterized by late maturity and large grains. 'Hillsdale', a soft red winter wheat line released by Michigan State University, was classified as a SWW wheat based on its pedigree. The other lines assigned to the SRW gene pool originated from Indiana ('Adder', 'Caldwell', and 'Clark'), Ohio ('Becker', 'Cardinal', and 'Dynasty'), and Wisconsin ('Charmany'). Seed company-developed SRW cultivars, 'P2548', 'P2550', 'P2555', and 'Twain', were included in this experiment. Compared to the SWW gene pool, lines in this pool are generally earlier in maturing and have smaller kernels.

Southern blot analysis

Southern blots were prepared with DNA extracted by a modified CTAB procedure (Saghai-Maroof et al. 1984), which was subsequently cleaved with one of three restriction enzymes (*Bam*HI, *Eco*RV, and *Hin*dIII, Boehringer Mannheim). For RFLP analysis, 48 low-copy, polymerase chain reaction (PCR) amplified and [^{32}P]-labeled DNA clones provided by Dr. M.E. Sorrells at Cornell University were used. These probes included 34 clones from genomic DNA (WG) of 'Chinese Spring', 12 from cDNA of barley (BCD), and 2 from oat cDNA (CDO) (Table 1). The references of these clones can be obtained from GrainGenes database, the Triticeae Genome Gopher. Thirty clones were selected from them and used as probes with *Hin*dIII for the development of RFLPs among 55 landrace wheats collected from Afghanistan, Iran, and Turkey (Table 1).

COP analysis

Pedigrees were obtained from several data sources: release notices, documents of wheat genealogy (Zeven and Zeven-Hissink 1976), GrainGenes data base (the Triticeae Genome Gopher), and personal communication with wheat breeders. COPs were computed for all pairs of lines as follows (Kempthorne 1969)

$$COP_{A,B} = COP_{A,C\times D} = 1/2(COP_{A,C} + COP_{A,D}) \quad [1]$$

where COP between the A and B lines is equal to the average of COPs between A and the parental lines of B (C and D). Ancestral lines that are of unknown parentage are considered landraces. The COP between ancestral landraces was presumed to be zero. Other assumptions required for calculation of COP followed Cox et al. (1986).

Data collection and analysis

DNA bands on autoradiograms were visually scored as present or absent. The frequency of polymorphic probes in each gene pool was determined by the following formula:

$$N_P/N_T, \quad [2]$$

where N_P = the number of probes exhibiting any polymorphism among accessions of a gene pool, and N_T = the total number of probes. The number and frequency of band patterns per probe were determined and used for calculation of the Polymorphic Information Content (PIC) index (Anderson et al. 1993) for each gene pool:

$$PIC_i = 1 - \Sigma P_{ij}^2 \quad [3]$$

where P_{ij} is the frequency among the assayed lines of the jth pattern of clone i. Genetic similarity based on RFLP markers between two lines, x and y, was estimated using Nei and Li's computation (1979):

$$\text{Genetic similarity } (GS)_{xy} = 2\ N_{xy}/(N_x + N_y) \quad [4]$$

where N_x and N_y are the number of bands for each line, and N_{xy} the number of bands in common between the two lines. The SAHN cluster routine (Rohlf 1992) using the UPGMA (unweighted pair group method, arithmetic average) option was used to generate dendrograms based on either RFLP-based GS estimates or COPs.

The normalized Mantel statistic Z (Mantel 1967) was used to assess the significance of the relationships among the various similarity matrices.

Table 1 The list of 48 probes used in the Southern blot analysis. Number of bands, banding patterns, and polymorphic information content (PIC) index for separate and combined gene pools are listed. PIC values illustrated here are computed from *Hin*dIII-generated RFLP data of each gene pool using Eq. 3

