

Changes in genetic diversity in the red winter wheat regions of the United States

(genetic vulnerability/coefficient of parentage/germ plasm/genetic uniformity/plant breeding)

T. S. COX*†‡, J. P. MURPHY§, AND D. M. RODGERS†¶

*U.S. Department of Agriculture, Agricultural Research Service, Manhattan, KS 66506; †Department of Agronomy, Kansas State University, Manhattan, KS 66506; and §Department of Crop Science, North Carolina State University, Raleigh, NC 27695-7601

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ABSTRACT Pedigree and acreage data were utilized to determine trends in genetic diversity of soft red winter (SRW) and hard red winter (HRW) wheats. Four uniformity estimates were computed: (a) \bar{r}_1 , the mean relationship among all cultivars grown in a given year; (b) \bar{r}_2 , the mean relationship among primary cultivars; (c) \bar{r}_3 , the mean relationship of primary cultivars weighted by acreage; and (d) \bar{r}_4 , the mean relationship of primary cultivars grown in different years, weighted by acreage. In the SRW region, there has been a slow but steady increase in relationship among cultivars (\bar{r}_1 and \bar{r}_2). There was a dramatic increase in field uniformity (\bar{r}_3) during the 1970s, but \bar{r}_3 had sharply decreased by 1984 to its lowest point ever (0.22). All uniformity estimates decreased sharply for HRW wheats from 1919 to 1949 and have decreased gradually since. Uniformity is higher in HRW than in SRW wheats, primarily because of the persistence of a core of HRW germ plasm from cultivar 'Turkey,' but the difference is diminishing. Both classes appear to be entering a new era of increasing diversity.

In 1972, the National Academy of Sciences reported that, for the major field crops of the United States, a small number of cultivars covered a large proportion of the acreage in production (1). Ten years later, there had been a noticeable increase in cultivar diversity in the cotton (*Gossypium hirsutum* L.) and soybean [*Glycine max* (L.) Merrill] crops, but the situation had not changed for wheat (*Triticum aestivum* L.) (2).

In the wheat-growing regions of the United States, genetic uniformity exists at three levels. First, large tracts of land, especially in the Great Plains, are sown with a single species of wheat. Second, a small number of cultivars, representing a very small sample of wheat germ plasm in general, accounts for a large proportion of the wheat acreage. Third, most cultivars used in production are related to other cultivars through common parents (3, 4). Extensive genetic uniformity can result in crop losses if there is uniform susceptibility to new pest or pathogen genotypes or to a severe stress. To avoid this problem and to sustain genetic gain, breeders periodically introduce new germ plasm into their populations.

Increases in genetic variability have been tempered by the tendency to concentrate on selections from matings between highly adapted cultivars that carry the many specific gene complexes necessary in a successful cultivar. Furthermore, superior cultivars are often grown on large proportions of the wheat acreage. Successful breeding, therefore, can inadvertently reduce genetic diversity in the field.

One approach to evaluating genetic diversity is through examination of the frequencies in commercial cultivars of known genes with individually identifiable effects, such as electrophoretic (5) or disease-resistance loci. Such data could

be gleaned from cultivar-acreage surveys conducted over time. This uniformity, though critical, fails to consider the total genomic diversity between cultivars that might contain high levels of uniformity for qualitative, but not for quantitative, traits.

In contrast, total genomic diversity may be estimated through analysis of pedigree data (3, 5–7). Our objective in this study was a comprehensive evaluation of the changes in genetic diversity in the hard red winter (HRW) and soft red winter (SRW) wheat gene pools in the United States during this century. Utilizing an estimate of coefficient of parentage (8, 9) based on pedigree analysis, in combination with cultivar-acreage survey data, we examined the effects of red winter wheat improvement on the levels of genetic diversity in two wheat-growing regions.

