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ORIGINAL PAPER

The genetic diversity of UK, US and Australian cultivars of *Triticum aestivum* measured by DArT markers and considered by genome

J. White · J. R. Law · I. MacKay · K. J. Chalmers · J. S. C. Smith · A. Kilian · W. Powell

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Abstract The genetic diversity of UK, US and Australian wheat varieties over the period of modern plant breeding is estimated using diversity array technology markers. Diversity is assessed by both genetic distance between varieties, by AMOVA and as the volumes of multi-dimensional convex hulls estimated from principal co-ordinate analysis. At the whole genome level the three populations are genetically distinct; this is also true of the B genome. However, the US and Australian D genomes are found to occupy the same region of diversity space and the A genomes for these countries are partially overlapping. The use of high-density genotyping with a common marker set allows an unprecedented direct comparison between the diversities of the national populations, between individual genomes and the fluctuation of diversity over time. The highest genetic diversity amongst varieties is reported in the Australian population followed by the US, which in turn is more diverse than the UK. However the average diversity of loci is higher in the US set than in the Australian. Non-random fluctuations in genetic diversity over time are observed.

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J. White (✉) · J. R. Law · I. MacKay · W. Powell
National Institute of Agricultural Botany,
Huntingdon Road, Cambridge CB3 OLE, UK
e-mail: jon.white@niab.com

K. J. Chalmers
Molecular Plant Breeding CRC,
School of Agriculture Food and Wine, University of Adelaide,
Waite Campus, PMB1 Glen, Osmond, Australia

J. S. C. Smith
Pioneer Hi-Bred International Inc., Johnston,
IA 501310184, USA

A. Kilian
DArT P/L, PO Box 7141, Yarralumla,
Canberra, ACT 2600, Australia

Introduction

What level of genetic diversity is deployed as part of modern wheat production is a complex question, which must be viewed at both strategic and operational levels. Operationally, elite germplasm is supplied to farmers as (morphologically) distinct and uniform varieties; this germplasm has been a corner-stone of the green revolution. However, each such variety contains within it very little genetic diversity. So, operationally, genetic diversity in modern agriculture is a function of the range of varieties grown by farmers in a given geographical area at a given time. Growers select only the most potentially profitable genotypes so only a small number of the available varieties are grown at any time. [Economic pressures militating against the maximisation of agricultural biodiversity are discussed in more detail by Rubenstein et al. (2005).] This situation is sometimes interpreted as evidence of reduced genetic diversity amongst modern varieties, and modern plant-breeding techniques (repeatedly crossing and selecting among the best available varieties) are cited as being detrimental to the maintenance of diversity [Fowler and Mooney 1990; Food and Agriculture Organisation of the United Nations (FAO) 1996; Whatley 1997; Altieri 1999; Jana 1999; Tuxill 1999; The Soil Association 2001; Picone and Van Tassel 2002; Intermediate Technology Development Group 2002; Colley 2002; Phillips and Wolfe 2004]. If true this would be of serious strategic concern since genetic diversity is the raw material from which new varieties suitable for changing economic, agricultural and natural environments are produced.

A fuller picture of genetic diversity amongst modern wheat varieties should take account of the fact that, in addition to wheat varieties deployed by farmers, there exist a larger number of contemporaneous varieties which are offered to the market but never widely grown. An even larger number of varieties achieve plant breeders rights (a form of intellectual property protection, see; DEFRA 2006; UPOV 2002) but are never marketed. Still greater numbers of breeding lines are maintained by plant breeders and in collections of historic varieties and landraces maintained in germplasm collections (Bioversity International 2007). Thus a potentially very diverse genetic resource exists additional to the small number of varieties deployed by growers. The question remains, however, whether the genetic diversity available has changed due to the activities of plant breeders?

To address this, many studies have now been conducted looking specifically at the change in the genetic diversity of the wheat variety pool over the past 100–150 years. Although these studies have consistently noted a reduction in diversity between landraces and modern cultivars, they have reached different conclusions as to the trend in diversity over the period of modern plant breeding. Reduced diversity over time is reported in Canada by Fu et al. (2005, 2006) and in China (Tian et al. 2005; Chenyang et al. 2006), whereas constant or increasing diversity is observed by Smale et al. (2002), Reif et al. (2005) and Warburton et al. (2006) among International Maize and Wheat Improvement Centre (CIMMYT) lines, Roussel et al. (2004) (France), Khlestkina et al. (2004) (Eurasia), Mercado et al. (1996) (N. America), Martynov et al. (2005) (Russia), Donini et al. (1997) (UK) Huang et al. (2007) (NW Europe) and Lang et al. (2004) (Hungary). Overall a picture of relatively constant genetic diversity over time is emerging although a deficit still remains in that each of the published studies uses different sets of molecular markers and so comparison between geographical areas—or extrapolation to conclusions about the diversity of the global wheat crop—can be no more than tentative.

Apart from the strategic importance of genetic diversity to agriculture there is an interesting question arising from the evolutionary history of the crop. The species, *Triticum aestivum*, evolved relatively recently and is an allohexaploid. The three genomes are designated A, B and D and originate from *T. urartu*, *T. speltoides* and *Aegilops Tauschii*, respectively (Dvorak et al. 1993; Baum and Bailey 2004). The relative diversities of these three genomes may themselves give insights into the evolution and domestication of the species.

Our objectives were: to add to the growing evidence of the effect of modern plant breeding on genetic diversity over time, to compare this effect in three different geographic locations, to assess the relative diversity of wheat in the three locations and to exploit the high density diversity array technology (DArT) wheat markers (Akbari et al. 2006) to allow some comparison at the level of individual wheat genomes.

Materials and methods

Sample selection

Variety sets were chosen to represent varieties released for commercial use principally during the period 1930–2005 in the UK (94 varieties), US (96 varieties) and Australia (50 varieties). Seeds were obtained from national and international germplasm collections. Lists of varieties together with date of commercialisation, utility group and breeder are given in Tables 1, 2 and 3.

DNA extraction—UK and US sets

Fifteen seeds were placed on filter paper (Munktell, 264001, 190 mm × 400 mm) which had been previously folded in half (190 mm × 200 mm) and saturated in tap water. Filter papers and seeds were sealed in light-proof aluminium boxes and stored at 4°C (48 h) both to imbibe and break residual dormancy. The boxes were then transferred to a germination room (20°C) until the coleoptile length was 1.5–3 cm (about 6 days).

