Short communication

Impact of Line 1 germplasm on South African Hereford cattle

V.L.R. Leesburg[1,2], M.D. MacNeil[1,2,3#], E. van Marle-Köster[4], O. Mapholi[3] & F.W.C. Neser[2]
[1] USDA Agricultural Research Service, Miles City, Montana 59301, USA
[2] University of the Free State, Department of Animal, Wildlife and Grassland Sciences, PO Box 339, Bloemfontein 9301, South Africa
[3] ARC-Animal Production Institute, Private Bag X2, Irene 0062, South Africa
[4] Department of Animal and Wildlife Sciences, University of Pretoria, Pretoria 0002, South Africa

(Received 30 August 2012; Accepted 3 May 2013; First published online 7 June 2013)

Copyright resides with the authors in terms of the Creative Commons Attribution 2.5 South African Licence.
See: http://creativecommons.org/licenses/by/2.5/za
Condition of use: The user may copy, distribute, transmit and adapt the work, but must recognise the authors and the South African Journal of Animal Science.

Abstract

The goal of this research was to document the influence of Line 1 Hereford cattle, developed by the United States Department of Agriculture at its research facility in Miles City, Montana, on Hereford cattle in South Africa. Analytical approaches made use of both recorded pedigree and microsatellite marker information. Cattle with recorded performance data in South Africa were mated with Line 1 Hereford sires *in silico* and inbreeding coefficients were calculated for the resulting progeny. The relationship between South African and Line 1 Hereford cattle populations was estimated as twice the maximum inbreeding coefficient for the progeny of each South African animal. The calculated pedigree relationship of Hereford cattle registered in South Africa with Line 1 was 24%. Thirty-six South African Hereford cattle and a sample of 64 Line 1 animals were genotyped with 34 microsatellite markers. Based on a Bayesian model-based clustering method, the probability that the South African Hereford cattle were members of Line 1 was 0.38 ± 0.08. This research documents one aspect of the far reaching effects of the Line 1 Hereford population.

Keywords: Gene flow, migration, relationship
[#]Corresponding author: macneil.deltag@gmail.com

In the earliest days of the 20th century, of all Hereford cattle exported from Great Britain approximately 91% went to North and South America, and some animals were also exported to Australia and South Africa. The first importation recorded by the Studbook Society of South Africa was in 1892 (South African Studbook Association, 1971). A bull named Southern Cross was imported in 1901 by George Moorcroft; and the first Hereford cows are thought to also have been imported at this time. In 1903, 27 cows and four bulls were imported by the Transvaal Government and a herd was established at the Potchefstroom College of Agriculture. The South African Hereford Breeder's Society was founded in 1917 (South African Studbook Association, 1971). Hereford cattle played an important role in several research programmes on beef cattle during the 1900's in South Africa. Hereford bulls were used in selection for improvement of growth traits in Afrikaner cattle. Further selection for an adapted Hereford with a smooth coat and eye pigmentation was done over a period of 15 years at the Mara Research Station in the Limpopo Province, a region with extreme summer temperatures and tick-borne diseases (Bonsma, 1949; 1980). These animals were used in development of the Bonsmara breed (Bonsma, 1980). Hereford cattle have been credited with having a major role in the development of the beef industry in South Africa (South African Hereford Cattle Breeders' Society, 2010). Since the establishment of the Hereford Society pedigreed herds were kept by

URL: http://www.sasas.co.za
ISSN 0375-1589 (print), ISSN 222-4062 (online)
Publisher: South African Society for Animal Science http://dx.doi.org/10.4314/sajas.v43i2.5

private breeders and with live importations until the late seventies and thereafter primarily semen and ova from the United Kingdom, United States of America (USA) and Australia (B. Coe, ABS Global, personal communication). The Hereford breed was one of the first breeds in South Africa to take part in the National performance testing scheme.

Following upon the experiments of G.H. Shull and others which demonstrated the value of heterosis in production of maize, inbred lines of livestock were initiated in the USA beginning in the 1920's (Sprague, 1962). In 1931, the U.S. Department of Agriculture (USDA), Bureau of Animal Industry, initiated projects on development of inbred lines of cattle that were superior in rate of gain, weight for day of age, carcass characteristics and fertility (Winters, 1931; Knapp *et al.*, 1951). Fort Keogh, the USDA range livestock experiment station, played a large part in this project by developing the first and several of these inbred lines of cattle, the most important and productive of these inbred lines being Line 1 Hereford cattle (Knapp *et al.*, 1951).