Probe[a]	Number of patterns/probe			Number of bands/probe			PIC		
	SRW[b] + SWW[c]	SRW	SWW	SRW + SWW	SRW	SWW	SRW + SWW	SRW	SWW
BCD 1066	2	2	1	5	5	5	0.35	0.50	0.00
BCD 1069[d]	2	2	1	4	4	4	0.10	0.16	0.00
BCD 1086[d]	4	4	2	5	5	4	0.53	0.68	0.30
BCD 120[d]	3	3	1	6	6	2	0.17	0.31	0.00
BCD 1230[d]	1	1	1	4	4	4	0.00	0.00	0.00
BCD 1278[d]	1	1	1	4	4	4	0.00	0.00	0.00
BCD 21[d]	5	4	3	5	5	5	0.60	0.70	0.43
BCD 327[d]	1	1	1	5	5	5	0.00	0.00	0.00
BCD 348[d]	8	8	2	12	12	8	0.67	0.87	0.16
BCD 386[d]	3	3	3	4	4	4	0.43	0.43	0.43
BCD 442[d]	1	1	1	3	3	3	0.00	0.00	0.00
BCD 808	1	1	1	7	7	7	0.00	0.00	0.00
CDO 1396[d]	1	1	1	5	5	5	0.00	0.00	0.00
CDO 920[d]	1	1	1	7	7	7	0.00	0.00	0.00
WG 1026[d]	5	3	3	17	16	12	0.47	0.40	0.49
WG 1042[d]	4	4	1	7	7	6	0.59	0.70	0.00
WG 1044	3	3	2	9	9	9	0.39	0.53	0.18
WG 114[d]	2	2	1	4	4	3	0.10	0.16	0.00
WG 180[d]	1	1	1	8	8	8	0.00	0.00	0.00
WG 181[d]	1	1	1	5	5	5	0.00	0.00	0.00
WG 184[d]	1	1	1	7	7	7	0.00	0.00	0.00
WG 190[d]	6	6	3	12	12	10	0.73	0.80	0.34
WG 212	1	1	1	4	4	4	0.00	0.00	0.00
WG 241	1	1	1	5	5	5	0.00	0.00	0.00
WG 286[d]	2	2	2	4	4	4	0.48	0.39	0.50
WG 296	2	2	1	12	12	11	0.16	0.30	0.00
WG 341[d]	2	2	2	7	7	7	0.39	0.50	0.16
WG 363[d]	2	2	1	3	3	2	0.10	0.16	0.00
WG 401	1	1	1	11	11	11	0.00	0.00	0.00
WG 405	1	1	1	9	9	9	0.00	0.00	0.00
WG 419	1	1	1	4	4	4	0.00	0.00	0.00
WG 466	1	1	1	2	2	2	0.00	0.00	0.00
WG 514[d]	4	3	2	8	7	8	0.57	0.56	0.30
WG 522[d]	1	1	1	9	9	9	0.00	0.00	0.00
WG 530	1	1	1	8	8	8	0.00	0.00	0.00
WG 583[d]	3	3	1	3	3	2	0.17	0.31	0.00
WG 605	2	2	1	5	5	4	0.10	0.20	0.00
WG 645	6	5	2	13	13	11	0.59	0.77	0.16
WG 669	2	2	2	5	5	5	0.16	0.16	0.16
WG 686[d]	2	2	2	11	11	11	0.34	0.41	0.30
WG 710	1	1	1	7	7	7	0.00	0.00	0.00
WG 727	1	1	1	5	5	5	0.00	0.00	0.00
WG 750	1	1	1	3	3	3	0.00	0.00	0.00
WG 822[d]	4	3	3	6	6	6	0.54	0.65	0.31
WG 876	2	2	1	5	5	4	0.10	0.16	0.00
WG 9[d]	3	3	2	7	7	5	0.49	0.59	0.30
WG 909[d]	2	2	1	4	4	4	0.16	0.30	0.00
WG 933[d]	1	1	1	2	2	2	0.00	0.00	0.00

[a] Information on chromosomal locations of each clone can be referred from the Grain Genes, the Triticeae Genome Gopher
[b] SRW: the Eastern U.S. soft red winter wheat gene pool
[c] SWW: the Eastern U.S. soft white winter wheat gene pool
[d] Clones used as probes for the RFLP analysis of 55 landrace accessions collected from Afghanistan, Iran, and Turkey

Expected GS estimates were computed from COPs of all line pairs by the following formula (Messmer et al. 1993):

$$GS_{EXP\ for\ X,Y} = GS_0 + [(1 - GS_0) \times COP_{X,Y}] \quad [5]$$

where mean GS (GS_0) of unrelated lines (COP = 0) was estimated by computation of RFLP-based mean GS of 55 accessions of Southwest Asian landraces of *T. aestivum*. Those landraces were presumed to be unrelated to each other.

