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PLANT GENETIC RESOURCES

*Spring Wheat Diversity in Irrigated Areas of Two Developing Countries

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ABSTRACT

Crop genetic diversity may not be apparent from plant phenotypes. Coefficients of parentage were used to examine genetic diversity and compare trends in spring wheat cultivars grown in the Yaqui Valley of Mexico (1972-1991) and the Punjab of Pakistan (1978-1990). Coefficients of parentage estimate probabilities of retaining latent diversity rather than focusing on the apparent diversity of highly heritable traits (e.g., rust resistance alleles). A small trend towards increased genetic diversity was found in the Pakistani Punjab. In the Yaqui Valley, large oscillations in diversity occurred without significant trends. In comparing the two regions, the latent genetic diversity in the Yaqui Valley based on parentage and area of production in a given year (weighted diversity) was 20% less than in the Punjab. However, the lower diversity was partially offset by rapid turnover in germplasm in the Yaqui Valley. The rate of change in germplasm (temporal diversity) was 22% lower in the Pakistani Punjab than in the Yaqui Valley. The temporal diversity of cultivars used by growers in the Yaqui Valley was greater than among cultivars recommended for use by the research services, indicating that growers replace germplasm faster than the changes in recommended cultivars. The opposite was found in the Punjab. In the Yaqui Valley, individual cultivars dominated production for 1 to 3 yr, while in the Punjab, one cultivar, 'Yecora' dominated production for 7 yr. We conclude that (i) cultivar improvement programs did not erode genetic diversity in production areas currently growing improved cultivars and (ii) patterns of cultivar use by farmers were more important than the composition of recommended cultivars in determining genetic diversity.

LATENT GENETIC DIVERSITY of a crop influences disease vulnerability and stability across variable environmental stresses. By contrast, apparent diversity is manifest in the deployment of specific resistance genes with different virulence/avirulence reactions. Latent diversity is the underlying genomic variation that is not obvious until challenged by the appropriate biotic or abiotic stress. A narrow genetic base may increase a crop's latent vulnerability to disease and insect epidemics. Disease epidemics related to low latent diversity of crops include the Victoria blight (*Helminthosporium victoriae* Meehan and Murphy) of oats (*Avena* spp.) (Coffman, 1977) and the Southern corn leaf blight (*Helminthosporium maydis* Nisik. and Miyake) of maize (*Zea mays* L.) crops (Tatum, 1971). The absence of resistance in U.S. wheat (*Triticum* spp.) cultivars to Russian wheat aphid (*Diuraphis noxia* Mordv.) during the late 1980s (Smith et al., 1991a) is another example of low latent diversity resulting in economic loss.

To reduce risk to growers, breeders must develop genetically diverse cultivars. Because of production constraints, quality considerations, or refusal to change, growers often restrict the diversity of a crop by limiting the number of cultivars grown from the available set. Therefore, diverse cultivars which are acceptable to growers must be developed. Monitoring crop genetic diversity can provide insights into the effects of breeding programs and grower decisions. Genetic diversity of

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Abbreviations: CIMMYT, International Maize and Wheat Improvement Center; COD, coefficient of diversity; COP, Coefficient of Parentage; INIFAP, National Institute for Research on Agriculture, Livestock and Forestry; r, the value of a coefficient of parentage; d, a measure of diversity $= 1 - r$.

crops is monitored through examination of cultivar morphology (Souza and Sorrells, 1991a), molecular markers (Cox et al., 1985; Smith et al., 1991b; Souza and Sorrells, 1991b), reaction to disease/insect pests, and origin or parentage (Cox et al., 1985; Souza and Sorrells, 1989; Dilday, 1990; and Martin et al., 1991). Parentage analysis, the least expensive of these methods when extensive pedigree records are available, has produced measures correlated to estimates of diversity in marker genes (Cox et al., 1985; Souza and Sorrells, 1991c).

Coefficients of parentage (COP) summarize genealogical information from an array of cultivars. Originally developed by Wright (1922) and Malecot (1948), the COP for two cultivars estimates the expected percentage of alleles common by descent at loci polymorphic within a population. St. Martin (1982) adapted the COP analysis to inbred crops by assuming that each cultivar is completely inbred, that cultivars without common parentage are unrelated; and that parents contribute equally to the offspring despite inbreeding and selection. These assumptions and the validity of the methodology have been addressed by Cox. et al. (1985), Cowen and Frey (1987), Souza and Sorrells (1989), Cuevas-Perez et al. (1992), and Martin et al. (1991). Highly selected qualitative loci, such as those that control response to leaf rust (*Puccinia recondita* Rob. ex Desm. f. sp. *tritici*), would not follow the assumption of random transmission of a large number of alleles. Therefore, parentage analysis represents primarily the transmission of latent diversity, which is not obvious from the challenge by current disease/insect race complexes.

This study used the COP to evaluate the effect of breeding programs on the latent genetic diversity of bread wheat (*Triticum aestivum* L.) in areas of two developing countries: the Yaqui Valley of the State of Sonora, Mexico, and the Punjab Province of Pakistan. The Yaqui Valley and the Pakistani Punjab represent regions with different cultivar release and dissemination mechanisms (Brennan and Byerlee, 1991). Both regions are characterized by irrigated wheat production under semi-arid conditions with approximately 140 000 ha sown in the Yaqui Valley and 5.25 million hectares in the Pakistani Punjab (Brennan and Byerlee, 1991). In both regions, wheat is the predominant cool season crop in a double crop rotation with warm season crops. However, in the Yaqui Valley wheat is grown commercially on farms averaging about 30 ha, while in the Pakistani Punjab most farmers operate less than 5 ha, and about half of the wheat is consumed on the farm. The extension and seed supply systems for cultivar replacement are more developed in the Yaqui Valley. The two regions were early beneficiaries of the Green Revolution through the release of semidwarf cultivars in Mexico in the early 1960s and in the Pakistani Punjab beginning in 1966. A criticism of the Green Revolution is that genetic diversity was reduced by the release and widespread cultivation of a few genetically uniform cultivars (Wilkes, 1992).

This study measured the changes over time in the latent diversity of recommended cultivars and cultivars grown by farmers in the two study areas. The evidence presented is the first analysis of the status of genetic diversity in these Green Revolution areas.