For each variety ten coleoptiles were selected and cut from the grain. Each of the ten coleoptiles 2 mm (grain end) was taken and combined for DNA extraction.

Qiagen DNeasy® 96-well plant kits were used for DNA extraction in accordance with the manufacturer's instructions. The Retsch MM300 Mixer Mill system was used for tissue disruption. The final eluate comprised 2 × 50 µl, combined.

DNA extraction—Australian set

The DNA was extracted from leaves of 2-week-old wheat seedlings using a modified cetyltrimethylammonium bromide method (Doyle and Doyle 1987).

DArT genotyping—all samples

DArT is an array based genotyping technology, the markers are binary and dominant. The bases of polymorphism in DArT genotyping are SNPs and INDELs at restriction enzyme cutting sites and large INDELs within restriction fragments.

The development of the marker set used in this study is described by Akbari et al. (2006). DArT genotyping of wheat is offered as a commercial service by Triticarte Pty Ltd, Yarralumla, ACT, Australia (www.triticarte.com.au)

Table 1 UK variety set

Year first commercialised	Variety name (synonym)	Country of origin	Breeder	Utility
1931	Iron III	Scandinavia	Unknown	Feed
1931	Little Joss	UK	Sir Rowland Biffen	Bread
1931	Squareheads Master (Standard Red)	UK	Adopted by Plant Breeding Institute	Biscuit
1931	Wilhelmina	Netherlands	Plant Breeding Inst Wageningen	Biscuit
1931	Yeoman	UK	Plant Breeding Institute	Bread
1935	Holdfast	UK	Plant Breeding Institute	Bread
1935	Juliana	Netherlands	Plant Breeding Inst Wageningen	Biscuit
1935	Steel	Scandinavia	Unknown	Bread
1938	Chevalier	Scandinavia	Unknown	–
1938	Crown	Scandinavia	Unknown	–
1938	Desprez 80 (Joncquois)	France	Desprez	Bread
1940	Warden	UK	Gartons Ltd	Bread
1940	Wilma	Netherlands	Plant Breeding Inst Wageningen	Biscuit
1942	Gartons 60	UK	Gartons Ltd	–
1942	Steadfast	UK	Plant Breeding Institute	Biscuit
1943	Bersee	France	M. Blondeau	Feed
1944	Jubilegem	Belgium	Belgia State Plant Breeding Institution	Feed
1944	Vilmorin 27	France	Vilmorin-Andrieux	Feed
1944	Vilmorin 29	France	Vilmorin-Andrieux	Feed
1947	Redman	UK	Gartons Ltd	Bread
1947	Victor	UK	Gartons Ltd	Biscuit
1950	Hybrid 46	UK	Marsters Ltd	Feed
1950	Pilot	UK	Gartons Ltd	Feed
1950	Staring	Netherlands	Central Bureaux, Rotterdam	Feed
1952	King II	Denmark	Pajbjerg Foundation	Feed
1953	Capelle Desprez	France	Desprez	Bread
1954	Masterpiece	UK	Gartons Ltd	Bread
1954	Minister	Belgium	State Plant Breeding Station, Gembloux	Biscuit
1956	Banco	Sweden	Weibullsholm	
1956	N59	UK	Milns Ltd	Feed
1957	Dominator	UK	Milns Ltd	–
1958	Milfast	UK	Milns Ltd	Bread
1960	Elite Lepeuple	France	Lepeuple	Bread
1960	Flamingo	Denmark	F. Heine	Biscuit
1960	Professeur Marchal	Belgium	Gembloux	Biscuit
1962	Champlein	France	Claude Beoist	Feed
1963	Thor	Sweden	Weibull	Feed
1964	Rothwell Perdix	Denmark	F. Heines	Biscuit
1965	Kloka	Denmark	Von Rumker	Feed
1965	Maris Widgeon	UK	Plant Breeding Institute	Bread
1968	Joss Cambier	France	Cambier	Feed
1968	Maris Ranger	UK	Plant Breeding Institute	Biscuit
1969	Cama	Belgium	Gembloux	Feed
1969	West Desprez	France	Desprez	Bread
1971	Maris Nimrod	UK	Plant Breeding Institute	Biscuit
1972	Bouquet	France	Desprez	Feed
1972	Maris Huntsman	UK	Plant Breeding Institute	Feed

Table 1 continued

Year first commercialised	Variety name (synonym)	Country of origin	Breeder	Utility
1973	Atou	France	Guilleman	Feed
1973	Val	Belgium	Jorion	Biscuit
1974	Flinor	France	Legland	Bread
1974	Mega	UK	Rothwell Plant Breeders	Feed
1975	Maris Fundin	UK	Plant Breeding Institute	Feed
1977	Kador	France	Ringot	Feed
1978	Armada	UK	Rothwell Plant Breeders	Bread
1978	Hustler	UK	Plant Breeding Institute	Feed
1979	Aquila	UK	Rothwell Plant Breeders	Feed
1979	Brigand	UK	Plant Breeding Institute	Biscuit
1979	Virtue	UK	Plant Breeding Institute	Feed
1980	Avalon	UK	Plant Breeding Institute	Bread
1980	Copain	France	Benoist	Bread
1981	Norman	UK	Plant Breeding Institute	Biscuit
1981	Rapier	UK	Miln Marsters	Biscuit
1982	Fenman	UK	Plant Breeding Institute	Biscuit
1983	Galahad	UK	Plant Breeding Institute	Feed
1983	Longbow	UK	Plant Breeding Institute	Biscuit
1983	Stetson	UK	Rothwell Plant Breeders	Feed
1984	Mission	UK	Rothwell Plant Breeders	Bread
1986	Mercia	UK	Plant Breeding Institute	Bread
1986	Slejpner	Sweden	Weibull	Feed
1988	Apollo	Denmark	Breun	Feed
1989	Riband	UK	Plant Breeding Institute	Biscuit
1990	Beaver	UK	Plant Breeding Institute	Feed
1990	Haven	UK	Plant Breeding Institute	Feed
1991	Hereward	UK	Plant Breeding Institute	Bread
1992	Admiral	UK	ICI	Biscuit
1992	Torfrida	UK	Plant Breeding Institute	Feed
1993	Brigadier	UK	ICI	Feed
1993	Genesis	France	Serasem	Bread
1993	Hunter	UK	Plant Breeding Institute	Feed
1993	Spark	UK	Nickerson	Bread
1994	Cadenza	UK	Cambridge Plant Breeders	Bread
1994	Flame	UK	Nickerson	Feed
1995	Soissons	France	Desprez	Bread
1997	Charger	UK	Plant Breeding Institute	Bread
1999	Claire	UK	Nickerson	Biscuit
1999	Malacca	UK	CPB Twyford	Bread
2001	Option	UK	Monsanto (Successor to Plant Breeding Institute)	Bread
2001	Tanker	UK	Elsoms	Feed
2003	Robigus	UK	CPB Twyford	Biscuit
2004	Dickson	Netherlands	Cebeco	Biscuit
2004	Smuggler	UK	Advanta	Feed
2004	Cordiale	UK	CPB Twyford	Bread
2004	Gladiator	UK	Monsanto (Successor to Plant Breeding Institute)	Feed
2005	Glasgow	Denmark	Saaten Union	Feed