Results

Analysis of RFLP diversity

As expected for an allohexaploid, most probe DNA sequences hybridized to 3 or more distinct DNA fragments of different sizes when restricted with a given enzyme. *Hin*dIII generated a total of 307 bands for the 22 lines, while *Eco*RV and *Bam*HI produced 293 and 250 bands, respectively (Table 2). On average, 78% of all bands were monomorphic. *Hin*dIII revealed a higher frequency of RFLPs than the other two enzymes from the perspective of either the number of bands or the banding patterns per probe (Table 3). Fewer than 55% of the probes detected polymorphism for the entire germplasm using any enzyme (Table 3).

There were more bands scored for a given enzyme in the SRW gene pool than in the SWW (e.g., 305 vs. 280 bands for *Hin*dIII) (Table 2). More bands were unique to the SRW gene pool than in the SWW gene pool (Table 2). For instance, only 2 of the 307 bands in the case of *Hin*dIII-based RFLPs were not detected in the SRW gene pool. Generally, the frequency of polymorphic probes in the SRW gene pool was higher than that in the SWW gene pool (Table 3).

The level of heterogeneity of RFLP marker states within and between gene pools was estimated by the computation of PIC indexes. PIC values for each probe computed from *Hin*dIII-RFLP data are summarized for the two gene pools separately and combined in Table 1. The range of probe PIC indexes for the entire germplasm was 0–0.73 (mean = 0.20). The range of probe PIC for the SRW gene pool was 0–0.87 (mean = 0.24), which was greater than that (0–0.50) of the SWW gene pool (Table 1). This indicated that the SRW lines were more genetically diverse than the SWW lines in terms of the number and frequency of banding patterns per probe.

Table 4 contains the summary of a pairwise analysis of RFLPs for all lines. Within the SWW gene pool, the average relative frequency of polymorphic probe-enzyme combinations for a pair of lines was 8.5%. The frequency of polymorphism depended on which lines were considered. The SWW line pairs with 'C4828' were the most polymorphic with an average relative frequency of 14% of probe-enzyme combinations. The other SWW line pairs revealed polymorphism with fewer than 12% of probe-enzyme combinations. Within the SRW gene pool, however, on average 22.1% of probe-enzyme combinations detected polymorphism in a pair of lines. This frequency was relatively independent of which lines were considered.

RFLP-based GS estimates of 55 pairs of the SRW wheat lines (= 0.959) were less than the average GS estimate (= 0.988) of the SWW wheat lines (data not shown). The average GS estimate between the two gene pools was 0.966. A dendrogram derived from UPGMA clustering of RFLP-based GS revealed that the SWW lines grouped together distinct from the SRW lines (Fig. 1).

Patterns of line subgrouping based on estimated GS varied slightly depending on the restriction enzyme. Correlations among the three RFLP-based GS matrices (one for each enzyme) were relatively strong ($r \geqslant 0.72$) when both gene pools were considered

Table 2 Proportion of monomorphism and uniqueness among total bands revealed by 48 probes with different restriction enzymes in individual and combined gene pools of Eastern U.S. soft wheat

	Total no. of bands			Band monomorphism[b]			Number of unique bands	
	R + W[a]	SRW	SWW	R + W	SRW	SWW	SRW	SWW
*Hin*dIII	307	305	280	0.75	0.75	0.89	27	2
*Eco*RV	293	292	265	0.77	0.78	0.93	28	1
*Bam*HI	250	249	237	0.82	0.83	0.91	13	1

[a] R + W: SRW + SWW
[b] Band monomorphism = no. of monomorphic bands/total no. of bands

Table 3 Summary of average values of PIC, no. of banding patterns, and number of bands revealed by each probe with different restriction enzymes in individual and combined gene pools of Eastern U.S. soft wheat

	Frequency of polymorphic probes			Mean PIC			Mean no. of patterns/probe			Mean no. of bands/probe		
	R + W[a]	SRW	SWW	R + W	SRW	SWW	R + W	SRW	SWW	R + W	SRW	SWW
*Hin*dIII	0.54	0.54	0.31	0.20	0.24	0.09	2.23	2.10	1.42	6.4	6.4	5.8
*Eco*RV	0.40	0.40	0.23	0.15	0.19	0.07	2.08	1.96	1.25	6.1	6.1	5.5
*Bam*HI	0.35	0.35	0.25	0.15	0.16	0.08	1.75	1.67	1.31	5.2	5.2	4.9