Dissemination of Line 1 Hereford germplasm began in 1948 with sales of bulls and females that were excess to research needs to local cattle producers. In time, buyers came from across the U.S. to purchase Line 1 Hereford cattle from Fort Keogh. Additionally, several successful seedstock herds were founded in the USA using Line 1 germplasm (Dickenson, 1984). Today, Hereford semen and embryos are frequently exported from some of these herds in the USA to South Africa (B. Coe, ABS Global, personal communication). However, there has been no direct export of germplasm from Fort Keogh to South Africa. The goal of this project was to estimate the relationship of Line 1 Hereford cattle at Fort Keogh Livestock and Range Research Laboratory with animals recorded in the South African Hereford Herdbook using pedigree and DNA marker information.

Pedigree data of 4 491 animals with performance records born in South Africa since 1938 were obtained from the South African Hereford Society. Of these, 1 972 animal were also present in records of the American Hereford Association (AHA). Ancestors of the animals present in the AHA database were identified to produce an extended pedigree containing 14 647 animals. The Line 1 pedigree was also traced to the earliest animals recorded by the AHA (American Hereford Cattle Breeders' Association, 1899).

The 1 972 South African Hereford cattle for which AHA registration numbers were available, were pseudo-mated to Line 1 Hereford sires used at Fort Keogh from 1958 to present. Inbreeding coefficients were then calculated for the "offspring" resulting from these "matings" using the algorithm developed by Henderson & Quaas (1976). Wright's (1922) coefficient of relationship of each South African animal to Line 1 was taken to be twice the maximum of the calculated inbreeding coefficients resulting from the pseudo matings between it and the Line 1 sires.

A sample of 64 Line 1 Hereford cattle was genotyped using a set of 34 microsatellite markers covering the 29 bovine autosomes (Kealey *et al.*, 2002; Tshipuliso *et al.*, 2008). Markers were chosen based on marker position, suitability for multiplex reactions and ease of scoring. The selected markers, their genomic location and primer sequences are shown in Table 1. At Fort Keogh, touchdown PCR was performed in MJ Research (St. Bruno, Quebec, Canada) thermocyclers. All genotypes were collected on a LiCor 4200 DNA Analysis System (LiCor Biosciences, Lincoln, Nebraska, USA). Genotypes were independently scored by two individuals and discrepancies resolved.

Members of the South African Hereford Breeders Society provided hair samples from 36 seed-stock bulls that had a major impact with regard to number of progeny produced in South Africa. DNA extraction was performed at the ARC Genetics Laboratory in Irene, South Africa, followed by PCR and genotyping using the ABI 3130 platform (Applied BioSystems, Foster City, California, USA). Genotypes were scored using GeneMapper v4.0 (Life Technologies, Grand Island, New York, USA).

To standardize genotype scoring at the separate locations, semen samples from three Hereford bulls (Huth Enhancer 2D, Gerber Killarney 058K, and LCG Master Duty 51J) were purchased from ABS Global. The DNA from these bulls was genotyped with the other samples at both locations.

The programme, STRUCTURE (version 2.3.2; Pritchard *et al.*, 2010), was used to compare the Line 1 Hereford and South African Hereford populations using the genotypic data. STRUCTURE implements a Bayesian model-based clustering method for inferring population structure using genotype data consisting of unlinked markers (Pritchard *et al.*, 2000b; Falush *et al.*, 2003; 2007; Pritchard *et al.*, 2010). Animals were identified *a priori* as being in two clusters (i.e., K = 2). The programme then estimated each animal's probability of membership in both clusters, which may vary across independent samples (Pritchard & Cox, 2002). Allele frequencies were assumed to be independent draws from population-specific distributions.

This is the original model used by Pritchard *et al*. (2000a) and has been shown to work well for many data sets in which the allele frequencies in the different populations can be expected to be reasonably divergent from each other (Pritchard *et al*., 2010). Following a burn-in of 10,000 samples, the run length was set at 200,000 samples. For samples from South Africa, the average probability of their membership in the Line 1 cluster was interpreted as a measure of their genetic relationship of these animals to Line 1 Hereford.