MATERIALS AND METHODS

Cultivar Use and Pedigrees

Semi-dwarf bread wheat cultivars grown from harvest 1978 to 1990 in the Punjab of Pakistan (Table 1) and bread wheat cultivars used in the Yaqui Valley of the State of Sonora in Mexico from harvest 1972 to 1991 (Table 2) were included

Table 1. Cultivars grown in the Pakistani Punjab region, 1978 to 1990, with year of release and percent of bread wheat area grown.

Cultivar	Year of release	Year 1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
Mexipak	1966	37	16	9	5	4	2	1	1	1	1	<1	<1	<1
Chenab 70	1970	27	25	9	5	4	4	2	2	2	1	<1	<1	<1
Blue Silver	1970	0†	0	<1	1	2	2	3	3	4	4	5	7	7
SA-42	1971	0	0	0	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1
Sandal	1971	1	<1	3	3	4	6	5	4	3	2	2	1	1
Lyallpur 73	1973	1	1	4	7	9	10	11	12	11	10	7	6	5
Pari 73	1973	0	<1	1	<1	<1	1	1	1	1	1	<1	<1	<1
Yecora	1970	31	50	64	67	61	50	35	20	12	8	4	3	2
Nuri	1970	2	<1	2	1	1	<1	<1	1	<1	<1	<1	<1	<1
SA-75	1975	<1	2	3	2	1	1	<1	<1	<1	0	<1	<1	<1
Lu-26	1976	0	0	<1	<1	1	1	2	2	1	1	1	1	1
HD-2009	1976	0	0	<1	<1	<1								
Pavon	1976	0	4	3	3	4	5	5	5	4	4	3	2	2
Sonalika	1977		<1	1	2	4	7	9	10	11	9	7	6	5
WL-711	1978		0	<1	<1	3	8	13	17	18	20	18	16	11
Chenab 79	1979			0										
Bahawalapur	1979		0	0	0	0	1	2	2	2	2	2	2	2
Punjab 81	1981					0	<1	4	11	15	16	16	16	14
Pakistan 81 (Pak 81)	1981					0	0	<1	5	10	18	29	35	43
Faisalabad 83	1983								0	0	0	<1	<1	1
Barani 83	1983							0	0	0	0	0	0	0
Kohinoor	1983											<1	<1	<1
Faisalabad 85	1985										0	0	<1	<1
Punjab 85	1985										0	0	0	<1
Pirsabak 85	1985										0	0	0	0
Other	–	<1	<1	<1	0	0	0	0	0	0	0	1	1	1

† Underlined values indicate cultivars recommended by research services.

in this study. Durum wheats (*Triticum turgidum* var. *durum* L.), important in some years in the Yaqui Valley, were not included. Tall stature wheats of Pakistan, which accounted for from 31% (1978) to 4% (1990) of production, were excluded because they are generally grown outside of the irrigated areas. The area proportion of cultivars grown in each year were obtained from regional crop reporting systems. Pedigrees were determined from Villareal and Rajaram (1988), Anonymous (1990), Zeven and Zeven-Hissink (1976) and Kephart (1993), and CIMMYT records. The pedigree of each cultivar was traced back to its *ancestral parents* (Souza and Sorrells, 1989), that is any parent which does not itself directly have a known or obvious parent such as landraces, local cultivars, or cultivars of unknown origin. Relationships among ancestral parents were not determined; they were assumed to be equally unrelated ($r = 0$).

Calculation of Coefficients of Parentage

St. Martin (1982) defined an algorithm for calculating COP (r) for inbred species: each cultivar is equal to itself and has an identity with itself of $r = 1$; each pair of cultivars without common parentage has an identity of $r = 0$; and each parent contributes equally to the progeny. Therefore, for unrelated parents, the relationship between parent and offspring is $r = 0.5$. When a pureline cultivar is extracted as a reselection from a parent, rather than selected from a cross, the relationship between parent and pureline reselection is arbitrarily set at $r = 0.75$. Methods employed by St. Martin (1982) were modified for this study to reflect the relative number of chromosomes or chromosome fragments likely to be contributed by each parent in interspecific crosses. When a durum wheat was used as a parent in a cross with bread wheat, equal contribution between parents was not assumed and the COP between the durum ($4x$) parent and the offspring was $r = 0.4$, and between the bread wheat ($6x$) parent and offspring was $r = 0.6$. When rye (*Secale cereale* L.) or another diploid cereal with a non-homeologous genome was used as a parent, it was assumed that half of a chromosome arm of the genome was transferred to the bread wheat offspring. The relationship between the diploid parent and the offspring was defined as $r = 1/84$ (0.012) and the relationship between the bread wheat parent and the offspring was $r = 83/84$ (0.988).

A single matrix (**R**) of all cultivars was calculated with the spreadsheet software EXCEL (Microsoft Corp., Redmond, WA) as described by Souza and Sorrells (1989). The relation-

Table 2. Cultivars grown in the Yaqui Valley of Mexico, 1972 to 1991, with year of release and the percent of bread wheat area grown.

Cultivar	Year of release	Year																			
		1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991
Mayo 48	1948		<1																		
Yaqui 50	1950				<1																
Kenya 52	1952			<1																	
Nainari	1960				<1																
Lerma Rojo 64	1964		<1																		
INIA 66	1966	55	<1	<1	<1						3	<1									
Siete Cerros	1966	32	9	7	<1					<1											
Super X	1966	7	2	1																	
Tobari	1966		<1	<1																	
Ciano 67	1967	2																			
Nuri	1970		2†	<1	<1	<1															
Potam	1970		<1	<1	<1	<1															
Saric	1970		3	4	3	<1															
Yecora	1970		30	55	33	3	<1	<1		<1											
Cajeme	1971	0	50	30	14	2					<1										
Tanori	1971	0	4	2	13	5	1														
Vicam	1971	0	0	<1	2	0															
Jupateco	1973			<1	30	64	75														
Torim	1973			0	3	26	19	14	8	5	5	2	1	3	0	0	0	0			
Anahuac	1975						<1	27	13	<1											
Cocoraque	1975					0	<1	31	2	2	<1	<1									
Zaragoza	1975					0	3														
Nacozari	1976						0	9	30	58	68	<1	<1								
Pavon	1976						0	18	36	19	8	1	<1	0	0						
Pima	1976							1	3	9	15	3	<1	<1	0						
Tesapaco	1976						0	1	0	2	1	<1									
Hermosillo	1977								5	5	<1	<1									
Ciano 79	1979									0	6	66	74	9	2	3	3	2	3	3	1
Imuris	1979									<1	2	13	10	1	<1	<1					
Tesia	1979									0	6	13	7	<1	0						
Genaro	1981											<1	4	46	44	17	16	4	<1		
Glennson	1981												2	20	23	21	11	<1			
Sonoita	1981												1	3	4	7	15	11	8	8	1
Tonichi	1981												<1	5	4	8	14	17	9	8	<1
Ures	1981												<1	7	6	7	15	5	4	4	0
Seri	1982												0	2	18	38	24	<1	<1		0
Opata	1985																3	60	60	60	24
Oasis	1986																	<1	11	11	20
Curcurpe	1986																	<1	3	3	8
Papago	1986																	<1	3	3	11
Esmeralda	1988																				<1
Cumpas	1988																			0	2
Bacanora	1988																			0	32
Rayon	1989																				0
Tepoca	1989																				0
Other		3	0	<1	<1	0	<1	0	2	<1	<1	1	<1	3	<1	<1	<1	0	<1	1	0

† Underlined values indicate cultivars recommended by research services.

ships among the cultivars grown in each region were summarized in dendrograms derived from cluster analysis which used the COP values in the **R** matrix as the similarity measure (Fig. 1 and 2). Ward's incremental sums of squares fusion strategy (SAS, 1985) was used to cluster cultivars within each region.

Summary of Diversity within Years

The *average diversity* is the average value of the COP among all cultivars (including the COP of a cultivar with itself) grown within each year and region subtracted from 1. This converts the COP value to a diversity measure using the formula $d_a = 1 - \mathbf{G}_i\mathbf{R}\mathbf{G}'_i$, where $\mathbf{G}_i$ is a row vector of weighting values, $\mathbf{G}'_i$ is its transpose and R is the matrix r values. Any cultivar grown on at least 0.1% of region's bread wheat area in year i received a weight in vector G of n^{-1} (n = number of cultivars grown on greater than 0.1% of area) and other cultivars received a weight of 0.

The *weighted diversity* value, weighted by the percent of the wheat area of each region sown to a cultivar, was estimated by the following formula: $d_w = 1 - \mathbf{A}_i\mathbf{R}\mathbf{A}'_i$ where the vector of weights $\mathbf{A}_i$ contained the area (expressed as a proportion of total bread wheat area) sown to each cultivar in the ith year (Cox et al., 1986).

The *recommended diversity* was estimated from the average COP among cultivars recommended by the local research systems (Mexico: INIFAP, Pakistan: National Coordinated Wheat Program of the Pakistan Agriculture Research) for each cropping year. The formula for recommended diversity is $d_r = 1 - \mathbf{E}_i\mathbf{R}\mathbf{E}'_i$ where $\mathbf{E}_i$ is a vector of research recommendations, where recommended cultivars have a weight of m^{-1} (m = number of cultivars recommended) and non-recommended cultivars are weighted 0. As a measure of the utilization of the possible diversity, the *reserve diversity* was estimated as $d_{rw} = d_r - d_w$.

A coefficient of diversity (COD) was calculated to estimate the degree to which a single cultivar and related germplasm dominated each region. Each COP in the vector of products from $\mathbf{A}_i\mathbf{R}$ was subtracted from 1 to form a vector of COD values, one element for each cultivar (where $\mathbf{A}_i$ and $\mathbf{R}$ are the same as in the weighted diversity estimate). The higher the COD value the greater the diversity within the cropping system. The cultivar with the lowest COD was the dominant cultivar or germplasm base for that region/year and was used to represent the regional diversity that year.

Measurement of Temporal Diversity

The change in the composition of a region's germplasm was summarized by *temporal diversity* measures (Cox et al., 1986). These were estimated by comparing the parental diversity between cultivars grown or recommended at the start and end of 5-yr periods. The formula $d_{at} = 1 - \mathbf{G}_i\mathbf{R}\mathbf{G}'_{i+4}$ estimates *average temporal diversity* where $\mathbf{G}_i$ and $\mathbf{R}$ are the same as used to calculate average diversity. The $\mathbf{G}'_{i+4}$ is the transpose of the G vector of the growing year, 4 yr after the year i. The weighted diversity and recommended diversity were each recalculated as the summation of the matrix products, using $i + 4$ rather than i, for the transpose of the weighting vector. Revised formulas also estimated *weighted temporal diversity* ($d_{wt} = 1 - \mathbf{A}_i\mathbf{R}\mathbf{A}'_{i+4}$) of all cultivars grown weighted by area of production and the *recommended temporal diversity* ($d_{rt} = 1 - \mathbf{E}_i\mathbf{R}\mathbf{E}'_{i+4}$) of cultivars recommended to growers.

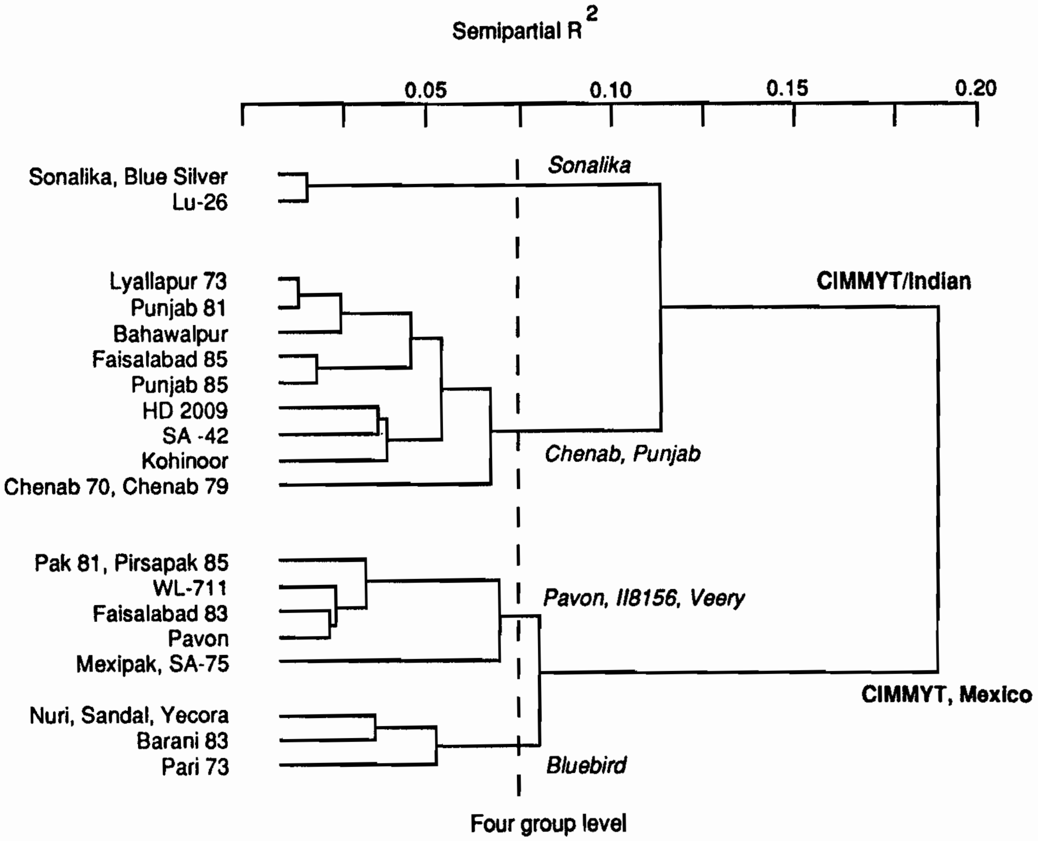

Fig. 1. Diversity of cultivars grown in the Pakistani Punjab from 1978 to 1990 based on cluster analysis of the parentage matrix.

Comparison of Similarity Measures

Linear regression trend lines were used to quantify changes over time for each diversity measure. *T*-tests were used to compare the across-years means of diversity measures. The standard errors of the across-year means were calculated from the variance of within-year means of each diversity measure within each region.

RESULTS

Diversity within the Pakistani Punjab, 1978-1990

Fourteen hexaploid spring wheat cultivars were released from 1978 to 1990 (1.2 cultivars per year). Two groups of cultivars were grown during the time period: (i) those predominantly of CIMMYT, Mexico parentage, and (ii) those of combined parentage from cultivars largely of CIMMYT and Indian subcontinent origins (Fig. 1). The lines of the CIMMYT group were clustered into 'Bluebird' sib-cultivars and a group highly related to 'I18156'. Within the CIMMYT/Indian group, the sister lines 'Blue Silver' and 'Sonalika,' together with 'LU26', a Sonalika derivative, were distinct from the main "Chenab/Punjab" group at an arbitrary four-group level.

Yecora was the dominant cultivar in Punjab from 1979 to 1984 (Table 1, Fig. 3a). Yecora and related wheats reached peak use in 1981, the only time the COD value dropped below 0.5. This indicated that Yecora and closely related cultivars accounted for greater than 50% of the germplasm utilized by growers in 1981. The average diversity values within years ranged from a low of 0.61 in 1978 to 0.78 in 1990 (Fig. 4a). The weighted diversity values show a trend towards greater use from 1981 to 1986 of diversite germplasm by growers and little change since 1987 (average trend 0.01 r yr^{-1}, $p < 0.01$, Table 3). The diversity among recommended cultivars shows no trend during this time period, remaining close to the average value of 0.74. The increase in d_w was not due, therefore, to broadening the genetic base of recommended cultivars but rather to (i) partial grower acceptance of new cultivars to replace Mexipak and Bluebird sisters ('Pari 73', 'Yecora', and 'Nuri') that dominated the production in the late 1970s and early 1980s, and (ii) retention by some growers of