[a] R + W: SRW + SWW

Table 4 Pairwise comparisons of RFLPs and mean genetic similarity estimates for the combined and separate gene pools. Number of total bands, number of polymorphic bands, and frequency of polymorphic probes generated by three different restriction enzymes and 48 probes were computed for all possible line pairs of each class, and then average values were calculated for pairs of lines

	SRW + SWW			SRW			SWW		
	H[a]	E[b]	B[c]	H	E	B	H	E	B
Mean no. of bands for a pair of lines	268	264	230	271	267	232	262	259	226
Mean no. of bands polymorphic for a pair of lines	19	15	11	24	22	14	8	5	5
Mean proportion of polymorphic bands for a pair of lines	0.07	0.06	0.05	0.09	0.08	0.06	0.03	0.02	0.02
Mean frequency of probes showing polymorphism for a pair of lines	0.21	0.15	0.16	0.27	0.21	0.19	0.10	0.07	0.09
Mean genetic similarity[d]	0.965	0.970	0.975	0.954	0.956	0.968	0.984	0.991	0.988

[a] H = Combination of 48 probes with *Hin*dIII
[b] E = Combination of 48 probes with *Eco*RV
[c] B = Combination of 48 probes with *Bam*HI
[d] Mean genetic similarity was estimated by Nei and Li's coefficient (1979)

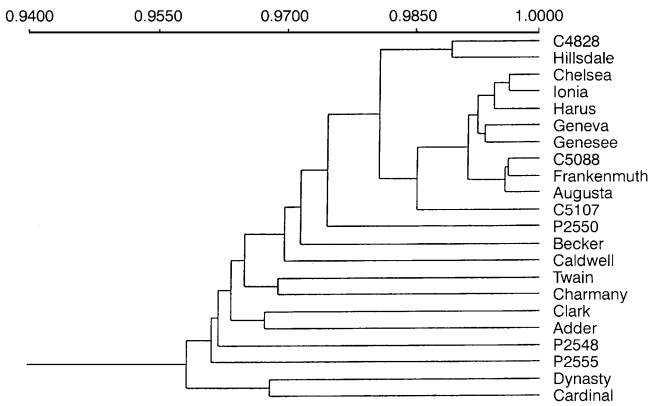

Fig. 1 Dendogram resulting from the cluster analysis of the RFLP-based Nei and Li's genetic similarity matrix among 22 Eastern U.S. soft wheat lines. GS matrix used for cluster analysis was constructed from RFLPs, which were generated from 48 probes and three restriction enzymes

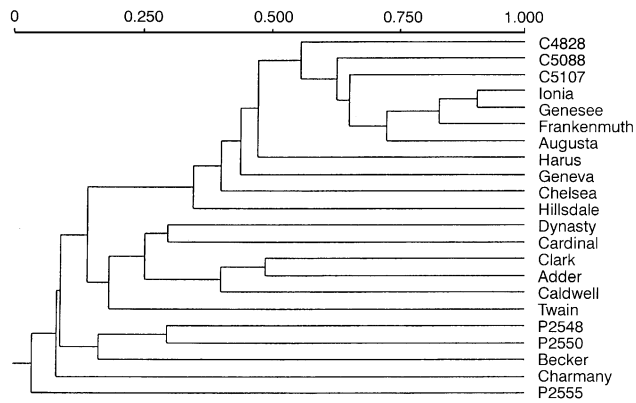

Fig. 2 Dendogram resulting from the cluster analysis of coefficients of parentage among 22 U.S. soft winter wheat lines

together (data not shown). However, *r* values between GS matrices for different enzymes for the SRW gene pool were relatively low compared to those for the SWW gene pool only (data not shown).

COP Analysis

COPs were calculated for 231 pairs of Eastern U.S. soft wheat lines (data not shown). There were 81 ancestral landrace lines for the 22 Eastern U.S. soft wheats. COP values ranged from 0.02 ('Hillsdale'-'P2555') to 0.90 ('Genesee'-'Ionia') with a mean of 0.21. Mean COP between members of the SWW and SRW gene pools was 0.11.

Mean COP within the SWW gene pool was 0.51 with a range from 0.25 for 'Chelsea'-'Hillsdale' to 0.90 for 'Genesee'-'Ionia'. 'Mediterranean' was the most important (mean COP with the SWW gene pool = 0.23) among the 53 ancestral lines for the SWW gene pool. Eleven SWW lines formed a subgroup in the COP-based dendrogram due to their high mutual level of coancestry (Fig. 2). Earlier released SWW-type lines (before 1980s) such as 'Genesee', 'Ionia', 'Frankenmuth', and 'Augusta' were more genetically related to each other than those that have recently been developed or released (Fig. 2).