Table 1 Microsatellite markers, their genomic locations, and primer sequences for markers used to assess molecular genetic relationship of South African Hereford cattle to Line1

Marker	BTA	cM	Primer sequences	
			Forward	Reverse
BMS574	1	14	ATGTTCTTTGACCACATGGATT	GAACAAGCATTCTGACCATAGC
URB014	1	142.1	CATTGGTAGGTGGGTTCTTTCC	GCAACCTAAGTGTCCATCAACAG
IDVGA-2	2	117.8	GTAGACAAGGAAGCCGCTGAGG	GAGAAAAGCCAAGAGCCAGACC
BMC5227	3	122.1	TGTGCGCTGTACAGTGAGTG	ATGTCAAGGTCAGGGAGGAA
AGLA227	4	101.5	TTAGAGCATAGTTGATTTAAAATG	CACAGGAAACTCTACTCAATATTC
BM8126	5	122.1	TCTTCCTCCGCAGACTGG	GAACCTGTGGATGAGCGG
BMS1315	5	32.5	AAGCCATTGATTGTAGATTGGG	GAGTTTCCTTTTTCCCCCAC
BL1038	6	122.3	GGCAAGCTAGAGTCAGACACG	GCAAAAGTCTAGGTGAAATGCC
BMS1247	7	132	TCAGCTCTCAGCAGCCTGTA	GGGGTTAATGGTGATCTGCA
BMS713	7	15.2	CCAAGGGAGGAAAAATAAGTTAA	ACCAGCAGTAGGTTGAGGTTAA
BMS836	8	114.2	GAAACTCTTTTCACTCTGCGC	GCTCTTAGGGATTGCTTCACC
RM321	8	15.8	CTATATTGTGTGCTTGAAATTTGC	TCTCACCTAGATGTCTCTGTATGTG
BMS1967	9	102.5	GGGCAGATGTGAGTAATTTTCC	AACTGAGCTGTATGGTGGACG
BMS2177	9	0	TTGCTAATGCAAATGTGTATGTG	GATCATGTCATCTGTGAAAAAAGA
BMS2614	10	98.4	ACTTTCTTTTCCTGTGGCTCG	CAGAGCTGGCACCAGAGG
CSSM038	10	7	TTCATATAAGCAGTTTATAAACGC	ATAGGATCTGGTAACTTACAGATG
BM827	11	0	GGGCTGGTCGTATGCTGAG	GTTGGACTTGCTGAAGTGACC
ILSTS028	11	105.3	TCCAGATTTTGTACCAGACC	GTCATGTCATACCTTTGAGC
BMS1316	12	98.7	CCTTCATGGAAGAAATTTTGTG	GGAGTTACAGTCCATGGGTTC
ILSTS059	13	34	AGTATGGTAAGGCCAAAGGG	CGACTTGTGTTGTTCAAAGC
BL1029	14	42.8	CAAATCAGCCTCTCCTCTTCC	GTGCTTCCAGAGACAATAAAGG
BMS2533	15	5.2	TGAAGTAAGTAAGCACACAAGCA	TTGATCATCTTTAGGTCCATCC
BM719	16	78	TTCTGCAAATGGGCTAGAGG	CACACCCTAGTTTGTAAGCAGC
ILSTS023	17	54.3	TCTAGAAGGCTGGGACTTGG	AGATTTCTGAAGTAGGGACC
INRA063	18	48.7	ATTTGCACAAGCTAAATCTAACC	AAACCACAGAAATGCTTGGAAG
BMC1013	19	98.4	AAAAATGATGCCAACCAAATT	TAGGTAGTGTTCCTTATTTCTCTGG
BMS745	19	15.9	TAGGGACTTGTTACCCGTGG	TGCAAGCTGTGAGGAGGAG
BMS1282	20	19.1	ACTCTTCCACAGTTGGCCTG	CCTCCTTCCTCCAGAGCC
IDVGA-45	21	31.8	GTGGTGGCAAAGAGTCAGA	AACAGCCCTGATTTCCATA
BM2613	22	51.3	AAGGAGAACCTCCATCCCTG	ATGGACAGAGGAACCCAGTG
BMS468	23	36	GTTAAGCAGAGGGTTTCCCC	TATTCCCAGGTGCTCTGAGG
BP28	25	22.6	AGGTGACAGGTGAGAGGGC	CCTCCACAACACCATCCTTC
CSSM036	27	39.8	GGATAACTCAACCACACGTCTCTG	AAGAAGTACTGGTTGCCAATCGTG
BMS510	28	22.1	TGCTGCATGATTCTCATTCC	AGCCTTCCTGTTCTCTGCTG
RM044	29	23.3	AAAGTGTTGGACATGACTGAAT	TTAACAATTAGCAACAGGAATAGG

Pedigree analysis: The initial file of 4 491 animals from South Africa contained 1 972 (44%) animals with a known AHA registration number. However, the South African Hereford Society identifies only 81 animals as being original to the American registry. The extended pedigree of these 1 972 animals, based on AHA records, contained an additional 14 647 unique animals. When these 14 647 animals were pseudo-mated to Line 1 sires, 1 990 (14%) produced a simulated progeny with a non-zero inbreeding coefficient thus indicating some relationship between the populations.