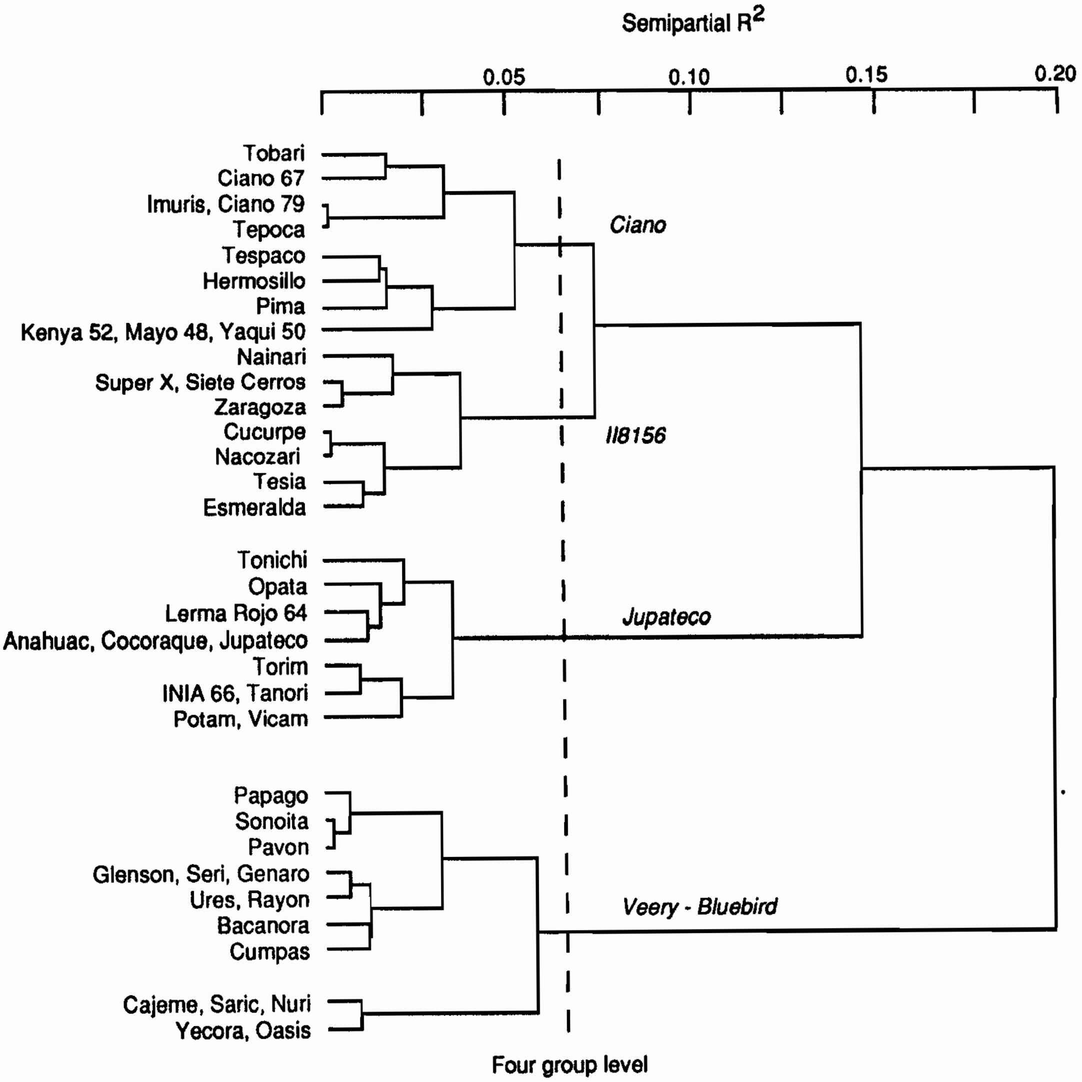

Fig. 2. Diversity of cultivars grown in the Yaqui Valley of Mexico from 1972 to 1991 based on cluster analysis of the parentage matrix.

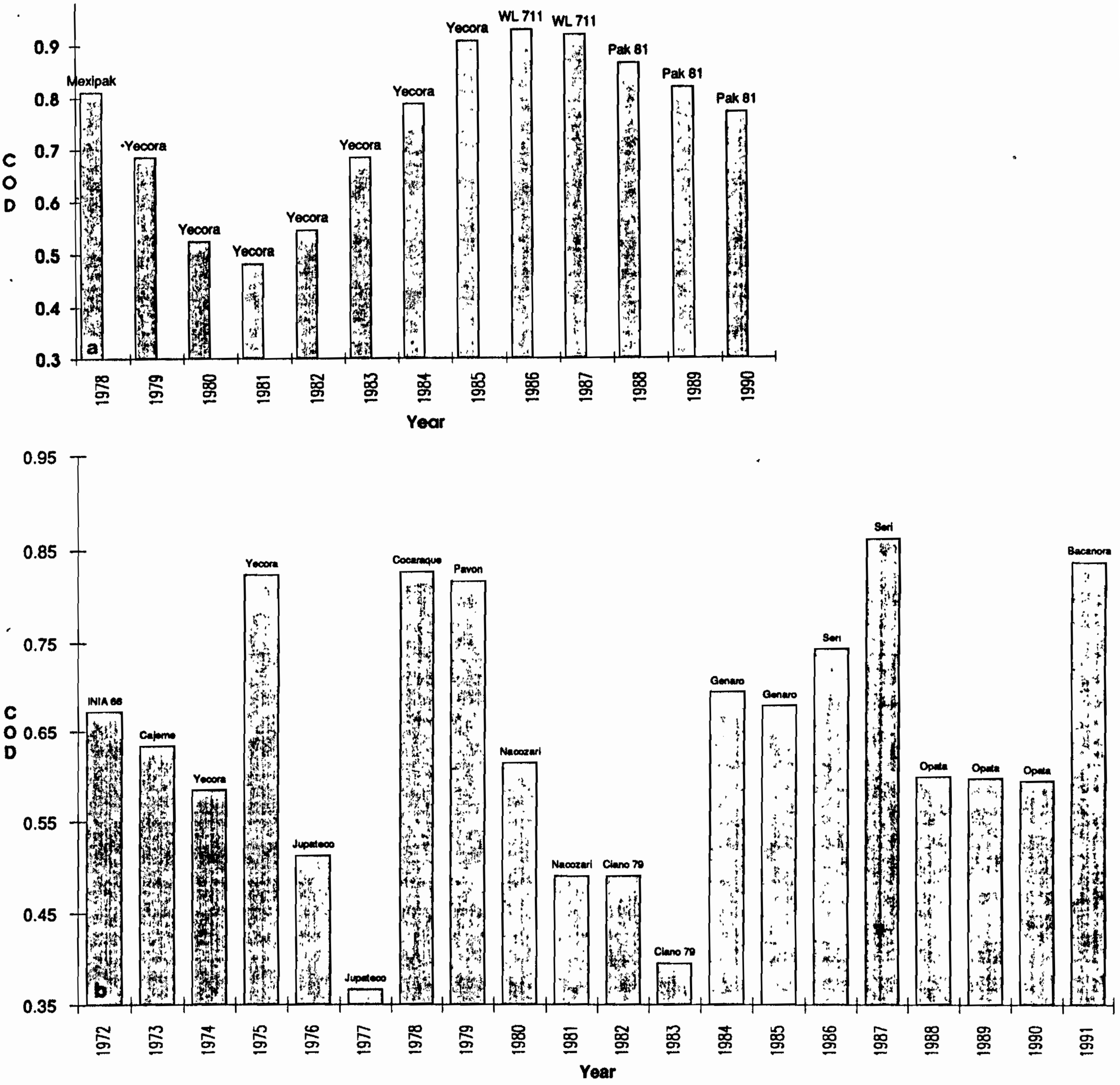

Fig. 3. Coefficients of diversity and dominant cultivar for a) the Pakistani Punjab, 1978 to 1990, and b) the Yaqui Valley of Mexico, 1972 to 1991.

older cultivars after being dropped from the recommended list. At the end of the period, nearly all of the cultivars grown still retained some portion of the production area (20 of 25 cultivars with greater than 0.1% of production area), indicating a slow turnover of germplasm in the Pakistani Punjab.

Average temporal diversity and recommended temporal diversity averaged across years were approximately the value of half-sibs (d_{at} and d_{rt} = 0.75; Table 3). The change in germplasm use by growers (d_{wt}) was slower than the change in recommended germplasm (d_{wt} = 0.64 vs. d_{rt} = 0.75, t-test $p < 0.01$, Table 3). The trend during this period was towards an increased rate of change in germplasm by growers (0.02 r yr^{-1}, $p < 0.01$; Table 3). The lowest d_{wt} values occurred in the period of 1979 to 1983 and the greatest was for the period 1983 to 1987 (Fig. 5a). A severe leaf rust epidemic in 1978 forced the transition from Mexipak (susceptible) to Yecora (resistant). The apparent diversity in leaf rust resistance did not confer latent diversity in the germplasm; during this time period temporal diversity remained relatively low. The rapid turnover in germplasm during the 1983 to 1987 period corresponded to the grower acceptance of 'Pak 81' (a Veery sib), derived from crossing of winter and spring wheats.

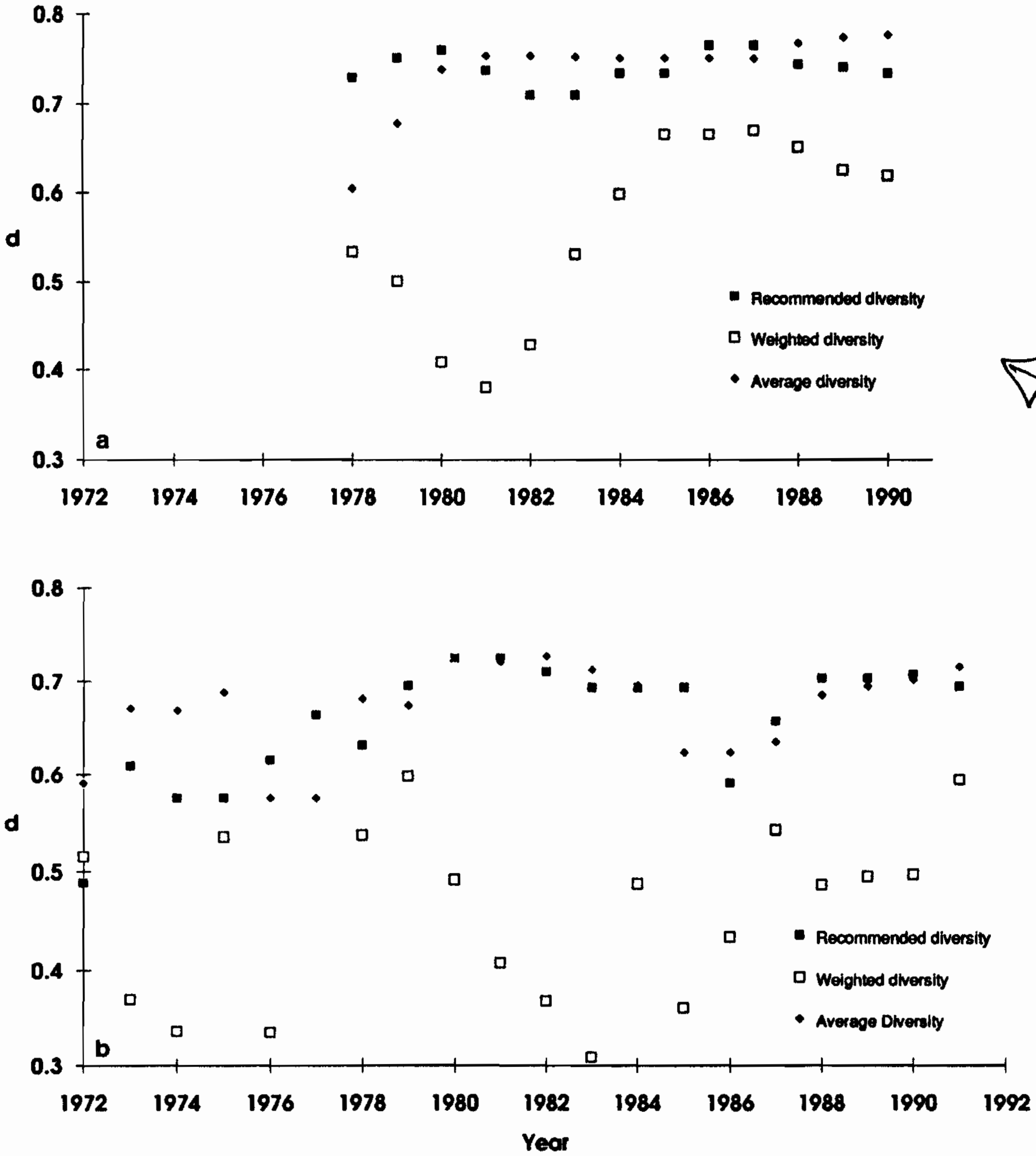

Fig. 4. Average diversity, weighted diversity, and recommended diversity of cultivars in a) the Pakistani Punjab, 1978 to 1990, and b) the Yaqui Valley of Mexico, 1972 to 1991.

Table 3. Means and distributions of parentage measures averaged across the time period 1972 to 1991 or 1978 to 1990.

							5-yr similarities		
Region	Parameter†	Average diversity d_a	Recommended diversity d_r	Weighted diversity d_w	Reserve diversity d_{rw}	Coefficient of diversity (COD)	Average temporal diversity d_{at}	Recommended temporal diversity d_{rt}	Weighted temporal diversity d_{wt}
Yaqui Valley 1972-1991	Mean	0.67	0.66	0.45	0.21	0.64	0.74	0.73	0.78
	Std. error	0.01	0.02	0.01	0.02	0.03	0.01	0.01	0.01
	Range	0.15	0.14	0.34	0.38	0.50	0.12	0.16	0.21
	Trend	0.00	0.01**	0.01	0.00	0.00	0.00	0.00	0.00
Yaqui Valley 1978-1990	Mean	0.68	0.69	0.46	0.22	0.65	0.75	0.75	0.80
	Std. error	0.01	0.01	0.02	0.02	0.03	0.01	0.01	0.01
	Range	0.10	0.13	0.24	0.29	0.47	0.10	0.11	0.10
	Trend	0.00	0.00	0.00	0.00	0.00	0.00	0.00	−0.01**
Pakistan Punjab 1978-1990	Mean	0.74	0.74	0.55	0.19	0.75	0.75	0.75	0.64
	Std. error	0.01	0.01	0.03	0.03	0.04	0.01	0.00	0.03
	Range	0.17	0.06	0.29	0.29	0.45	0.08	0.05	0.20
	Trend	0.01**	0.00	0.02**	0.02**	−0.02*	0.00	0.00	0.02**

*, ** Linear trend significantly different from zero at $P = 0.05$ and 0.01, respectively.

† Means: mean diversity estimated as an average of the yearly diversity values. Standard error: $SE = (\hat{\sigma}^2 n^{-1})^{0.5}$, where $\hat{\sigma}^2$ is the variance of the yearly diversity averages and n is the number of years for which an average diversity was estimated.

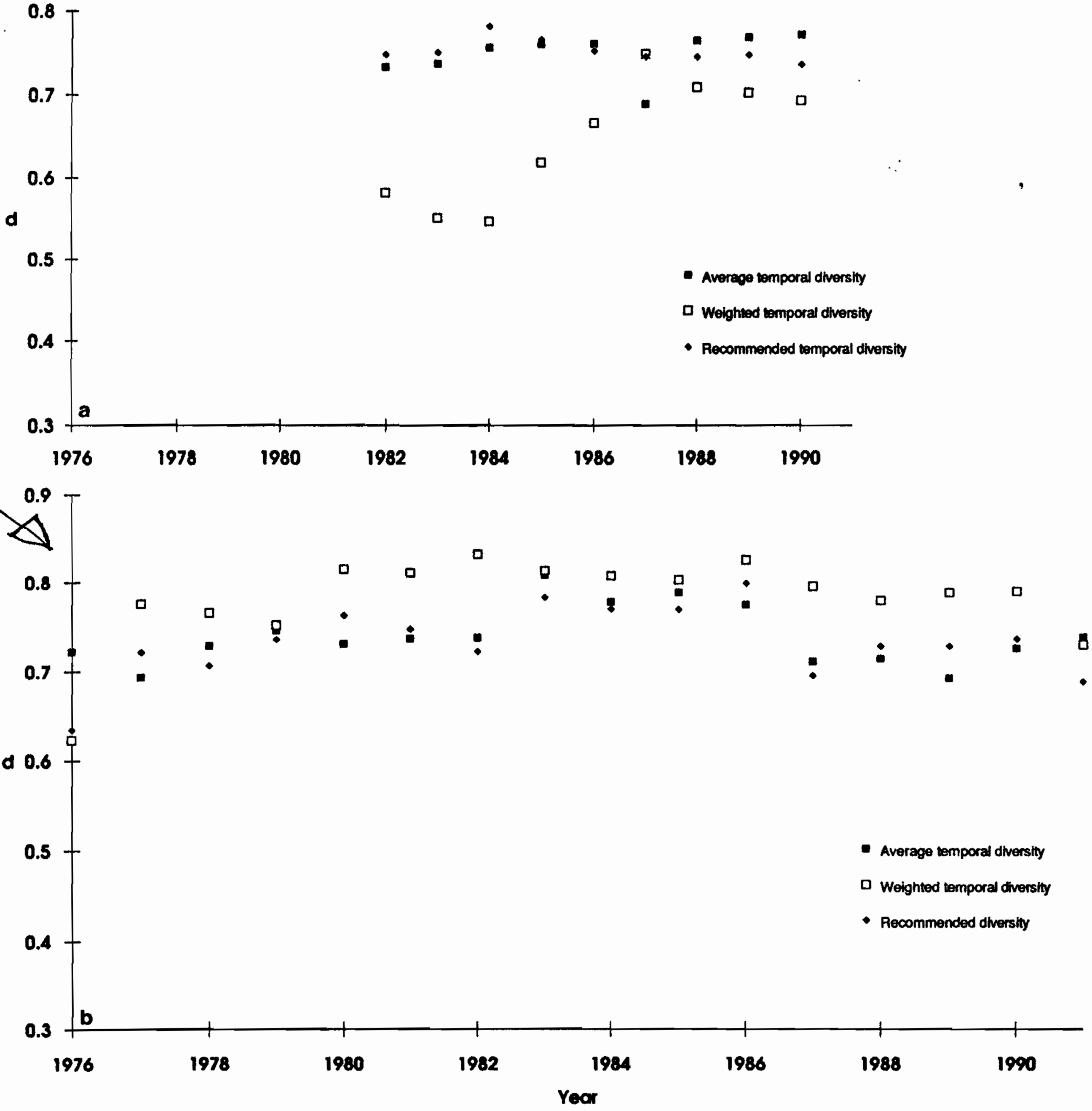

Fig. 5. Average temporal diversity, weighted temporal diversity, and recommended diversity of cultivars in a) the Pakistani Punjab, 1978 to 1990, and b) the Yaqui Valley of Mexico, 1972 to 1991; comparisons of diversity designated by the last year of the 5-yr period.

Diversity in the Yaqui Valley, 1971-1991

From 1971 to 1991, 43 hexaploid spring wheats were grown in the Yaqui Valley of Mexico. Fourteen were released prior to 1971 for a release frequency of 1.5 cultivars per year. A number of the cultivars grown in the Yaqui Valley during this period were sister lines, different genotypes derived from the same cross. In addition, lines derived from backcrossing to the dominant cultivars were grown. As a result a number of the cultivars grown were quite closely related.

Cluster analysis of the COP values produced groups of cultivars which were closely related. The close groups of cultivars were distantly linked to each other (Fig. 2). This would be expected when a number of sister cultivars, backcross derivatives, and half-sister cultivars are considered as was the case for the Yaqui region. The *Ciano 67, II8156, Jupateco,* and *Veery-Bluebird* clusters, designated by the dominant parentage of the cluster, were identified at the arbitrary four-group level.

The average diversity of the cultivars grown in any one year ranged from 0.58 in 1976 to 0.78 in 1982, with an average across years of 0.67 (Table 3, Fig. 4b). The d_a values had no overall trend (significant linear regression coefficient) during this time period. The weighted diversity

(d_w) also showed no significant trend over years and was characterized by large year-to-year swings (range in d_w: 0.34), approximately 225% greater than the range of the average diversity values. The average d_w across years was 0.45, 33% lower than the average d_a value (*t*-test, $p < 0.01$).

The lower mean and greater range of d_w in comparison to d_a represent successive cycles of cultivar acceptance. Wide-spread acceptance of one or several closely related cultivars was followed by a period of rapid decline with the introduction of a new set of superior cultivars of which one or two would eventually predominate. In two time periods, 1977 and 1981 to 1983, the utilization of a limited set of cultivars or sister lines was so great that the COD value dropped below 0.50. This is an indication that greater than 50% of the parentage variation was related to the dominant cultivars (Jupateco in 1977, 'Nacozari' in 1981, and Ciano 79 in 1982 to 1983). In contrast to the utilization of cultivars by Yaqui Valley growers, recommended diversity (d_r) increased steadily until 1980 with little fluctuation afterwards (average trend: 0.01 yr^{-1}, $p < 0.01$; range: 0.14). The average across years was 0.66 and 0.21 for the recommended and reserve diversities, respectively. Therefore, if growers had grown the recommended cultivars in equal areas, the diversity of the cultivars grown in the Yaqui Valley could have increased 47%.