The Eastern U.S. SRW gene pool had more complex parentages than the SWW gene pool. Mean COP within this pool was 0.15 and the range of COP values was from 0.03 ('Twain'-'P2555') to 0.49 ('Adder'-'Clark'). Sixty-five ancestral landrace lines were identified for this gene pool; 'Mediterranean' and 'Turkey Red (syn. 'Turkey')' were the most important with mean COPs of

0.17 and 0.08, respectively. In contrast to the SWW gene pool, the SRW-type lines did not form a simple subgroup in the COP-based dendrogram (Fig. 2). Nevertheless, grouping patterns of some related lines within this gene pool likely corresponded to their developmental origins. For example, 'Dynasty' and 'Cardinal' were from the Ohio Agricultural Experiment Station (AES), 'Clark', 'Adder', and 'Caldwell' from the Indiana AES, and 'P2548' and 'P2550' from Pioneer Hi-Bred International, Inc. (Fig. 2).

Relationship between RFLPs and COPs

The correlation between RFLP-based GS (using combined data from all three restriction enzymes) and COP was moderate ($r = 0.73$, $P < 0.01$) when all 231 pairs of Eastern U.S. soft winter wheat lines were considered. However, the associations between the two different parameters within the individual SRW and SWW gene pools were substantially lower (r value of 0.23 and 0.28, respectively). RFLP-based GS estimates are plotted against COP values in Fig. 3. Most pairs of lines within the SRW gene pool were distributed only on the left side of the plot along the COP axis. In contrast, line pairs within the SWW gene pool or between the SWW and SRW gene pools were distributed throughout the plot.

Expected GS estimates were calculated by using Eq. 5 and COP values. Mean RFLP-based GS for 55 unrelated landrace lines from Southwest Asia (COP = 0) was 0.905, which was used as an estimate of the proportion of alleles alike *in state* not *by descent* (GS_0). Expected GS values (GS_{EXP}) plotted against COPs were compared with the corresponding RFLP-based GS (GS_{OBS}) for a pair of lines (Fig. 3). Generally, GS_{EXP} was below the level of GS_{OBS} along the COPs and increasingly large differences between two parameters were observed as COP declined (Fig. 3).

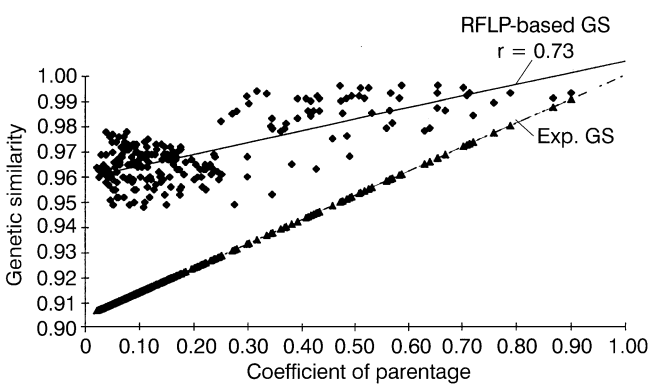

Fig. 3 The plot of RFLP-based genetic similarity (GS_{OBS}) and expected GS (GS_{EXP}) vs. coefficients of parentage for 231 pairs of the Eastern U.S. soft winter wheat lines

Discussion

Comparison of the genetic diversity of the Eastern U.S. SRW and SWW wheat gene pools

The level of DNA polymorphism was quite low in the Eastern U.S. soft winter wheat pools. Fewer than 10% of bands detected between 2 lines were polymorphic, irrespective of the gene pools and restriction enzymes. The majority of DNA clones were noninformative with low PIC values (Table 1). Some DNA clones with high PIC values based on one gene pool were not always informative for the other, such as BCD 1066, BCD 120 and WG 1042 (Table 1). This could be related to the homogeneity of key genome segments in either gene pool.

Limited variation in these pools is closely related with the narrow genetic background of this species, which might be due to only a few events of hexaploidization between *T. turgidum* and *T. tauschii*. Along with selection and genetic drift during cultivar development, breeding strategies using a limited range of elite parents also seemed to contribute to a decline of genetic diversity.