MATERIALS AND METHODS

The pedigrees of most SRW and HRW wheat cultivars grown commercially between 1919 and 1984 were traced back to 74 introductions and parents of introductions which had no known relationship to any other introduction or cultivar (3). Coefficients of parentage, r (8, 9), were computed for all pairwise combinations of cultivars. The following assumptions were made in the algorithm used to compute r values: (i) a cultivar derived from a cross obtained half of its genes from each parent; (ii) all ancestors, cultivars, and parental lines were homozygous and homogeneous; (iii) the ancestors were unrelated to each other ($r = 0$); (iv) the r value between a selection from a cultivar and the cultivar equaled 0.75; and (v) the r value between two selections from the same cultivar was $r = (0.75)^2 = 0.56$. The contradiction between assumption ii on one hand and assumptions iv and v on the other was necessary in order to take into account those few cultivars from which unique variants have been selected.

The coefficient of parentage, and the computer algorithm used to compute it, is based on the simple principle that the relationship between two cultivars or lines X and Y is determined by the degree of relationship between the parents of X and Y. Symbolically, if the parents of X are A and B and the parents of Y are C and D, then $r_{XY} = \frac{1}{4}(r_{AC} + r_{AD} + r_{BC} + r_{BD})$. Of course, r_{AC} depends on the relationship (r) between the parents of A and C, etc. A matrix of r values was produced using such computations, subject to assumptions i–v above.

The uniformity estimates (\bar{r}_n values) in Table 1 were computed for the HRW and SRW classes, separately, using data from Cox *et al.* (3) and cultivar-acreage distribution survey data for the HRW and SRW wheat-growing regions in the United States from 1919 to 1984 (refs. 10–17 and Stan-

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Abbreviations: HRW wheat, hard red winter wheat; SRW wheat, soft red winter wheat.

‡To whom reprint requests should be addressed.

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Table 1. Formulas for uniformity estimates \bar{r}_1 – \bar{r}_4

Uniformity estimate*	Description
$\bar{r}_1 = \frac{2}{m_y(m_y - 1)} \sum_{i=1}^{m_y} \sum_{j=1}^{i-1} r_{ij}$	Mean r among all cultivars grown on at least 0.01% of the acreage of a class in year y
$\bar{r}_2 = \frac{2}{n_y(n_y - 1)} \sum_{i=1}^{n_y} \sum_{j=1}^{i-1} r_{ij}$	Mean r among all cultivars grown on at least 1.0% of the acreage of a class in year y
$\bar{r}_3 = \sum_{i=1}^{n_y} \sum_{j=1}^{n_y} p_{iy} p_{jy} r_{ij}$	Mean r weighted by acreage—i.e., the mean degree of relationship between two plants selected at random from anywhere in the region of interest in year y
$\bar{r}_4 = \sum_{i=1}^{n_y} \sum_{j=1}^{n_z} p_{iy} p_{jz} r_{ij}$	Mean r , weighted by acreage, between years y and z

*Where cultivars 1 through n_y or n_z were grown on at least 1.0% of the acreage in year y or z , respectively, and cultivars $n_y + 1$ through m_y were grown on less than 1.0% in year y . The estimated coefficient of parentage between cultivars i and j was r_{ij} , and the fraction of the acreage occupied by cultivar i was p_{iy} and p_{iz} in years y and z , respectively.

standardization Division of the Federal Grain Inspection Service, unpublished data).

We computed four estimates of genetic diversity (Table 1). (a) \bar{r}_1 was the mean coefficient of parentage between all cultivar pairs within a class reported as grown commercially. This estimated the total genetic uniformity of germ plasm available to growers and was computed at 10-year intervals from 1919 to 1979 inclusive, plus 1984. (b) \bar{r}_2 was the mean coefficient of parentage between all cultivar pairs within a class reported to be grown commercially on 1% or more of the total acreage of that class. It represented uniformity of the primary cultivars within a class at the survey date and was computed at 5-year intervals between 1919 and 1984 inclusive. (c) \bar{r}_3 was the sum over all pairwise combinations of primary cultivars i and j of the product (proportion of wheat acreage in primary cultivars occupied by cultivar i) \times (proportion occupied by j) \times (coefficient of parentage between i and j) for a given year. It was an estimate of field uniformity, or the mean degree of relationship between any two plants selected at random from the HRW or SRW region in a given year, and was computed at the same intervals as \bar{r}_2 . (d) \bar{r}_4 was computed in the same way as \bar{r}_3 , but using coefficients of parentage between cultivars from different years, weighted by the product of their proportional acreages in their respective years. It was an estimate of uniformity over time—i.e., the mean relationship between two plants selected at random in a region in different years.

Note that \bar{r}_3 will always be larger than \bar{r}_1 or \bar{r}_2 for a given class and year because of the inclusion of r values between cultivars and themselves, which are always unity in computation of \bar{r}_3 . The estimates \bar{r}_1 and \bar{r}_2 include only intercultural r values; therefore, \bar{r}_1 and \bar{r}_2 are independent of the number of cultivars, unlike \bar{r}_3 and \bar{r}_4 .

RESULTS

The number of cultivars in commercial production provides a crude estimate of genetic uniformity (Table 2). The total number of commercially available SRW cultivars fluctuated between 55 in 1919 and 70 in 1979 before increasing to 98 in 1984. The number of widely grown, or primary, SRW cultivars has varied between 12 and 23. In contrast, the total number of commercially available HRW cultivars has increased from only 5 in 1919 to 164 in 1984. The number of

Table 2. Number of cultivars grown, number of primary cultivars* grown, and percentage of area covered by primary cultivars in the SRW and HRW wheat regions of the United States

Year	No. of cultivars				Percentage of area in primary cultivars	
	Total		Primary		SRW	HRW
	SRW	HRW	SRW	HRW		
1919	55	5	15	1	89	99
1929	65	26	20	4	93	97
1939	60	21	21	10	93	95
1949	67	30	22	15	91	95
1959	69	45	12	16	87	94
1969	63	72	14	21	90	90
1979	70	102	15	19	89	80
1984	98	164	23	20	88	79

*Those cultivars sown on 1% or more total acreage in class.

primary HRW cultivars has increased accordingly and appeared to level out around 20. The primary cultivars have accounted for approximately 90% or more of the total acreage in their respective classes in most years.

Genetic uniformity in the HRW region has been greater than in the SRW region throughout the century (Figs. 1 and 2). The differences in \bar{r}_n values were greatest in 1919, when there were 55 SRW and only 5 HRW cultivars and virtually the entire HRW acreage was occupied by the single cultivar 'Turkey.' The \bar{r}_3 of 1.00 for HRW in 1919 is an overestimate of true genetic uniformity, since Turkey was a heterogeneous landrace. However, it is unlikely that other early HRW cultivars, many of which were plant selections out of Turkey, were more genetically heterogeneous than modern cultivars, which are often selected in the early generations from crosses.

Both \bar{r}_1 and \bar{r}_2 have increased slightly over 65 years in the SRW region (Fig. 1). Regression analysis (data not shown) showed statistically significant increases of 0.001 per year for both \bar{r}_1 and \bar{r}_2 . Mean uniformity among all available cultivars, \bar{r}_1 , was slightly but consistently lower than that among the primary cultivars, \bar{r}_2 . A deviation from the characteristic parallelism of these two estimates occurred in 1979, when seven of the primary cultivars were 'Arthur' and close relatives.

Field uniformity, \bar{r}_3 , did not always follow trends in uniformity among SRW cultivars. The \bar{r}_3 fluctuated slightly around 0.30 between 1919 and 1949. The increase to 0.40 in 1954 resulted from a 65% share of the SRW acreage sown

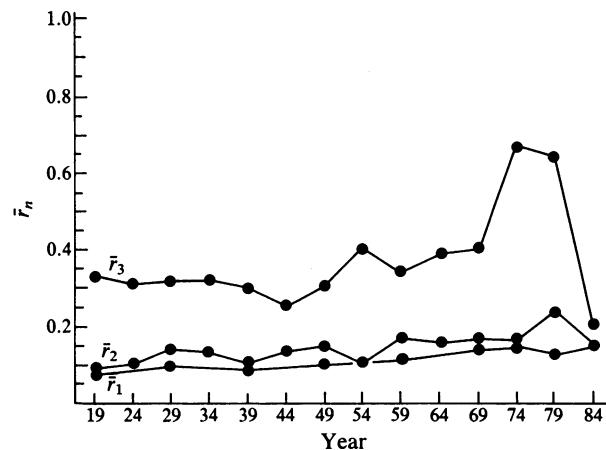


FIG. 1. Mean degree of relationship among available cultivars (\bar{r}_1), primary cultivars (\bar{r}_2), and primary cultivars weighted by proportional acreage (\bar{r}_3) in selected years between 1919 and 1984 in the SRW wheat class.

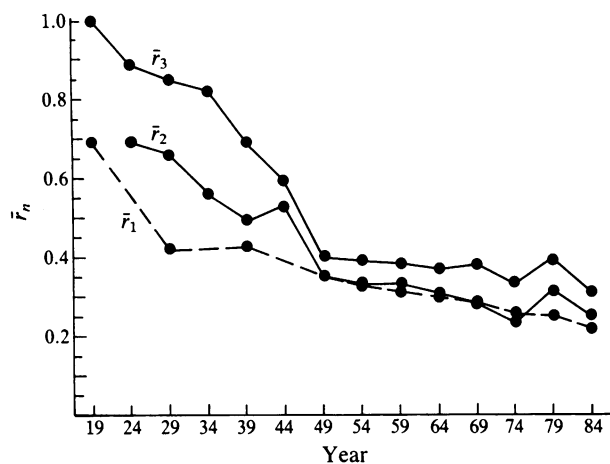


FIG. 2. Mean degree of relationship among available cultivars (\bar{r}_1), primary cultivars (\bar{r}_2), and primary cultivars weighted by proportional acreage (\bar{r}_3) in selected years between 1919 and 1984 in the HRW wheat class.

with a group of four related cultivars, 'Vigo,' 'Seneca,' 'Thorne,' and 'Butler.' Mean r for the six pairwise combinations among these four cultivars was 0.47. A marked increase in \bar{r}_3 to 0.67 in 1974 resulted from the widespread popularity of Arthur and the very closely related 'Arthur 71,' which together accounted for 68% of the total acreage in that year. The percentage of the total acreage sown with these two cultivars decreased to 47% in 1979, but \bar{r}_3 remained at 0.64 because the majority of the difference in acreage was sown with the closely related cultivar 'Abe' (r between Arthur and Abe = 0.95). A dramatic plunge in \bar{r}_3 occurred in 1984. Nine cultivars ('Caldwell,' 'Coker 747,' 'Hart,' 'Arthur,' 'Arthur 71,' 'McNair 1003,' 'Pike,' 'Coker 762,' and 'Pioneer 2550') accounted for 65% of the SRW acreage, but no single cultivar was predominant. With the exception of Arthur, Arthur 71, and Coker 747, the r values between pairwise combinations of these nine cultivars were all less than 0.35.

All \bar{r}_n values have decreased over the years in the HRW region (Fig. 2). Regression analysis showed statistically significant decreases of 0.003 and 0.007 per year for \bar{r}_1 and \bar{r}_2 , respectively. In 1979, \bar{r}_2 increased temporarily, and in 1984 remained higher than in 1974, because of the ubiquity of 'Scout'-type wheats in the parentage of primary cultivars. But, after having leveled off through the 1960s and '70s, \bar{r}_1 was at its lowest point ever (0.22) in 1984, indicating a new infusion of genetic diversity by breeders into recently released cultivars.

Field uniformity, \bar{r}_3 , decreased steeply from 1.00 in 1919 to 0.40 in 1949 for the HRW region and has gradually fallen since. The "transition year" 1949 marked a shift in the bulk of HRW acreage from the two cultivars Turkey and 'Tenmarq' to the four less closely interrelated cultivars 'Pawnee,' 'Wichita,' 'Triumph,' and 'Comanche'; however, all four were derived from crosses involving selections from Turkey. Scout, which had a Pawnee sib, Turkey, and two Turkey selections ('Nebred' and 'Cheyenne') in its pedigree, first appeared in large acreages in the survey in 1969. By 1979, there was a transitory increase in \bar{r}_3 , when over 35% of the HRW acreage was sown with Scout or its selections and backcross derivatives. This increase coincided with a decrease in the number (Table 2) and an increase in the similarity (Fig. 2, \bar{r}_2) of primary cultivars in 1979; however, \bar{r}_3 , as in the SRW region, was at its lowest point ever in 1984.

Whereas \bar{r}_3 indicates the level of genetic uniformity in a given year, \bar{r}_4 is a dynamic indicator of the continuity of germ plasm over time. The value of \bar{r}_4 varied from a low of 0.12 for 1984 vs. 1949, to a high of 0.65 for 1974 vs. 1979 in the SRW

Table 3. Mean coefficient of parentage ($\bar{r}_4 \times 100$) between primary cultivars from different years, weighted by the product of the proportional acreages

	1984	1979	1969	1959	1949	1939	1929	1919
1984		32	29	22	22	30	33	36
1979	26		35	27	27	37	41	44
1969	15	16		33	32	42	45	49
1959	14	15	25		37	42	43	46
1949	12	13	18	23		43	44	47
1939	13	15	22	24	23		75	79
1929	13	16	22	25	24	30		90
1919	13	15	21	25	24	29	32	

HRW wheat above diagonal; SRW wheat below diagonal.

region. Table 3 shows \bar{r}_4 values for every tenth year only, plus 1984. Predictably, consecutive dates were more similar than those separated in time, because of overlap of cultivars and germ plasm. For a period extending into the 1950s, \bar{r}_4 values involving the year 1919 remained fairly constant in the SRW region. Subsequently, they gradually decreased to approximately 0.13, the \bar{r}_4 for 1919 with 1984. This pattern resulted from the slower rate of supplantation in the cultivar population during the earlier period. For example, 8 of the 22 primary cultivars grown in 1919 were still classified as primary cultivars 30 years later. Changes in the cultivar population accelerated over the past three decades; by 1959, none of the primary cultivars of 1919 were still in that same category; those cultivars, in turn, had been completely replaced by 1969. In 1984, only 2 of 20 primary cultivars also had been classified as primary cultivars in 1974.

In the HRW region, \bar{r}_4 estimates involving 1984 were highest for 1984 vs. 1919–1929 and 1984 vs. 1979 (Table 3), indicating that the basic Turkey germ plasm has persisted in the HRW gene pool up to the present, and that some of the diversity introduced in the 1940s and '50s has been eliminated from the gene pool. The mean \bar{r}_4 for 1944 vs. the previous five surveyed years (from 1919 to 1939) was 0.65. This degree of relationship between current and recently grown cultivars decreased at an accelerated rate, until the mean \bar{r}_4 for 1984 vs. the five surveyed years between 1959 and 1979 was 0.27.

DISCUSSION

Genetic diversity has increased tremendously in HRW germ plasm and decreased slightly in SRW germ plasm during this century. In 1984, \bar{r}_1 was 0.15 and 0.22 for SRW and HRW wheats, respectively, compared with 0.08 and 0.41 in 1919. Rates of increase in \bar{r}_1 and \bar{r}_2 were each about 1% of the century mean per year for SRW wheats, but \bar{r}_1 and \bar{r}_2 decreased at rates of 1 and 2% per year, respectively, for HRW wheats.

The transitory peak in \bar{r}_3 that occurred in both regions during the 1970s has passed. If we take the mean r of 0.05 between the SRW and HRW cultivar clusters estimated by Murphy *et al.* (4) and an acreage ratio of 4:1 for HRW vs. SRW wheats, the mean \bar{r}_3 over the entire red winter wheat region was 0.29 in 1979 and 0.22 in 1984.

Increased or decreased genetic diversity is not an end in itself for plant breeders, but a by-product of crossing and selection. In winter wheat, the most important stimulus for increased genetic diversity has been the need for resistance to diseases and insects; the need to maintain end-product quality has tended to decrease diversity. SRW breeders have taken the genetic diversity available in their region, augmented it by crossing with other gene pools, and concentrated the best germ plasm in modern cultivars. A slight, but not a severe, increase in cultivar similarity (\bar{r}_1) has resulted. HRW breeders, in contrast, began with a single cultivar, Turkey. By making selections from Turkey in the first half of this

century and crossing with wheats from other classes (most notably 'Kawvale,' 'Florence,' and 'Marquis'), they greatly diversified the germ plasm. More recently, HRW breeders have introduced further genetic diversity, including genes from SRW cultivars and semidwarf spring and winter wheat lines.

Evidence of the occurrence of genetic diversity over time (2) in the red winter wheats is provided in Table 3. The rate and amount of change in genetic diversity, as measured herein, does not necessarily have a cyclical pattern or any relationship to the typical life span of wheat cultivars. In the SRW region, there were three approximate periods within which relationships between dates were relatively high and relationships with dates from other periods were lower: 1919–1954; 1954–1969; and 1974–1979. Relatively high levels of relationship were maintained during the period from 1919 to the 1950s. The list of available cultivars changed slowly over time. Cultivars were closely related to each other and to older cultivars and landraces such as 'Mediterranean,' 'Flint,' 'Purplestraw,' 'Poole,' 'Gypsy,' and 'Valley.'

Cultivars that were predominant during the second period ('Monon,' 'Knox,' 'Vermillion,' 'Redcoat,' 'Dual,' 'Benhur,' 'Blueboy,' 'Atlas 66,' and 'GA 1123') were developed from complex crosses sometimes including exotic germ plasm. This resulted in an overall decrease in \bar{r}_4 with dates in the previous period.

The third period, which probably extends beyond the suggested limit of 1979, was dominated by the cultivar Arthur and its relatives. In a cluster analysis based upon coefficient of parentage (4), Knox and Arthur relatives formed separate clusters. This relatively low level of relationship would partially account for the sharp delineation in \bar{r}_4 between 1969 and the three subsequent dates. The dramatic drop in \bar{r}_3 (Table 2) and the small \bar{r}_4 for 1979 with 1984 suggests that we are entering another period of diversity over time.

In the HRW region, there was little diversity over time until the 1950s (Table 3). Since then, the core of Turkey germ plasm has been maintained, with a more rapid turnover of the germ plasm surrounding that core. The genetic relationship between a field of Turkey in 1919 and today's average HRW wheat field (i.e., \bar{r}_4 for 1919 vs. 1984) is larger than \bar{r}_4 for 1979 vs. 1984! There has been diversity over time in the HRW region, but a considerable portion of the germ plasm has not seen any turnover.

Duvick (2) stated that as the numbers of public and private breeding programs increased, the rate of change in diversity over time would accelerate. Trends over the next decade will provide the critical data, but it is noteworthy that 9 of the 20 primary SRW cultivars in 1984 were bred by private industry, representing the highest fraction of pure-line cultivars in that category from that source ever. Nevertheless, sheer numbers of cultivars do not necessarily determine genetic diversity. For example, a 126% increase in the number of HRW cultivars between 1959 and 1979 (Table 2) produced no perceptible change in overall diversity (\bar{r}_3) during that period (Fig. 2).

Comparison of \bar{r}_1 with \bar{r}_2 in both classes shows that, in general, widely grown cultivars represent a narrower gene pool than the complete set of released cultivars. Further, a given wheat grower cannot choose from the set of all released cultivars, since only a handful are adapted to the conditions in his or her area and represent the most recent genetic improvements.

Field uniformity, \bar{r}_3 , is, of course, only partially under the control of breeders. It depends heavily on the number of cultivars grown and on the acreages they occupy; however, except for the peak in the 1970s for the SRW region, \bar{r}_3 has

approximately paralleled \bar{r}_1 and \bar{r}_2 . We have averaged across entire regions to obtain \bar{r}_3 . The degree of uniformity could be much higher, say, in a particular state where one or two cultivars are extremely popular.

Genetic uniformity in crops does not inevitably lead to calamitous epidemics, nor does genetic diversity alone prevent them. Diversity, however, provides a partial insurance policy against crop loss as well as the raw material for further genetic progress. Since we cannot foresee the future, it is important to monitor trends in crop genetic diversity. Present trends in the red winter wheat region are encouraging.

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