The cultivars grown in the Yaqui Valley changed rapidly with only 'Opata' dominating production for more than 2 yr (Table 2, Fig. 4b). The average temporal diversity of cultivars across 5-yr periods was 0.74. The recommended temporal and average temporal diversity were almost identical. The weighted temporal diversity was 0.78, significantly higher than the recommended temporal diversity (*t*-test, $p < 0.01$). This indicates that the growers changed germplasm at a higher rate than the rate of change recommended by the research service.

DISCUSSION

Average Diversity

The diversity of spring bread wheats within these two regions was somewhat lower than the diversity found in other crop studies that used an average diversity or COP measurement. The average diversity of cultivars from 1981 to 1990 in the Yaqui Valley and the Pakistani Punjab was $d_a = 0.75$ and 0.78, respectively (data not shown). Estimates of average diversity for the USA are 0.81 for soybean cultivars of the 1970s (Cox et al., 1985), 0.81 among U.S. two-rowed and 0.88 among six-rowed barley cultivars grown from 1971 to 1990 (Martin et al., 1991), and 0.81 for US oat cultivars grown from 1971 to 1985 (Souza et al., 1989). Among rice (*Oryza sativa* L.) cultivars in Latin America for the years 1971 to 1989 d_w ranged from 1.00 in Chile to 0.68 in El Salvador (Cuevas-Perez et al., 1992). Among U.S. hard red winter wheat cultivars the d_a and d_w values in 1984 were 0.75 and 0.65, respectively. For soft red winter wheats in 1984, d_a was 0.85 and d_w was 0.80 (Cox et al., 1986). Weighted diversity for both classes of red winter wheat was higher than found in spring wheats of the Punjab and Yaqui Valley.

The diversity of wheats grown in the Yaqui Valley and the Pakistan Punjab are not unusually low compared to other crops and regions. However, for both of these regions, the average diversity and weighted diversity typically ranged between a half-sib and full-sib relationship. This study points to a limitation in attempts to diversify germplasm as only a narrow range of germplasm is typically accepted by growers.

The Pakistani Punjab had higher diversity values than the Yaqui valley, both for recommended cultivars (recommended diversity) and area of cultivars grown by growers (weighted diversity). Comparison of the three measures of diversity for 1978-1990 confirms that the Punjab had significantly more diversity among cultivars than the Yaqui Valley ($p < 0.05$, Table 3). This is probably due in part to the greater geographic area of the Punjab. The weighted diversity was also calculated for the rice-wheat area of the Punjab which is similar in area to the Yaqui Valley. For the years 1984 and 1986-1990, when data are available, the weighted diversity was 0.51, lower than for the Yaqui Valley (Byerlee, 1993, unpublished data). The average diversity was also enhanced in the Punjab because of the long term persistence of cultivars. All the cultivars in production in 1978 were still in production at the end of the study (Table 1). By contrast, none of the cultivars grown in 1978 in the Yaqui Valley were still in production in 1990 (Table 2). For both regions, the magnitude of reserve diversity was comparable. If growers were to grow cultivars recommended by the research services equally (that is, use all the recommended diversity) diversity could be increased by approximately 0.20 (Table 3). However, this would probably lead to a reduction in yields and grower satisfaction. For example, in the Pakistan Punjab, the dominant cultivar in the late 1980s, Pak 81, consistently yielded more than other cultivars (Byerlee, 1993).

Diversity through Time

The 5-yr temporal diversity measures indicate that both regions have comparable rates of germplasm replacement with average temporal diversity and recommended temporal diversity of approximately 0.75. The comparable rate of replacement of recommended cultivars (Table 3) indicates that research programs in both regions are similar in their ability to identify and release new germplasm. However, from 1978 to 1990, the Yaqui Valley germplasm was retired at a significantly higher rate ($d_{wt} = 0.80$) than in the Punjab ($d_{wt} = 0.64$, *t*-test $p < 0.05$, Table 3). The area-weighted lifespan of cultivars in Pakistan's Punjab was 10.9 yr compared with 3.7 yr in the Yaqui Valley (Brennan and Byerlee, 1991). Therefore, any potential impact of genetic uniformity in the Yaqui Valley is at least partially offset by the high rate of germplasm replacement. The 1977 leaf rust epiphytotic in the Yaqui Valley was controlled in the first year through fungicide application when genetic control of the disease broke down (Dubin and Torres, 1981). In that year the susceptible genotype, Jupateco, was sown to 75% of the bread wheat area but was completely replaced by resistant cultivars in 1978 (Table 2) greatly reducing both disease loss and fungicide requirements. Because these options for epiphytotic control are not now available in many developing countries, the 1977 to 1978 transition in the Yaqui Valley may be a unique situation.

Effect of Breeding Programs on Diversity

Degradation of recommended diversity (the diversity of cultivars with acceptable characteristics) was not observed in either growing region. Therefore, plant breeding programs did not reduce diversity. Instead widespread acceptance by growers of a limited number of cultivars was the major force reducing latent diversity. The rapid cycling of the Yaqui Valley was not observed in the Punjab probably because of the larger area involved and a less developed cultivar dispersal system rather than breeding program differences. The trend towards greater diversity observed in the Punjab may reflect real gains in the release and acceptance of diverse cultivars or be part of a cycle of longer duration than observed in the Yaqui Valley. However, disease epiphytotics in both regions are forces encouraging spatial and temporal diversity. For example, in the years immediately after leaf rust epiphytotics in the Yaqui Valley (e.g., 1977 and 1986) and in the Punjab (1978) diversity increased as the dominant cultivar was replaced by several cultivars. In the absence of disease pressure, germplasm diversity may not be maintained by breeding programs or growers. Breeding programs are challenged to develop several diverse cultivars with peak yield levels to limit the tendency of growers to choose mono-cultivar systems. Heisey (1990) suggested mechanisms for encouraging temporal diversity, including (i) more rapid seed multiplication, (ii) distinct naming of cultivars for better name recognition by growers, (iii) private sector incentives for seed sales and promotion, and (iv) more aggressive on-farm demonstration of new cultivars.

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