The Eastern U.S. SWW gene pool has been developed from a narrow genetic background, as revealed in the coefficient of parentage analysis. A relatively small number of varieties that dominated cultivated areas in the late 1940s to the middle 1970s have been recurrently used as breeding parents for the development of the SWW gene pool (Patterson and Allan 1981). Mean COPs of the SWW gene pool analyzed here with these predominant varieties are 0.49 ('Yorkwin'), 0.24 ('Cornell 595'), 0.67 ('Genesee'), and 0.58 ('Yorkstar'). Mean COP of 'Genesee', one of the SWW lines surveyed in this study and quite a good source of yield potential in the 1950s, was much higher with the other SWW lines than with the 11 SRW type lines (= 0.13).

The predominance of a few elite lines as breeding parents is also common in the development of the Eastern U.S. SRW gene pool. However, the results presented here confirm the conclusion of Patterson and Allan (1981) that the genetic base of the SRW gene pool is broader than that of the SWW gene pool on the pedigree basis. The higher number of unique RFLP bands and banding patterns detected in the SRW gene pool were consistent with the relatively greater pedigree-based genetic diversity estimates.

Relationship between marker-based GS and COP as measures of genetic diversity

There was a significant correlation of two different measures of genetic relationships for all pairs of the Eastern U.S. soft winter wheat lines. However, genetic

relationships revealed by the two diversity measures were not always consistent, as revealed from their poor correlation when an individual gene pool was considered. Consequently, the relationship between RFLP-based GS and COPs might be biased due to sampling effects.

Nei and Li's GS based on RFLP banding patterns is not always satisfactorily reliable as a measure of genetic distance between individuals. Its calculation may be affected by cryptic allelism such as null allelles of RFLP loci. When multiple polymorphic codominant loci are present, as is probably the case in this study, GS would be biased to underestimate its true value.

As reviewed in other reports (Cox et al. 1985; Graner et al. 1994; Messmer et al. 1993), impractical assumptions required for the computation of COPs may also be a source of the poor relationship between the two diversity measures. For example, alleles are not always transmitted equally from female and male parents to progeny. Also, breeding parents are not always completely homozygous and homogeneous.

Moreover, the base populations of unrelated ancestral lines may vary in the amounts of alleles alike *in state*, so that COPs underestimate the true GS. In fact, the calculated GS_0 from the Southwest Asian landrace population is 0.905, while the GS_0 of the 231 pairs of the Eastern U.S. soft winter wheat lines, as estimated by the regression of RFLP-based GS_{OBS} on COPs, is approximately 0.96 (Fig. 3). This suggests that the true GS_0 of the base population of ancestral parents is probably high for the Eastern U.S. soft winter wheat germplasm pool. As Cox et al. (1985) and Graner et al. (1994) postulated, poor relationships between the two measures may result partially from high levels of GS between unrelated lines. Our results also revealed that the 231 genotype pairs distributed with a short range of the RFLP-based GS as compared to that of the COPs in the plot (Fig. 3).

The unknown effects of selection and genetic drift on the allelic frequency changes during inbred development may reduce the reliability of COPs as measures of genetic relationship. For example, the transmission of alleles, especially those controlling qualitative traits with high heritability, is clearly influenced by intensive selection pressure in the breeding program, which results in a biased contribution from one parent with favorable alleles to the progeny generation (Cox et al. 1985; Souza and Sorrells 1989).

DNA marker/COP-assisted breeding strategies in common wheat

The expansion of the genetic base has been one of the major pursuits in the soft winter wheat breeding program since the genetic improvement of characters is dependent upon the amount of useful diversity. For this purpose, world germplasm collections may provide great promise as a reservoir of genetic variation in spite of their unknown genetic nature. Within the Eastern U.S. soft winter wheat pools, the near equivalence of the SRW wheat gene pool in performance along with its latent genetic diversity points to its utility as a tool in the expansion of the germplasm base of the SWW wheat gene pool. With the increasing availability of molecular maps, the use of DNA markers would assist the manipulation of genetic diversity by accessing the polymorphism on the basis of map information and characterizing genomic regions that differentiate between pools and entries. The pedigree-based sampling of genotypes in classical breeding schemes would also offer another potential for expanding the genetic bases of gene pools. Even though COPs cannot completely estimate genomic similarity between individuals, the approach using pedigree information is still effective to monitor the change in field diversity and to select parents for the development of breeding cycles.

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