Table 2 Australian variety set

Release date	Line	State	Breeder
1901	Federation	NSW	W. Farrer, Lambrigg
1915	Nabawa	NSW	Chapman Experiment Farm. Cross made in NSW at Wagga, reselected at Chapman farm WA
1924	Ranee	Vic	Werribee State Farm
1927	Dundee	NSW	Cowra Experiment Farm
1930–1940	Dirk	SA	Roseworthy Agricultural College
1945	Gabo	NSW	Sydney University
1946	Insignia	Vic	State Research Farm, Werribee, Mallee Research Station
1950	Veranopolis		Brazilian
1952	Spica	Qld	Roma State Farm
1956	Olympic	Vic	Longerenong Agricultural College
1959	Heron	NSW	Wagga Agricultural Institute
1960	Falcon	NSW	Wagga Agricultural Research Institute
1960	GAMENYA	NSW	Sydney University
1960	Mengavi	NSW	Sydney University
1960's	WW80		NSW Wagga Research Institute
1963	Festiguay	NSW	Department of Agriculture, NSW
1963	Raven	NSW	Wagga Research Institute
1966	Glaive	SA	Roseworthy Agricultural College
1967	TIMGALEN	NSW	University of Sydney, North West Wheat Research Institute
1969	GATCHER	NSW	Sydney University
1969	Halberd	SA	Roseworthy Agricultural College
1973	Condor	NSW	Agricultural Research Institute Wagga Wagga
1973	Kite	NSW	Agriculture
1973	WW15		Introduction from CIMMYT
1974	Madden	WA	
1974	OXLEY	Qld	University of Queensland/Queensland Department of Primary Industries
1977	COOK	Qld	Queensland Department of Primary Industries
1977	Tincurrin	WA	Agriculture WA
1978	Millewa		Introduction from CIMMYT
1978	WARIGAL	SA	Waite Institute
1979	Banks	NSW	Queensland Wheat Research Institute
1981	Aroona	SA	Waite Institute University of Adelaide
1982	Eradu	WA	Agriculture WA
1982	Hartog	Qld	Queensland Department of Primary Industries
1982	Matong	Vic	Department of Agriculture, Victoria
1984	Dagger	SA	Roseworthy Agricultural College
1984	Meering	Vic	Horsham, Agriculture Victoria
1984	Spear	SA	Roseworthy Agricultural College
1985	Machete	SA	Roseworthy Agricultural College
1985	Rosella	NSW	NSW Agriculture
1986	Lowan	Vic	Horsham, Agriculture Victoria
1986	Schombergk	SA	Waite Institute University of Adelaide
1986	Sunco	NSW	The University of Sydney Plant Breeding Institute
1988	Molineux	SA	Waite Institute, University of Adelaide
1988	Tatiara	SA	Waite Institute, University of Adelaide
1989	CD87		Cross Made at Horsham, Agriculture Victoria, Unreleased line

Table 2 continued

Release date	Line	State	Breeder
1989	Janz	Qld	Queensland Wheat Research Institute
1990	Cunningham	Qld	Queensland Wheat Research Institute
1991	Excalibur	SA	Roseworthy Agricultural College
1991	Yarralinka	SA	Waite Institute University of Adelaide
1992	CADOUX	WA	Agriculture Western Australia
1992	Sunland	NSW	The University of Sydney Plant Breeding Institute
1992	Sunstate	NSW	The University of Sydney Plant Breeding Institute
1993	Amery	WA	Agriculture Western Australia
1993	Barunga	SA	Waite Institute University of Adelaide
1987	BD159	Vic	Horsham, Agriculture Victoria
1993	Beulah	Vic	Horsham, Agriculture Victoria
1993	Goroke	Vic	Horsham, Agriculture Victoria
1993	Tasman	Qld	Queensland Wheat Research Institute
1993	Trident	SA	Roseworthy Agricultural College
1994	Cascades	WA	Agriculture Western Australia
1994	Frame	SA	Waite, University of Adelaide
1994	Sunvale	NSW	The University of Sydney Plant Breeding Institute
1994	Tammin	WA	Agriculture Western Australia
1996	Carnamah	WA	Agriculture Western Australia
1996	Goldmark	Vic	Horsham, Agriculture Victoria
1997	Diamondbird	NSW	NSW Agriculture (selection from CIMMYT introduction Pavon)
1997	Krichauff	SA	University of Adelaide, Waite Institute
1997	Westonia	WA	Agriculture Western Australia
1998	Bowie	SA	Roseworthy Agricultural College
1998	Camm	WA	Agriculture Western Australia
1998	H45	NSW	Sunprime Seeds, Tamworth
1999	Kukri	SA	Roseworthy
1999	YITPI	SA	Waite, University of Adelaide

SA South Australia, *WA* Western Australia, *NSW* New South Wales, *Vic* Victoria, *Qld* Queensland

who conducted the analyses for this study. DArT technology is protected by patent No. WO 01/73119.

Genetic distance

Average genetic distance (Nei and Takizaki 1983) between varieties was used as an index of genetic diversity. Calculation was performed using PowerMarker software (Lui and Muse 2005) which produced a matrix of distance between all possible pairs of varieties. In the analysis the dominant biallelic DArT marker data were treated as haploid data. The varieties were sub-divided by group (US, UK, AUS) and sorted in order of date of first release. A rolling five variety mean genetic distance was then calculated through the time series together with a corresponding five variety mean date of first release.

Genetic distance was calculated using all available markers and then markers in sub-sets corresponding to the A, B and D genomes. A summary of the markers used is given in Table 4.

Principle co-ordinate analysis

To assess and visualize the positions of varieties in diversity space (as opposed to just the genetic distances between the varieties) principle co-ordinate analysis was applied separately to markers in each genome and to all markers together (Koebner et al. 2003). Varieties were identified by country of origin in these analyses. Principal co-ordinate analyses were computed using GenStat [Release 9.1 Copyright 2006, Lawes Agricultural Trust (Rothamsted Experimental Station) supplied by VSN International].

Volumes of convex hulls

The volumes of convex hulls in five dimensions were used as an alternative measure of genetic diversity.

The convex hull of a set of points is the smallest convex set that contains the points. In two-dimensions (2D) it is possible to join the extreme points from the PCO plot on the plane, this can be considered as defining the diversity space—see Donini

Table 3 US variety set

Year first commercialised	Variety name	Origin/breeder	Utility
1845	Red May	Virginia selection from White May early 1800s?	SRW
1871	Fultz	Abraham Fultz, Mifflin County, PA	SRW
1900	Turkey	Settlers in the plains states brought it in from Russia, Black Sea region	HRW
1884	Currell	W.E. Currell, VA	SRW
1880	Poole	Unknown	SRW
1886	Fulcaster	S.M. Schindel, Hagerstown, MD	SRW
1940	Red Chief	Earl G. Clark, Sedgwick, KS	HRW
1907	Leap	J.S. Leap, VA	SRW
1908	Trumbull	C.G. Williams, Ohio Agricultural Experiment Station, Wooster, OH	SRW
1917	Blackhull	Earl G. Clark, Sedgwick, KS	HRW
1917	Kanred	Samuel C. Salmon, Kansas Agricultural Experiment Station, Manhattan, KS	HRW
1918	Nebraska No. 60	T.A. Kiesselbach, University of Nebraska, Nebraska Agricultural Experiment Station, Lincoln, NE	HRW
1918	Nittany	C.F. Noll, Pennsylvania Agricultural Experiment Station, State College, PA	SRW
1955	Vermillion	Purdue University Agricultural Experiment Station and USDA-ARS	SRW
1921	Redhart	Coker's Pedigreed Seed Co., Hartsville, SC	SRW
1923	Ridit	E.F. Gaines, Washington Agricultural Experiment Station, Pullman, WA	HRW
1924	Purkof	A.T. Wiancko, Purdue University, W. Lafayette, IN	HRW
1933	Early Blackhull	A.P. Haeberle, Clearwater, KS	HRW
1929	Kawvale	Kansas Agricultural Experiment Station, Manhattan, KS	SRW
1932	Tenmarq	Kansas Agricultural Experiment Station, Manhattan, KS	HRW
1933	Cheyenne	T.A. Kiesselbach, University of Nebraska, Nebraska Agricultural Experiment Station, Lincoln, NE	HRW
1987	Clark	Purdue University Agricultural Experiment Station and USDA-ARS	SRW
1935	Chiefkan	Earl G. Clark, Sedgwick, KS	HRW
1937	Thorne	L.E. Thatcher, Ohio State University, OARDC, Wooster, OH	SRW
1938	Nebred	T.A. Kiesselbach, University of Nebraska, Nebraska Agricultural Experiment Station, Lincoln, NE	HRW
1940	Triumph	Joseph E. Danne, El Reno, OK	HRW
1941	Pawnee	University of Nebraska, Nebraska Agricultural Experiment Station, Lincoln, NE	HRW
1944	Westar	Texas Agricultural Experiment Station and USDA Division of Cereal Crops and Diseases	HRW
1944	Wichita	Kansas Agricultural Experiment Station, Manhattan, KS	HRW
1946	BlueJacket	Earl G. Clark, Sedgwick, KS	HRW
1946	Vigo	Purdue University Agricultural Experiment Station and USDA-BPI	SRW
1947	Butler	C.A. Lamb, Ohio State University, OARDC, Wooster, OH	SRW
1947	Chancellor	Georgia Agricultural Experiment Station in cooperation with USDA Cereal Crops and Diseases	SRW
1947	Royal	L.H. Smith, University of Illinois, Illinois Agricultural Experiment Station, Urbana, IL	SRW
1976	Vona	Dr James R. Welsh, Colorado State University, Fort Collins, CO	HRW
1950	Seneca	C.A. Lamb, Ohio State University, OARDC, Wooster, OH	SRW
1950	Kiowa	Kansas Agricultural Experiment Station, Manhattan, KS	HRW
1953	Knox	Purdue University Agricultural Experiment Station and USDA-ARS	SRW
1955	Dual	Purdue University Agricultural Experiment Station and USDA-ARS	SRW
1956	Bison	Kansas Agricultural Experiment Station and USDA-ARS	HRW
1957	Super Triumph	Joseph E. Danne, El Reno, OK	HRW
1942	Improved Triumph	Joseph E. Danne, El Reno, OK	HRW

Table 3 continued

Year first commercialised	Variety name	Origin/breeder	Utility
1959	Monon	Purdue University Agricultural Experiment Station and USDA-ARS	SRW
1951	Pennoll	C.F. Noll, Pennsylvania Agricultural Experiment Station, State College, PA	SRW
1959	Wakeland	North Carolina State University, North Carolina Agricultural Experiment Station, Raleigh, North Carolina	SRW
1960	Kaw	Kansas and Oklahoma Agricultural Experiment Stations	HRW
1960	Ottawa	Kansas Agricultural Experiment Station and USDA-ARS	HRW
1960	Redcoat	Purdue University Agricultural Experiment Station and USDA-ARS	SRW
1960	Warrior	Nebraska Agricultural Experiment Station and the USDA-ARS-CR	HRW
1967	Blueboy	North Carolina State University, North Carolina Agricultural Experiment Station, Raleigh, North Carolina	SRW
1964	Scout	Nebraska Agricultural Experiment Station and the USDA-ARS-CR	HRW
1966	Parker	Kansas Agricultural Experiment Station and USDA-ARS	HRW
1966	Sturdy	Texas Agricultural Experiment Station and the USDA-ARS-CR	HRW
1967	Scout 66	Nebraska Agricultural Experiment Station and the USDA-ARS-CR	HRW
1968	Arthur	Purdue University Agricultural Experiment Station and USDA-ARS	SRW
1968	Logan	Dr Howard N. Lafever, Ohio State University, OARDC, Wooster, OH	SRW
1970	Eagle	Kansas Agricultural Experiment Station and USDA-ARS	HRW
1971	Arthur 71	Purdue University Agricultural Experiment Station and USDA-ARS	SRW
1971	Centurk	Nebraska Agricultural Experiment Station and the USDA-ARS-CR	HRW
1972	Abe	Purdue University Agricultural Experiment Station and USDA-ARS	SRW
1971	Coker 68-15	Howard F. Harrison, Coker's Pedigreed Seed Co., Hartsville, SC	SRW
1976	Coker 747	Howard F. Harrison, Coker's Pedigreed Seed Co., Hartsville, SC	SRW
1976	Hart	University of Missouri, Columbia, Missouri	SRW
1976	Larned	Kansas Agricultural Experiment Station and SEA-USDA	HRW
1978	Newton	Kansas Agricultural Experiment Station and USDA-ARS	HRW
1979	TAM 105	Texas Agricultural Experiment Station and AR-SEA-USDA	HRW
1971	TAM W-101	Kenneth B. Porter, Texas A&M University, Texas A&M University Agricultural Research and Extension Centre, Amarillo, TX	HRW
1979	TAM W-105	Texas Agricultural Experiment Station and AR-SEA-USDA	HRW
1980	Coker 762	Coker's Pedigreed Seed Co., Hartsville, SC	SRW
1977	McNair 1003	McNair Seed Company, Laurinburg, North Carolina	SRW
1980	Pike	University of Missouri, Columbia, Missouri	SRW
1981	Caldwell	Purdue University Agricultural Experiment Station and USDA-ARS	SRW
1982	Hawk	North American Plant Breeders Inc., Berthoud, CO	HRW
1984	TAM 107	Texas Agricultural Experiment Station and the USDA-ARS	HRW
1986	Cardinal	Dr Howard N. Lafever, Ohio State University, OARDC, Wooster, OH	SRW
1987	2180	Pioneer Hi-Bred International Inc., Hutchinson, KS	HRW
1934	Clarkan	Earl G. Clark, Sedgwick, KS	SRW
1987	Dynasty	Dr Howard N. Lafever, Ohio State University, OARDC, Wooster, OH	SRW
1988	2548	Pioneer Hi-Bred International, Inc., Windfall, IN	SRW
1988	Karl	Kansas Agricultural Experiment Station and the USDA-ARS	HRW
1988	2163	Pioneer Hi-Bred International Inc., Hutchinson, KS	HRW
1990	Madison	Virginia Polytechnic Institute and State University, Blacksburg, VA	SRW
1990	Wakefield	Virginia Polytechnic Institute and State University, Blacksburg, VA	SRW
1991	Tomahawk	AgriPro, KS	HRW
1993	Alliance	Nebraska Agricultural Experiment Station and the USDA-ARS	HRW
1994	Jagger	Kansas Agricultural Experiment Station and the USDA-ARS	HRW

Table 3 continued

Year first commercialised	Variety name	Origin/breeder	Utility
1995	2137	Kansas Agricultural Experiment Station and the USDA-ARS (Pioneer germplasm)	HRW
1997	Coker 9663	Coker (Northrup, King & Company), Bay AR	SRW
1995	Hopewell	Dr Howard N. Lafever, Ohio State University, OARDC, Wooster, OH	SRW
1998	2174	Oklahoma Agricultural Experiment Station, Stillwater, OK (Pioneer germplasm)	HRW
2002	Jagalene	AgriPro, KS	HRW
1998	Patton	AgriPro, Lafayette, IN	SRW
1999	Roane	Virginia Polytechnic Institute and State University, Blacksburg, VA	SRW
2001	2145	Kansas Agricultural Experiment Station, Hays, KS (Pioneer germplasm)	HRW
2001	25R78	Pioneer Hi-Bred International Inc., Windfall, IN	SRW
2002	25R47	Pioneer Hi-Bred International Inc., Windfall, IN	SRW

Table 4 The distribution of all markers available by genome

Distribution by genome	DarT markers
Total available	379
A genome	130
B genome	188
D genome	54
Unmapped	7

et al. (1997), Law et al. (1997a, b). However, even in 2D the computation of the area of a convex hull is complex and the complexity increases when volumes are required even for modest higher dimensional problems. In this study the volumes of multi-dimensional convex hulls were calculated using the Qhull© (1998–2003) software which implements the Quickhull algorithm of Barber et al. (1996).

Statistical analysis

AMOVA (calculated using Arlequin version 2.0) was used to apportion variance—and hence diversity—to country and decade by country and 20-year period by country. This analysis was conducted for the whole genome and for the individual genomes. Both 10 and 20-year groups were examined to ensure that the results observed for the decadal groups were not merely artefacts of small sample sizes.

Statistical significance of the difference between mean genetic distances was assessed by *t*-test.

The diversity flux over time was tested to determine if the number of clear peaks and troughs were likely to have occurred by chance. We developed an algorithm to recognise sustained change in gradient of the curve of diversity over time. Each change from positive to negative gradient was counted as a peak and negative to positive was counted as a trough. The varieties were then randomly re-ordered with respect to time and the number of clear peaks and troughs was recalculated, this process was repeated 1,000 times. The number of peaks and troughs observed in our data was compared with the number observed in each of the 1,000 permutations to determine the significance of our observations.

Results

Genetic diversity, measured at the whole genome level, is different between the three national sample sets. The order of genetic diversity is AUS > USA > UK. This is true if genetic diversity is measured either as average genetic distance between varieties or as the volumes of convex hulls (see; Tables 7, 8). This agreement between methods does not persist at the level of individual genomes; whilst the average genetic distance method continues to rank the countries in the same order, ranking on the basis of the areas of convex hulls differs. The low diversity of the UK D genome relative to those of the US and Australia is evident in both Tables 7 and 8. However, differences between countries in terms of the volumes for other genomes are less noticeable and we have not yet developed tools to test their statistical significance.

The difference between means of genetic distance between varieties between countries was, in the majority of cases, highly significant (*t*-test; see notes to Table 7). However, by combining genomes between countries we show that the average diversity of the three genomes in the whole data set are similar and, frequently, statistically indistinguishable (Table 7). When all the data are combined the D genome is significantly less diverse than the A and B genomes, despite the high D genome diversity noted in the Australian population. This latter finding is consistent with the deficit in D genome markers reported for DArT by Akbari et al. (2006) (and also noted by these authors for other marker systems).

Results of the analysis of diversity change over time are presented in Fig. 1. This analysis serves to illustrate the

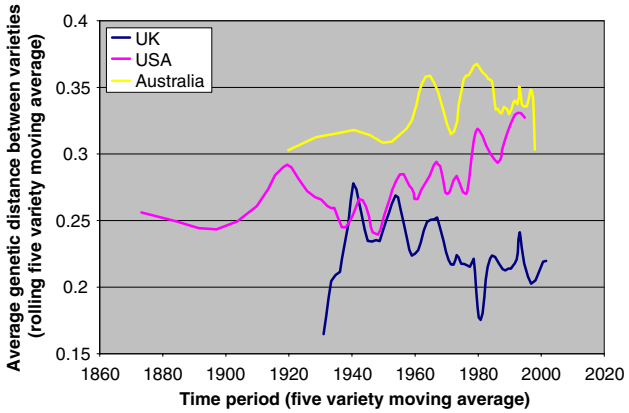

Fig. 1 Significant ($P = 0.001$) non-random fluctuation in genetic diversity between countries over time, all genomes

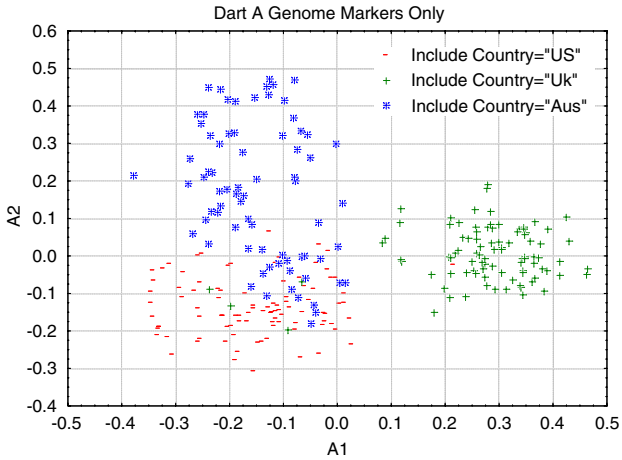

Fig. 2 Distribution of varieties in 2D PCO space (A genome)

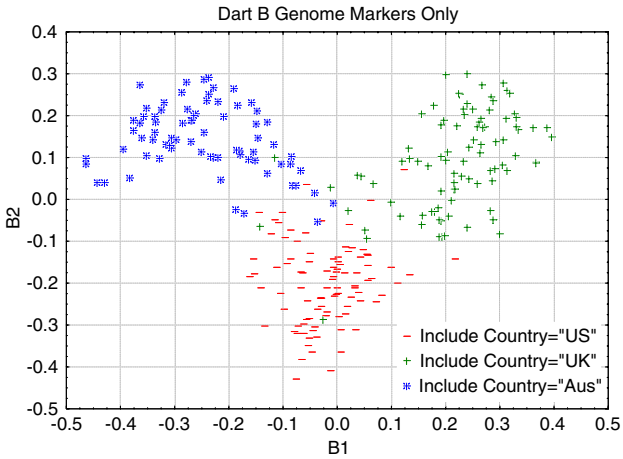

Fig. 3 Distribution of varieties in 2D PCO space (B genome)

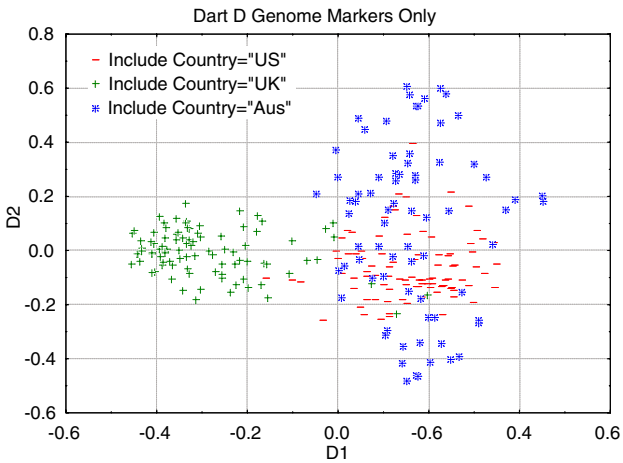

Fig. 4 Distribution of varieties in 2D PCO space (D genome)

difference in the average genetic distance between varieties between the three populations over time and also the changes within each population. Over the time period there has been an upward trend in diversity in the US whereas diversity in Australia and the UK has remained relatively constant. The fluctuations in diversity evident in Fig. 1 were found, by a permutation test, to be a rare outcome; less than 1% of all the (1,000) random permutations produced an equal or greater number of peaks and troughs. We are confident, therefore, that the fluctuation in diversity is real and not an artefact of the data manipulation. We also examined diversity flux over time within genomes within countries (data not presented) and found similar trends.

In addition to the question of relative diversity between countries and genomes we used principal co-ordinate analysis to determine the extent to which the three populations represent distinct areas of diversity space. Results show the three national populations are distinct with respect to the B genome (Fig. 2), but that in the case of A and D genome space the US and Australian populations are overlapping (Fig. 3, 4). This is particularly notable in the D genome. The UK population remains well distinguished in all cases. Analysis of the distinction between the populations on the basis of the whole genome (PCO and genetic distance, data not presented) shows complete distinction between the populations. On this basis it seems likely that each national population represents only a fraction of a larger gene pool.

AMOVA was used to apportion variance (diversity) between the country of origin and the decade of first registration for the three genomes, and for each genome individually. The country of origin accounts for about 10–20% of the diversity detected by DArT. This is greater than the variation accounted for by the decade (of first registration) within countries. It is interesting to note that about 80% of the diversity remains unaccounted for either by time or country of origin (see Tables 5, 6). We are currently

Table 5 AMOVA—decadal groups

	df	Sums of squares				Components of variance (% of total variation)			
		ABD all loci	A all loci	B all loci	D all loci	ABD all loci	A all loci	B all loci	D all loci
Between countries	*2*	1,853	487	859	363	4.88 (18.79)	1.28 (18.00)	2.27 (19.83)	0.97 (20.94)
Between decades within countries	*20*	1,307	358	581	218	2.08 (8.01)	0.57 (8.00)	0.94 (8.17)	0.34 (7.32)
Within decades within countries	*503*	9,565	2,643	4,146	1,672	19.02 (73.19)	5.26 (73.99)	8.24 (72.00)	3.32 (71.74)
Total components of variance (=100%)	*525*	12,725	3,488	5,586	2,253	25.98 (100)	7.10 (100)	11.45 (100)	4.63 (100)

Significance test (1,023 permutations): for all components of variance $P <= 0.001$

Table 6 AMOVA—20 year groups

	df	Sums of squares				Components of variance (% of total variation)			
		ABD all loci	A all loci	B all loci	D all loci	ABD all loci	A all loci	B all loci	D all loci
Between countries	*2*	1,853	487	859	363	4.71 (18.13)	1.22 (17.27)	2.19 (19.19)	0.94 (20.3)
Between 20 year groups within countries	*9*	897	230	359	138	1.70 (6.56)	0.48 (6.80)	0.75 (6.57)	0.28 (6.13)
Within 20 year groups within countries	*514*	10,055	2,772	4,368	1,752	19.56 (75.31)	5.39 (75.93)	8.50 (74.24)	3.41 (73.57)
Total	*525*	12,725	3,489	5,586	2,253	25.98 (100)	7.10 (100)	11.45 (100)	4.63 (100)

Significance test (1,023 permutations): for all components of variance $P <= 0.001$

investigating other factors which contribute to the maintenance or erosion of diversity using an extended marker set.

Discussion

We have attempted to inform the debate about the effect of plant breeding on the genetic diversity of varieties available to farmers in three geographic areas. In addition we have attempted to dissect the underlying diversity of the three wheat genomes and make similar comparisons between genomes and locations. The data set has also allowed some consideration of the diversity of the national sample sets as fractions of the total diversity of all the samples tested. We measured genetic diversity in three ways; the average genetic distance between varieties, the proportion of total diversity accounted in AMOVA and as the area of convex hulls in diversity space defined by principle co-ordinate analysis. Alternative metrics of distance and diversity could have been employed (e.g. coefficient of parentage, Smale et al. 2002) to test for increasing relatedness between varieties over time but we believe that the combination methods we used here were at least as good since they took account of genotypic similarity and were not confounded by backcrossing and selection which are often obscured in published pedigrees.

Considering whole genome diversity; in agreement with the consensus of other studies, our analyses show there is little evidence of a reduction in genetic diversity over the period of modern plant breeding. AMOVA (Tables 5, 6) shows only a small proportion of variance is attributable to decadal or 20-year intervals and Fig. 1 shows graphically an upward trend in diversity in the US and broadly constant diversity in the UK and Australia.

Figure 1 also illustrates that within these broad trends there are fluctuations in the genetic diversity of varieties over time; of particular interest is the sharp reduction in diversity in the UK set in the period 1976–1985. Reference to Table 1 shows that this corresponds to a period during which varieties from a single breeder [Plant Breeding Institute (PBI)] completely dominated the UK market. It is also coincident with the introduction of genetically (*rht2*) based semi-dwarf growth habit by PBI in its winter wheat. It is possible that there was a reduction in diversity due to selective sweep combined with the period when almost all varieties came from the PBI breeding programme which might itself represent a smaller gene pool than that of the whole UK set. An analogous situation is reported by Warburton et al. (2006) where strong selection in CIMMYT spring wheat in the period 1945–1965 led to much improved varieties but also to reduced genetic diversity. CIMMYT have latterly reversed this trend by including wheat from geographically diverse locations and synthetic material (hexaploid wheat produced by artificial hybridisation of durum wheat with *Ae. Tauschii*) in subsequent breeding programmes. To try better to understand the factors leading to short term fluctuations in diversity within our samples we are currently re-investigating the question using an extended marker set.

The use of a common marker set allows comparison to be made between the three national populations. Overall the order of decreasing genetic diversity is Australia > US > UK, this is evident in both PCO and genetic distance analysis. It is interesting to consider these differences in diversity in the light of the recent history of the three national wheat populations. The diversity of the Australian wheat population is considerably higher than that of the UK and US. This is consistent with the known history of Australian wheat varieties which in the nineteenth century originated variously from the UK, South Africa, Italy, Canada, India and the USA. In the twentieth century material from CIMMYT (including, most recently, material derived from synthetics) has added further to the diversity of the available gene pool (O'Brien et al. 2001). Intuitively, the range of climatic conditions in Australia will also increase the diversity in the national population where sub-sets of varieties are adapted to specific regions; Table 2 indicates the region for which the varieties have been released.

In contrast, the less diverse gene pool in the UK may reflect the long period during which wheat landraces have been adapted to the UK environment. In the late nineteenth century, selection from within this population may have served to create a well adapted, but narrow, genetic base. Subsequent introgression of traits from European, US and Japanese material has involved backcrossing to maintain a UK tolerant ideotype, potentially attenuating the expansion of the gene pool from these introductions (for a review of the UK wheat gene pool see Angus 2001).

The US varieties exhibit a level of diversity between that of the UK and Australia. The history of wheat breeding in the US has some similarities with that of Australia in that the crop was introduced in the recent past and then adapted by selection and latterly breeding. However, for soft and hard winter wheat the number of geographical sources of original germplasm is quite small. US hard red winter wheat (HRW) originates from material introduced from Europe, notably the variety Turkey (and selections thereof) which originated in the Ukraine. The addition of germplasm from other sources has been slow, such that modern HRW derives as much as 50% of its genes from this one variety. Soft winter wheat (SRW) has a longer history in the US but its origins are not particularly diverse in that until the latter part of the nineteenth century European varieties were imported for use with little local selection (for a review of the US wheat gene pool see Carver et al. 2001; Bacon 2001). Subsequent breeding and regional adaptation together with steady introduction of new material probably accounts for the rising trend in diversity over time.

Apart from establishing the level of genetic diversity these data also show separation of the populations in diversity space (Fig. 2, 3, 4). The three populations are distinct on a whole genome basis and also with respect to the B genome. AMOVA (Tables 5, 6) shows that country of origin accounts for 20% of the total diversity.

This distinction between the populations is entirely consistent with the known genetic history of the national crops—being developed independently over the past 100 years with strong selection for adaptation to local environment and significantly different founder populations. Paradoxically, however, the US and Australian populations are partially overlapping with respect to the A and more particularly D genomes. These findings raise questions about the relationship between the US and Australian sets—why are they so similar in these genomes? It is possible that since both populations are grown under drought stress that selection for early flowering or other beneficial traits has led to the introgression of similar combinations of alleles in the A and D genomes? If this were so then the diversity of these national D genomes ought to have been lowered, in fact in Australia the D genome is most diverse. It might be that the D genome is globally least diverse (as reflected in the relative lack of polymorphic markers found in this genome by Akbari et al. 2006 and others) and therefore not subject to selection by breeders—plasticity from the A and B genomes being sufficient. If this were true then D genome diversity might, on average, persist independent of breeder selection elsewhere in the genome and it is the diversity of environment in the US and Australia which has led to the introduction of a wide range of genetic material; the D genome has been extensively sampled but selection has generally been directed at A and B genome loci.

Within each national set it is possible to rank the genomes in order of increasing diversity (Table 7). In the UK set the D genome is markedly less diverse than the A or B genomes; conversely the Australian D genome is more diverse than the corresponding A and B genomes. In the US there is very little difference in diversity between the three genomes. Taking the data together as a sample of the diversity of the global wheat gene pool suggests there is, in fact, little difference in the average genetic distances between varieties between A and B genomes although the D genome is less diverse overall. It appears, therefore, that total diversity is achieved by different routes in the three populations.

Erosion of genetic diversity due to breeding could occur not just at the national level but in the species as a whole. At the national level we, and others, have shown little evidence of reduction in genetic diversity but for the species as a whole it is difficult to assess what is happening because different studies have used different marker systems. In this study we are able not only to use the volume of the convex hulls as an index of genetic diversity within a population but also the volume of diversity space unaccounted for by the three populations can be used to give a clue as to the magnitude of the species diversity, or at least an estimate of its minimum. Table 8 shows that in the whole genome and

Table 7 Average genetic distance between varieties by genome and country of origin

Country	Genome	Average genetic distance	Group
UK	D	0.237	1
UK	A,B,D	0.289	2
UK	B	0.297	3
UK	A	0.306	4
US	B	0.343	5
US	D	0.346	5
US	A,B,D	0.349	5
US	A	0.359	6
AUS	A	0.374	7
US/UK/AUS	D	0.393	8
US/UK/AUS	A,B,D	0.399	9
US/UK/AUS	B	0.399	9
US/UK/AUS	A	0.402	10
AUS	A,B,D	0.405	11
AUS	B	0.406	11
AUS	D	0.431	12

Within a numbered group the means are not significantly different from each other ($P <= 0.05$)

Table 8 Comparison of the volumes of convex hulls (five dimensions) by genome and country of origin

Genome	US (%)	UK (%)	AUS (%)	US/UK/AUS (%)
Whole genome	4	3	6	100
A genome	12	9	8	100
B genome	9	11	8	100
D genome	21	8	19	100

Volume expressed as a percentage of the volume occupied by the dataset combined over countries

in the A and B genome the proportion of the total diversity space occupied by each national set is relatively small. Even taken as an aggregate and ignoring the fact that in the A genome there is some overlap between the US and Australia less than 30% of the volume is occupied by varieties (A and B genomes) and only 13% of the volume of the whole genome hull. This suggests that the potential diversity of the species is at least three times greater than that captured in this experiment. Whether this diversity is extant in other national variety populations and seed banks is an interesting question and it would be worthwhile to sample wheat from other geographical areas and to analyse them with this marker set to establish how they relate to this study in terms of total diversity and position in diversity space. In this context the D genome should be considered separately; the complete overlap of the Australian and US varieties in diversity space and the lower overall average genetic distance between varieties suggest it may be less diverse. However, in terms of the volume of the convex hulls occupied by the samples we find about 30% of the total for the genome (assuming the Australian and US samples are occupying the same space), which suggests that whilst the D genome might be less diverse its diversity has still been sampled to about the same level as the A and B genomes. To some extent this also argues against the possibility of breeders actively selecting traits in the D genome for adaptation to Australia and the US.

Finally, since they are still relatively new, a brief discussion of the performance of the DArT markers is appropriate. DArT markers have performed well in this study. Although their biallelic nature limits to some extent the range of analyses possible, this is compensated for by the wide genome coverage. For example, allelic diversity (Nei 1987) expressed as the sum of the squares of the frequencies of each allele at a locus is less informative (at the locus level) using DArT markers than it would be with multi-allelic SSRs. However the large number of markers allows a precise average value to be obtained which compensates for the deficiency at the individual marker level. Indeed, we considered using allelic diversity as an additional test statistic but found that a moving average of allelic diversity over all loci in time series gave essentially the same fluctuating curves and relative ranking between countries as did average genetic distance. Dominance of the DArT markers may present potential difficulties in the analysis of out-breeding species, in this study; however, since wheat is a self-pollinating species and the varieties have all have been inbred the level of heterozygosity will be low and this is unlikely to be a problem.

DArT has potential for widespread use; genetic maps are becoming available with many of the DArT markers mapped relative to familiar SSRs. The density of the genome coverage suggests DArT may have potential in association mapping and certainly as a basis for genetic diversity studies it has great potential. The benefit of conducting a widespread screen of the global genetic diversity of a species with common markers with known map positions cannot easily be overstated.

Knowing that the genetic diversity of the crop in these countries has remained at least constant for the past 70 years is reassuring. The suggestion that no more than 30% of the genetic diversity of the species is captured in these three populations underlines the importance of in situ and ex situ conservation of wheat germplasm throughout the world. It also suggests the need to add a wider range of wheat samples to this dataset in order to try to measure the total genetic diversity of the species. If this could be done it might serve as a basis for monitoring temporal trends in diversity on a global basis and ensuring that the core diversity of the species was protected in germplasm collections,

even if it were not deployed in elite varieties. There is no doubt that climate change will re-define the wheat ideotype for many geographical areas and it is only the conservation of genetic diversity which will ensure that breeders have the raw materials with which to respond.

Conclusion

Overall, the data do not support the hypothesis that modern plant breeding leads to a reduction in available diversity.

In common with the general consensus of other authors, we conclude that the genetic diversity of wheat varieties available to growers in the UK, US and Australia is no lower today than it was 70 years ago. However, we note significant fluctuations in diversity over time. The data presented suggest that at the species level the genetic diversities of wheat A and B genomes are similar but that the D genome may be less diverse.

The UK, US and Australia have developed wheat gene pools in partial isolation from each other and from different founder populations, the populations are, unsurprisingly, genetically distinct.

For the first time (to our knowledge) the genetic diversity of three, genetically very distinct, wheat populations have been compared using a common marker system. The results suggest that not more than a third of global wheat genetic diversity is represented by these samples and that DArT markers could readily be used to explore its full extent.

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