The average relationship between the South African Hereford population and the Line 1 herd at Miles City, MT USA was 10.6%. For those South African animals that were related to Line 1, their average relationship was 24%; which is approximately equivalent to having a grandparent from Line 1. The estimated relationships between Line 1 and South African Hereford cattle were distributed on the interval 0% to 82%; with 139 South African Hereford cattle having a relationship to Line 1 greater than 70%.

Many large scale genetic evaluations involve animals with incomplete pedigrees (Lutaaya *et al.*, 1999). Regular inbreeding algorithms (Quaas, 1976), based on the definition by Wright (1922), calculate the relationship of animals with at least one parent missing as zero. Even if both parents are known, inbreeding could be underestimated if some of their ancestors are unidentified. If the proportion of missing ancestors or parents is large the relationship trend could be seriously underestimated for a population (Lutaaya *et al.*, 1999). The American Hereford Association database, used for comparison, is practically complete since 1960 and contains millions of records. The corresponding pedigree from South Africa is much smaller, although also comprehensive and highly informative.

Genomic analysis: Numerous studies have used microsatellite markers to describe the relationships between breeds and their history (e.g. MacHugh *et al.*, 1994; Moazami-Goudarzi *et al.*, 1997; Beja-Pereira *et al.*, 2003). The probability of the sampled South African Hereford cattle being members of Line 1, based on microsatellite genotypes, is shown in Figure 1. This probability was distributed on the interval 0.23 to 0.58, with mean and median = 0.38 and standard deviation = 0.08.

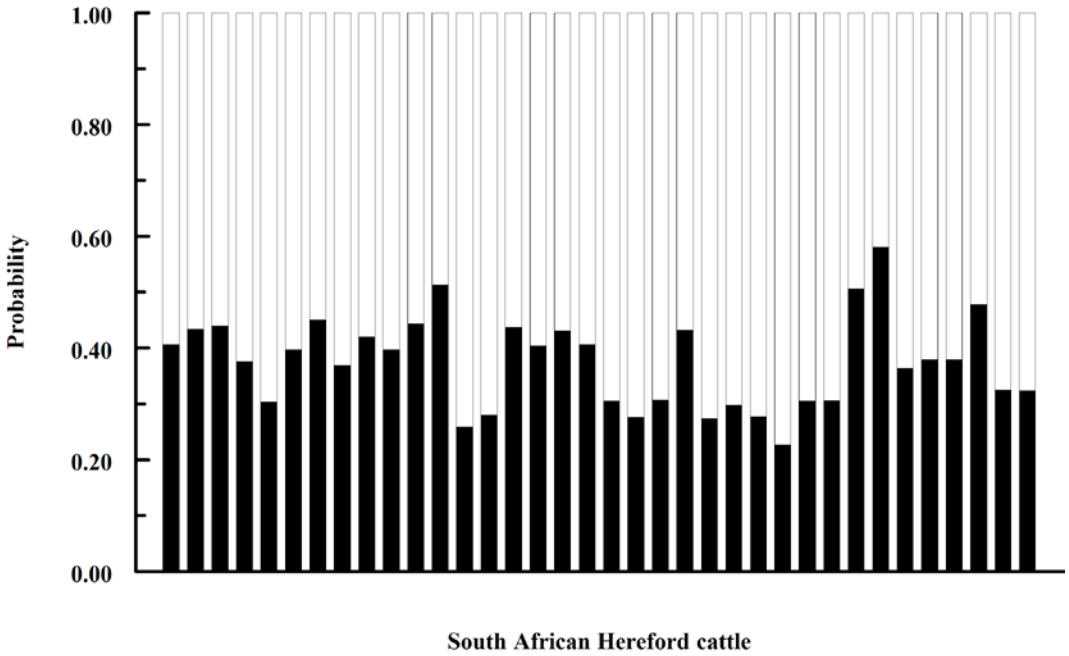

Figure 1 Probability of Hereford cattle sampled from South Africa being members of the Line 1 Hereford population from Fort Keogh, Miles City, Montana USA. Each vertical bar represents an individual animal that originated from South Africa.

In interpreting results of the pedigree and genomic analyses, it is important to recognize that relationship coefficients are based on genome wide expectations of allelic identity by descent whereas the probability of membership is based on observed allele sharing. Thus, while the statistics are related

probabilities, they are not strictly proportional. Rosenberg *et al.* (2002) suggested overall similarity of populations is evident given the geographically widespread nature of most alleles and the ability to conduct molecular genetic analyses. However, the ability to derive pedigree-based relationships may be much more difficult due to lack of international coordination for integration of the data and concerns of breeders and breed associations for private property rights (Golden *et al.*, 2009).

Since 1934, there has been no immigration into the Line 1 Hereford population. Annual production sales have resulted in emigration from Line 1 to North American herds. In the latter part of the 20th century, cryogenically preserved semen and embryos facilitated trade in of genetics (Board of Agriculture, 1993) and has resulted in the influence of Line 1 on the South African Hereford population, as documented here.

References

American Hereford Cattle Breeder's Association, 1899. The American Hereford record and Hereford herd book. Vol I-II.

Beja-Pereira A., Alexandrino, P., Bessa, I., Carretero, Y., Dunner, S., Ferrand, N., Jordana, J., Laloe, D., Moazami-Goudarzi, K. & Canon, J., 2003. Genetic characterization of southwestern European bovine breeds: a historical and biogeographical reassessment with a set of 16 microsatellites. J. Hered. 94, 243-250.

Board of Agriculture, 1993. Livestock: Managing Global Genetic Resources. Committee on Managing Global Genetic Resources: Agricultural Imperatives. National Research Council. Nat. Acad. Press, Washington, D.C. Accessed 23/02/2010. http://www.nap.edu/openbook.php?record_id=1584

Bonsma, J.C., 1949. Breeding cattle for increased adaptability to tropical environments. J. Agric. Sci. 39, 204-221.

Bonsma, J.C., 1980. Livestock Production. A global approach. Tafelberg, Goodwood, Cape Town, South Africa

Dickenson, H.H., 1984. The influence of Line 1 in the Hereford breed. In: Proc. Ft Keogh Livestock and Range Research Laboratory. 1984 Field Day, Miles City, Montana.

Falush, D., Stephens, M. & Pritchard, J.K., 2003. Inference of population structure: Extensions to linked loci and correlated allele frequencies. Genetics 164, 1567-1587.

Falush, D., Stephens, M. & Pritchard, J.K., 2007. Inference of population structure using multilocus genotype data: dominant markers and null alleles. Mol. Ecol. Notes 7, 574-578.

Golden, B.L., Garrick, D.J. & Benyshek, L.L., 2009. Milestones in beef cattle genetic evaluation. J. Anim. Sci. 87, E3-E10.

Henderson, C.R. & Quaas, R.L., 1976. Multiple trait evaluation using relatives' records. J. Anim. Sci. 43, 1188-1197.

Kealey, C.G., MacNeil, M.D. & Golden, B.L., 2002. Genetic distance between a multi-breed composite and two inbred lines of Hereford cattle. Proc. West. Sec. Am. Soc. Anim. Sci. 53, 127-131.

Knapp, B., Church, R.C. & Flower, A.E., 1951. Genetic history of Line 1 Hereford cattle at the United States Range Livestock Experiment Station, Miles City, Montana. Bull. No. 479.

Lutaaya, E., Misztal, I., Bertrand, J.K. & Mabry, J.W., 1999. Inbreeding in populations with incomplete pedigrees. J. Anim. Breed. Genet. 116, 475-480.

MacHugh D.E, Loftus, R.T., Bradley, D.G., Sharp, P.M. & Cunningham, P., 1994. Microsatellite DNA variation within and among European cattle breeds. Proc. Roy. Soc. Lond. Ser. B. 256, 25-31.

Moazami-Goudarzi, K., Laloë, D., Furet, J.P. & Grosclaude, F., 1997. Analysis of genetic relationships between 10 cattle breeds with 17 microsatellites. Anim. Genet. 28, 338-345.

Pritchard, J.K. & Cox, N.J., 2002. The allelic architecture of human disease genes: common disease - common variant - or not? Hum. Molec. Genet. 11, 2417-2423.

Pritchard, J. K., Stephens, M. & Donnelly, P., 2000a. Inference of population structure using multilocus genotype data. Genetics 155, 945-959.

Pritchard, J.K., Stephens, M., Rosenberg, N.A. & Donnelly, P., 2000b. Association mapping in structured populations. Am. J. Hum. Genet. 67, 170-181.

Pritchard, J.K., Wen, X. & Falush, D., 2010. Documentation for STRUCTURE software: Version 2.3. Dept. of Human Genetics, University of Chicago. Dept. of Statistics. University of Oxford. http://pritch.bsd.uchicago.edu/structure.html

Quaas, R.L., 1976. Computing the diagonal elements and inverse of a large numerator relationship matrix. Biometrics 32, 949-953.

Rosenberg, N.A., Pritchard, J.K., Weber, J.L., