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Origin and diversity of North American hard spring wheats

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Abstract Genetic diversity is an important safeguard against crop vulnerability to biotic and abiotic stresses. Coefficient-of-parentage (COP) values of 248 North American hard spring wheat (*Triticum aestivum* L. em. Thell) cultivars released from 1901 to 1991 were used to estimate the genetic similarity of cultivars. COP values were used: to (1) quantify germ plasm sources and their contributions to the North American hard spring wheat gene pool; (2) measure changes in genetic diversity through time; and (3) identify major groupings of related cultivars. Landraces and local cultivars that contributed to the formation of the gene pool were: spring wheat (64%), winter wheat (16%), *T. turgidum* var. *durum* L. (10%), and *T. turgidum* var. *emmer* L. (8%). 'Fife', 'Hard Red Calcutta', and 'Turkey Red' accounted for 18%, 13%, and 8%, respectively, of the hard spring wheat origins. 'Era' and 'Butte' in the US, and 'Neepawa' and 'HY 320' in Canada, were the most commonly used named parents of cultivars released from 1981 to 1991. Both Canada and US had the greatest level of similarity among new cultivar releases in the 1930s (Canada: r=0.39, US: r=0.34). Genetic similarity in the US declined to r=0.14 in the 1940s and remained relatively constant thereafter. Similarity among released Canadian cultivars remained relatively high until the 1970s when the introduction of new market classes resulted in a 50% reduction in genetic similarity to approximately the same level of similarity found in the US. Cluster analysis was used to group cultivars released after 1941 into 13 clusters of similar genotypes. The cultivar clusters may have value for the stratified sampling of spring wheat germ plasm or in identifying diverse germ plasm for intermating.

Key words Spring wheat (*Triticum aestivum*) · Genetic diversity · Coefficient of parentage

Introduction

Hard-endosperm spring wheats are one of the primary types of wheat produced in North America. In the United States, approximately a third of wheat production is hard red spring (HRS) wheat produced primarily in the northern Great Plains. Few hard spring cultivars are white; however, interest in hard white spring wheats has increased recently (Morris 1992). The production of hard red spring wheat in the northern Great Plains dates to the introduction of 'Fife' by David Fife of Canada in 1842 (Ausemus and Rietz 1962). Between the introduction of Fife and the release of 'Marquis' in 1911, approximately 30 named spring wheat cultivars were developed or introduced to North America (Kephart 1994). Many were selections or crosses derived from Fife. The release of 'Marquis' ('Hard Red Calcutta'/'Red Fife') led to the replacement of many local cultivars and a subsequent loss of crop diversity. Marquis reached a peak US production of nearly 5.5 million ha in 1929 and was still produced on 900 ha in 1984 (Kephart 1994). Because of its broad adaptation and good baking quality, Marquis was a dominant parent in US and Canadian breeding programs. 'Thatcher' (Marquis/'Iumillo'emmer//Marquis/'Kanred') replaced Marquis in importance reaching a peak production area (2.5 million ha) in the US in 1939 (Kephart 1994). Thatcher also replaced Marquis as the quality standard for Canadian and US spring wheats. Although plant introductions have been widely used in breeding to improve disease resistance (Cox 1991) and lodging resistance (Dalrymple 1980), the impact of these introductions on broadening genetic diversity in spring wheats is uncertain. The prevalence of backcrossing and cyclical mating to adapted wheats may have re-

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stricted the diversification of breeding programs away from the Marquis-Thatcher germ plasm.

Pedigree analysis is a technique to study genetic diversity providing helpful genetic information regarding the preservation of diversity (Souza et al. 1994), the selection of parents (Souza and Sorrells 1991), and in tracing genetically related phenomena from ancestor to ancestor (Dilday 1990). The coefficient of parentage (COP) is the probability that a random allele at a random locus in one individual is identical by descent to a random allele at the same locus in the other individual. Computation of the COP value (r) requires a detailed pedigree of all genotypes and the assumption that the original ancestors of the relevant gene pool are unrelated (Murphy et al. 1986). The coefficient of parentage was originally developed by Wright (1922) and Malecot (1948). St. Martin (1982) adapted the COP 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.

The objectives of the present study were to: (1) determine the relative importance of specific wheat landraces and introductions; (2) use the COP (r) to measure genetic diversity changes through time in US and Canadian hard spring wheats; and (3) to identify major groupings of related cultivars within the hard spring wheats gene pool.

Materials and methods

The parentage similarity of 248 hard-kerneled spring wheats (white and red) was examined using COP estimates. These represent all recorded cultivars released or grown in the US and Canada from 1901 to 1991. The parentage of a cultivar was traced back to its ancestral parents. Cultivars without known or obvious parents were designated as ancestral parents. Examples of these would be landraces, local cultivars, or cultivars of unknown origin.

Parentage information was extracted from: (1) original registration notices from scientific publications in Crop Science, Agronomy Journal, and Canadian Journal of Plant Science; (2) published summaries of pedigrees [Villarreal and Rajaram (1988), Zeven and Zeven-Hissink (1978), Kephart (1994)] and, (3) primary sources such as breeding records at CIMMYT, North Dakota State University (Frohberg 1993, Personal Communication), USDA-ARS, St. Paul, Minn. (Busch 1993, Personal Communication), and the Agriculture Canada Research Station at Manitoba (Czarnecki 1993, Personal Communication).

The surveyed cultivars and their parents were included in a relationship matrix that was numerically estimated using Microsoft Excel, version 4.0 (Microsoft Corp., Redmond, Wash.), a microcomputer-based spreadsheet program, and followed the methodology described by Souza and Sorrells (1989). Cultivars with unknown pedigrees were not included in the coefficient calculation. The relative relationship of these 25 cultivars is included in the discussion. The r values for all the pairwise combinations were estimated under the assumptions made for inbred species (St. Martin 1982; Murphy et al. 1986). The assumptions used were: (1) a cultivar derived from a cross traces half of its genes from each parent; (2) all ancestral parents, cultivars, and parental lines were homozygous and homogeneous; (3) the ancestral parents were unrelated (r=0); (4) the r value between a selection from a cultivar and the cultivar equalled 0.75 (this included cases of induced mutations); and (5) the r value between a cultivar and itself was 1.0.

The percent ancestral contribution was defined in two analyses as the percent of a cultivar's, or group of cultivars', parentage that could be traced to a specific genotype (landrace or cultivar). The COP values of an ancestral parent were summed for all improved cultivars within a group and standardized to a percentage by dividing by the sum of all COP values for the group. In the first analysis, cultivars were divided into two groups: cultivars released from 1901 to 1940 and cultivars released from 1941 to 1991. The percent ancestral contribution of specific landraces and local varieties were estimated for each group to determine the origins of the hard spring germ plasm.

The second analysis examined the 83 cultivars released from 1981 to 1991 and determined which improved cultivars contributed directly to the parentage of current spring wheats. The pedigree of each spring wheat was traced back until reaching a named cultivar or plant introduction (Beer et al. 1995). Breeding lines which had been used as parents of cultivars were traced through their pedigree back to named cultivars. ND122 and several other widely used breeding lines were exceptions and were treated as cultivars. The direct COP value between a parental cultivar and a progeny cultivar was calculated, excluding collateral relationships that may have existed between parents and progeny due to common parents further back in the pedigree. The COP value of each parent was summed across all 83 progeny cultivars and divided by 83 to estimate the percent ancestral contribution. For some CIMMYT lines, multiple sister lines were used as parents usually without specific designation of selection numbers. In the case of Bajio, Bluebird and Veery sibs, COP values were pooled for all sibs from a common cross.

Changes in genetic similarity were estimated by dividing cultivars into 10-year groups based on release date. Similarity among cultivars was calculated by averaging the off-diagonal elements of the COP matrix of all possible combinations of cultivars released within a 10 year time-frame. Statistical Analysis System (SAS), version 6.08, was used to perform the cluster analyses of 192 hard spring cultivars released after 1941. The subroutine PROC CLUSTER was used to analyze the matrix of COP values (SAS 1989). Cultivars were clustered using the Unweighted Pair Group Method of clustering.

Results and discussion

One-hundred and forty five landraces, local cultivars, and plant introductions were identified as ancestral parents of the North American hard spring cultivars. 'Fife', 'Hard Red Calcutta', and 'Turkey Red' had the largest percent ancestral contribution to the hard spring wheats released from 1901 to 1991 (Table 1). 'Kenya 324', a leaf rust resistance source, had the largest contribution of ancestral parents that did not appear in the North American germ plasm prior to 1941. Mating between market classes has been an important part of hard spring development since the turn of the century. Turkey Red hard red winter, 'Iumillo' durum, 'Yaroslav' emmer, and 'Khapli' emmer appeared in pedigrees of hard red spring wheats prior to 1940, largely through intermediate parents such as Hope and Thatcher. Tetraploid *Triticum* species and hexaploid winter wheats accounted for 18 and 16% of the ancestral contribution, respectively, (including the ancestral parents listed in Table 1 and minor ancestral parents not listed in Table 1).

The base of ancestral parents has expanded slowly through time. Prior to 1940, four ancestral parents accounted for 52% of the parentage. After 1940, the top four ancestral parents accounted for 43% of the parentage. The narrow genetic origin of the hard spring wheats is similar to that of the hard red winter wheat crop in the US in the first half of this century, when most cultivars were derived

Table 1 Ancestral parents of North American hard spring wheat cultivars (lines with >1% total contribution)

Ancestral parent	Origin	Type	Total contribution (%)	Contribution 1901–40 (%)	Contribution 1941–91 (%)
Fife	Poland	Spring wheat	18.2	26.7	15.1
Hard Red Calcutta	India	Spring wheat	12.7	13.8	11.6
Turkey Red	Ukraine	Winter wheat	7.7	3.7	9.0
Iumillo	Spain	Durum	5.6	1.7	7.5
Khapli	India	Emmer	4.2	2.8	4.6
Kenya 324	Kenya	Spring wheat	4.2		5.5
Yaroslav	Europe	Emmer	3.6	2.7	3.9
Steinwedel	S. Africa	Spring wheat	3.0		3.9
Akakomughi	Japan	Winter wheat	2.4		3.0
Kota	Russia	Spring wheat	2.3	3.6	1.9
Ladoga	Russia	Spring wheat	2.3	7.6	0.4
PI 94701	Israel	Durum	2.1	1.3	2.2
Alfredo Chaves 6	Brazil	Spring wheat	1.9		2.5
Polyssu	Brazil	Spring wheat	1.9		2.5
Java	Russia	Spring wheat	1.7	2.4	1.0
Marroqui	Morrocco	Spring wheat	1.5		2.0
Gypsum	USA	Spring wheat	1.3	1.6	1.1
Kenya BF9906	Kenya	Spring wheat	1.2		1.6
Red Egyptian	Egypt	Spring wheat	1.2		1.6
Supreza	Brazil	Spring wheat	1.2		1.6
Gehun	India	Spring wheat	1.1	3.6	0.3

either through selection of Turkey Red or from crossing to selections of Turkey Red (Cox et al. 1986). The top four ancestral parents of the US and Canadian oat (*Avena sativa* L.) crop from 1951 to 1986 had a total parent ancestral contribution of 37% (Souza and Sorrells 1989), slightly lower than the contribution by the four most important ancestral parents of the hard spring wheat crop.

Breeders have favored either backcrossing or repeated cycles of mating to adapted germ plasm for the introduction of new germ plasm into the hard spring crop. This is indicated by the continued importance of the ancestral parents of Thatcher (Fife, Hard Red Calcutta, Turkey Red, Iumillo) in recently released spring wheats and the relative unimportance of new introductions. For example, 'Akakomughi' is an ancestral parent of many spring wheats through widespread use as a dwarfing source and as a parent of 'Mentana' (Borojevic 1983) and Mentana's progeny 'Frontana', a source of leaf rust (*Puccinia recondita* Rob. ex Desm. f. sp. *tritici*) resistance (Roelfs et al. 1992). Despite this use as a parent, Akakomughi had an ancestral contribution of less than 3% to the cultivars released after 1940 (Table 1) and only slightly more than 3% for cultivars released from 1981 to 1991 (data not shown) when it appeared in the pedigree of 92% of the cultivars. 'Daruma', the source of the *Rht*1 and *Rht*2 dwarfing genes also widely used throughout the spring wheat production region (Dalrymple 1980), had an ancestral contribution of 0.6% for cultivars released from 1981 to 1991, due to widespread use of recurrent mating in order to transfer the dwarfing factors into traditional hard spring germ plasm.

The most common geographic origin of the ancestral parents was from western Europe (32% of parentage), followed by the Indian sub-continent (21%) areas in the former Soviet Union (20%), and the continent of Africa (13%, Table 1). Wheats described as Brazilian or North American, such as 'Polyssu' and 'Gypsum', were derived from germ plasm originating in Europe or Asia, but their exact ancestry is obscure.

'Neepawa' and 'HY 320' were the most common parents of spring wheats released from 1981 to 1991 in Canada, while 'Era' and 'Butte' were the most common parents of US cultivars released in the US during the same period (Table 2). Neepawa was widely used as a direct parent for cultivars in the Canadian Western Red Spring class and as a recurrent parent in backcrossing programs to de-

Table 2 Percent ancestral contribution of the ten most-common parents of US and Canadian hard spring wheats released from 1981 to 1991

Parents of Canadian wheats		Parents of US wheats	
Parent	%[a]	Parent	%
Neepawa	18.6	Era	12.1
HY 320	10.1	Butte	5.2
Chris	6.0	Bajio sibs	4.9
Tobari 66	5.4	Waldron	4.3
Fortuna	4.8	Plainsman V	3.0
Glenlea	4.8	Blubird sibs	3.0
Kolibri	4.8	Marshall	2.6
Benito	3.6	Len	2.6
Manitou	3.6	Veery sibs	2.2
CT 615[b]	2.4	Borah	2.2
Columbus[b]	2.4		
Total	63.8		42.0

[a] Percent of pedigrees descendent from a specific parent for cultivars with-defined parentage

[b] CT 615 and Columbus tied for the 10th rank

velop rust resistant breeding lines such as BW63 (Townley-Smith et al. 1993). HY 320 is the standard for the Canadian Prairie Spring class and was used as a parent for other wheats within that market class. The ten most common parents in Canada accounted for 64% of the pedigrees of new hard spring cultivars. In the US, the ten most common parents accounted for only 42% of the pedigrees. This difference was largely due to fewer cultivars having been released in Canada than in the US. Within the US cultivars, the parents Bajio, Bluebird and Veery from the CIMMYT program represented a significant introduction of non-US spring wheat material. 'Red River 68', a selection of the Bajio cross, is also a parent of 'Plainsman V' one of the other important parents of current US spring cultivars (Table 2). 'Tobari 66', also a Bajio selection, from CIMMYT and 'Kolibri' from Germany represent introductions of new germ plasm into Canadian cultivars. The average similarity among the ten most common parents was lower in the US (r=0.15) than in Canada (r=0.23). This may reflect less stringent US market class requirements which allow US breeders a greater diversity in parental selection than is available to Canadian breeders.

The genetic similarity of the hard spring market classes in this century has changed through time. From 1901 to 1920 very low similarities existed among cultivars in both Canada and the US (Table 3). Even though 17 cultivars were developed in this time period, all were derived from crosses of local cultivars of divergent origins or from the introduction of local cultivars from other countries (e.g., 'Kota' and 'Chul' from Russia). Marquis' success as a cultivar led in turn to its widespread use as a parent. By the 1930s, the average similarity of cultivars had risen above r=0.34 in both countries, largely due to a high degree of similarity in new releases with Marquis. The average similarity between Marquis and the cultivars released during the 1930s was r=0.54. After this time period the genetic similarity declined in the US, reaching r=0.14 during the 1940s and thereafter remaining constant. In Canada, genetic similarity remained higher than in the US, fluctuating between r=0.20 and 0.34 until the 1970s. Additional market classes such as Canadian Prairie Spring and Canadian Western Extra Strong allowed new types of germ plasm to be utilized in released cultivars. The additional germ plasm used to develop these market classes reduced the genetic similarity of released cultivars by half from the 1960s to the 1970s (from r=0.34 to r=0.16).

Table 3 Mean coefficient of parentage (r) values of North American hard red spring wheat cultivars through time

Time period	Canada			USA		
	n[a]	Mean[b]	SE[c]	*n*	Mean	SE
1901–1910	2	0.00	0.00	4	0.00	0.00
1911–1920	6	0.13	0.09	5	0.00	0.00
1921–1930	5	0.15	0.07	8	0.14	0.05
1931–1940	6	0.39	0.05	10	0.34	0.04
1941–1950	4	0.20	0.04	13	0.14	0.04
1951–1960	5	0.24	0.06	8	0.12	0.05
1961–1970	4	0.34	0.08	29	0.10	0.02
1971–1980	11	0.16	0.04	46	0.16	0.02
1981–1990	17	0.18	0.06	65	0.14	0.02

[a] *n* = number of cultivars
[b] Mean = mean r values
[c] SE = standard error

Although the genetic similarity among US and Canadian cultivars is equivalent after 1970, this value may be biased due to a high number of private US cultivars with unknown pedigrees. If cultivars with unknown pedigrees are included, the similarity among US cultivars for the 1970's is r=0.11. For the 1980s the pedigree similarity among all US cultivars was r=0.09. Of the 22 cultivars released from 1971 to 1991 with unknown parentage, ten were selected from male-sterile-facilitated intermating populations which were composed of US hard red spring germ plasm intermated with desert southwest, semidwarf spring wheats. Another ten of the unknown pedigree wheats were derived directly or indirectly from CIMMYT germ plasm and would most likely have a high similarity to other US cultivars derived from CIMMYT germ plasm, such as 'Peak' and 'Yecora Rojo'. Therefore, if an exact pedigree could be obtained for the unknown US cultivars it is unlikely that this would significantly change the genetic similarity values from the range of r=0.14 to 0.16. US and Canadian hard spring wheats released from 1971 to 1990 had approximately the same level of similarity. However, the diversity of germ plasm in the US is in a single market class while in Canada multiple market classes exist with a high degree of similarity within a class and a low degree of similarity between classes.

The level of similarity of the North American spring wheat crop, compares favorably to other small grains crops. The average similarity among hard spring wheats during the 1980s for both Canada and the US was more than a third lower than the level found among hard red winter wheats grown in the US in 1984, but approximately the same as the soft red winter wheats grown at the same time (Cox et al. 1986). The similarity of spring wheat cultivars available from 1981 to 1990 in the Yaqui Valley of Mexico and the Punjab of Pakistan was r=0.25 and r=0.22, respectively (Souza et al. 1994). Both values were significantly higher that the hard spring wheats of this study for the same time period (Table 3). Martin et al. (1991) found similarities among 2-row and 6-row barleys grown from 1971 to 1990 of r=0.19 and r=0.12, respectively. Both values are within the same range as the spring wheats of this study. The US and Canadian oat crop has a lower pedigree similarity with average COP values of r=0.08 for the 10-year period from 1976 to 1985 (Souza and Sorrells 1989), approximately half the level of similarity of the US and Canadian hard spring cultivars.

The temporal pattern of pedigree similarity in the hard spring wheats is consistent with other small grains. Although a large number of local wheat cultivars were available to North American growers in the late nineteenth century through plant introductions and farmer selection (Clark et al. 1922), a few cultivars came to dominate production in the spring and winter wheat crops, greatly in-

Table 4 Spring wheats released from 1971 to 1991 clustered by pedigree similarity

Name	Release date	Origin	State
Cluster A			
Dundas	1979	CAN	PEI
Shasta	1976	USA	Calif.
Tadinia	1984	USA	Calif.
Cluster B			
Bounty 208	1971	Mex/USA[a]	Colo.
Colano	1971	MEX/USA	Colo.
Cutler	1991	CAN	Alberta
Funks W-433	1971	MEX/USA	Ariz.
Funks W-434	1971	MEX/USA	Ariz.
Funks W-444	1974	MEX/USA	Ariz.
Klasic	1982	USA	Calif.
Lark	1974	MEX/USA	Calif.
Norak	1984	USA	Ariz.
Osolo	1980	USA	Colo.
Peak	1971	MEX/USA	Idaho
Peak 72	1972	MEX/USA	Idaho
Probrand 771	1980	USA	Minn.
Protor	1975	MEX/USA	Minn.
Sawtell	1978	USA	Idaho
Serra	1988	USA	Calif.
Solar	1984	USA	Minn.
Tanori 71	1975	MEX/USA	Calif.
Cluster C			
Anza	1971	MEX/USA	Calif.
Bluesky	1987	CAN	Alberta
Bronze Chief	1985	USA	Mont.
Eureka	1978	USA	S.D.
Express	1991	USA	Mont.
Glenlea	1972	CAN	Man
Glenman	1985	USA	Mont.
Guard	1983	USA	S.D.
Hipro	1984	MEX/USA	Calif.
Kodiak Dwarf	1984	USA	Mont.
Laura	1986	CAN	Sask
MyKay	1981	USA	Idaho
Mindoro	1984	MEX/USA	Calif.
Nomad	1989	USA	Mont.
Pioneer 2370	1989	USA	Mont.
Pioneer 2385	1987	USA	Mont.
Portola	1975	USA	Calif.
Powell	1979	USA	Utah
Probrand 751	1980	USA	Minn.
Probrand 775	1984	USA	Calif.
Probred	1974	USA	Minn.
Prodax	1972	MEX/USA	Minn.
Prospur	1975	USA	Minn.
Vandal	1991	USA	Idaho
Wildcat	1987	CAN	Alberta
WS[b] 1616	1972	MEX/USA	Calif.
WS 6	1973	MEX/USA	Calif.
Yolo	1981	USA	Calif.
Cluster D			
AC Tabor	1991	CAN	Sask
CDC Biggar	1989	CAN	Sask
Genesis	1988	CAN	Sask
HY 320	1985	CAN	Sask
Cluster E			
Angus	1978	USA	Minn.
Benito	1979	CAN	Man
Bergen	1990	USA	Colo.
Bounty 309	1974	USA	Colo.
Buckshot	1983	USA	Colo.
CDC Makwa	1990	CAN	Sask
CDC Teal	1991	CAN	Sask
Conway	1986	CAN	Sask
Copper	1987	USA	Idaho
Courtney	1983	USA	Calif.
Cutless	1986	USA	N.D
Erik	1983	USA	Colo.
Gus	1989	USA	N.D.
Kitt	1975	USA	Minn.
Lancer	1985	CAN	Sask
Leader	1981	CAN	Sask
Lew	1976	USA	Mont.
Marberg	1980	USA	Mont.
Marshall	1982	USA	Minn.
Minnpro	1989	USA	Minn.
Napayo	1972	CAN	Man
Pioneer 2369	1982	USA	Minn.
Pioneer 2375	1989	USA	Minn.
Pondera	1980	USA	Mont.
PR 2360	1981	USA	Mont.
Profit 75	1974	USA	Calif.
Prospect	1988	USA	S.D
Roblin	1986	CAN	Man
Sinton	1975	CAN	Sask
Spillman	1987	USA	Wash.
Stoa	1984	USA	N.D.
Success	1984	USA	Colo.
Tioga	1974	USA	N.D.
W 2501	1988	USA	Colo.
W 2502	1988	USA	Colo.
Walera	1984	USA	Minn.
Wared	1972	USA	Wash.
Wheaton	1983	USA	Minn.
WS 25	1976	MEX/USA	Calif.
Cluster F			
AC Minto	1991	CAN	Man
Borah	1974	USA	Idaho
Columbus	1980	CAN	Man
Katepwa	1981	CAN	Man
Kenyon	1985	CAN	Sask
Pasqua	1990	CAN	Man
Cluster G			
Barton	1975	USA	N.D.
Canuck	1974	CAN	Sask
Chester	1976	CAN	Alberta
Dalen	1991	USA	Colo.
Leif	1985	USA	Minn.
Nordic	1986	USA	Colo.
Rick	1988	USA	Utah
Shield	1986	USA	S.D.
Wynne	1982	USA	Utah
Cluster H			
Alex	1981	USA	N.D.
Bannock	1972	USA	Idaho
Hi-Line	1991	USA	Mont.
Newana	1976	USA	Mont.
Norana	1973	USA	Mont.
Pinnacle	1989	USA	Idaho
Shortana	1971	USA	Mont.

Table 4 Continued

Name	Release date	Origin	State
Cluster I			
Amidon	1988	USA	N.D.
Celtic	1986	USA	Colo.
Coteau	1978	USA	N.D.
Ellar	1974	USA	N.D.
Fjeld	1989	USA	Colo.
Len	1979	USA	N.D.
Norquay	1974	CAN	Man
Nowesta	1973	USA	N.D.
Olaf	1973	USA	N.D.
Probrand 711	1984	USA	Minn.
SU 28-1	1976	USA	N.D.
Telemark	1987	USA	Colo.
Tracey	1979	USA	Calif.
Cluster J			
Butte	1977	USA	N.D.
Butte 86	1986	USA	N.D.
Centa	1982	USA	S.D.
Grandin	1989	USA	N.D.
James	1979	USA	S.D.
Sharp	1990	USA	S.D.
Vance	1989	USA	Minn.
Cluster K			
Henry	1944	USA	Wis.
Lathrop	1961	USA	Wis.
Cluster L			
Belvedere	1985	CAN	PEI
Golden 86	1986	USA	Mont.
Laval-19	1978	CAN	Quebec
Max	1986	CAN/FDR	Nova Scot.
Milton	1981	CAN	PEI
Panther	1989	USA	Mont.
Sorrel	1989	USA	Mont.
Tammy	1986	USA	Calif.
Vernon	1979	CAN	PEI
Vigal	1990	USA	Alaska
Wampum	1978	USA	Wash.
Cultivars with unknown or unrecorded pedigrees			
Accord	1991	USA	Mont.
Aim	1979	USA	Mont.
Apex 83	1983	USA	Mont.
Baker	1987	USA	Ariz.
Brute	1985	USA	Mont.
Cavalier	1990	USA	Ariz.
Challenger	1983	USA	Ariz.
Chena	1990	USA/FIN	Alaska
Discovery	1986	USA	Mont.
DK-22S	1978	USA	Tex.
DK-33S	1978	USA	Tex.
DK-49S	1978	USA	Tex.
Funks W-406	1971	USA	Ariz.
Funks W-408	1971	USA	Ariz.
Nordak	1971	USA	N.D.
Norseman	1984	USA	Colo.
Poco Red	1991	USA	Ariz.
Rambo	1986	USA	Mont.
WB[c] 906R	1980	USA	Mont.
WB 911	1981	USA	Mont.
WB 926	1987	USA	Mont.
WS 1	1974	USA	Calif.

[a] CIMMYT, Mexico developed wheats released in the US
[b] WS: World Seeds
[c] WB: Westbred

creasing genetic similarity. As breeders began crossing to introduce disease and insect resistance, the similarity of the wheat crops declined. This is consistent with other studies of wheat and barley (Cox et al. 1986; Martin et al. 1991; Souza et al. 1994) in concluding that agricultural systems with well-developed cereal breeding programs tend toward lower levels of similarity among released cultivars and can maintain low levels of similarity for extended periods of time. Wheat producers in North America (Cox et al. 1986), and in other wheat production areas (Souza et al. 1994), tend to choose a limited number of cultivars from among those available. The effect of relative areas of cultivar production is generally to increase the level of genetic similarity in a production system (Souza et al. 1994). Area of production was not examined in this study, but it can be assumed that grower selection among cultivars would increase the similarity of hard spring crop above the estimates presented in this study. In Canada, where the dominant market class is CSRS, the high similarity of cultivars in that class ($r>0.5$) and large production area would significantly raise an area-adjusted similarity value.

Groups of similar cultivars were formed by applying cluster analysis to the COP matrix for cultivars released from 1941 to 1991. The clustering procedure was stopped when the clusters (designated clusters A to L) accounted for 80% of the variation within the COP matrix. Cultivars released after 1971 are presented in Table 4 listed by cluster. The largest number of cultivars could be divided roughly into three sets. Clusters E to J represents the core of the hard spring germ plasm, consisting of 63 cultivars with strong COP similarities to older germ plasm such as Thatcher and strong similarities to each other. The close relationship of these six clusters is supported by the plot of the principal-component coefficients of the matrix of COP similarity between cultivar clusters (Fig. 1). The second group of cultivars was represented by clusters A to C, which represent 63 cultivars with a high frequency of CIMMYT germ plasm appearing in their pedigrees. Cluster L represents a third group of 22 cultivars with low similarity to each other ($r=0.08$) and to other clusters (below $r=0.3$). Most of the cultivars in cluster L are utility wheats from Canada with significant European parentage (e.g.,

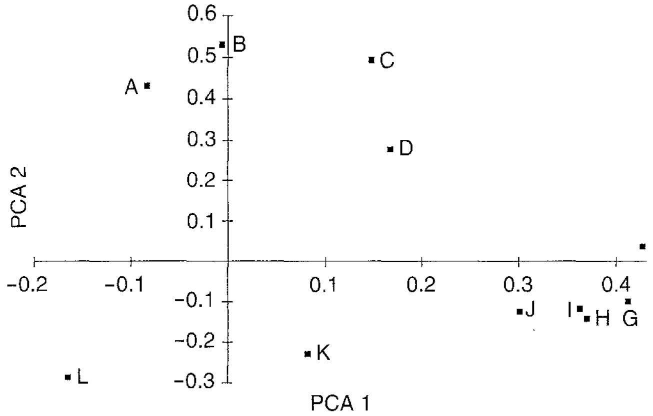

Fig. 1 Similarity of pedigree clusters A to L plotted using principal component analysis: prinicpal component axis 1 (*PCA 1*) and 2 (*PCA 2*) accounted for 65% of the variation in the matrix of parentage similarity among the 12 clusters

'Max and 'Vernon') or private cultivars from the US with unusual or partially incomplete pedigrees (e.g., 'Sorrel'). In addition to these three large groups, cluster D has six cultivars, including HY 320 and cultivars derived from HY 320. Cluster K contains 'Henry' and 'Lathrop', a backcross derivative of Henry.

Within the group of cultivars in clusters E to J, clusters E and F and clusters F and H were the most similar (average r>0.30 between cultivars in the paired clusters). Cluster F is composed of 17 cultivars of which only five were released after 1970 and all have a high degree of pedigree similarity to Thatcher. Cluster-E cultivars were derived from introgression of CIMMYT germ plasm into the Thatcher background. Cultivars in cluster H were derived from backcrosses to 'Centana' (pedigree: Pilot 13/ Thatcher//Pilot 13; backcross examples: 'Shortana', 'Norana', and 'Bannock') or from the pyramiding of parents closely related to 'Centana' (e.g. 'Hi-Line'). Clusters G and J are the least similar clusters (average r between clusters: 0.08) among the core clusters E to J. Cluster J contains cultivars derived from Butte or germ plasm closely related to Butte.

The clusters presented here represent a stratification of the hard spring germ plasm. Sampling of cultivars for genetic or physiology studies could utilize these clusters in sampling a cross-section of the North American hard spring germ plasm with a minimum number of cultivars. Cowen and Frey (1987) and Souza and Sorrells (1991) have suggested that intermating parents with low, rather than high, genetic similarity would result in progeny populations with higher genetic variances. The optimum parental combinations would be parents that are well adapted to the environment of selection and have low COP values. For example, cluster F represents the core Thatcher-derived hard spring germ plasm and clusters A and L are least similar to cluster F (average similarity of A and L with F, r=0.05). Therefore, crosses between these clusters should result in progeny with greater genetic variation than crosses among cultivars within cluster F (average similarity r=0.61) or crosses between clusters E and F (average similarity, r=0.32).

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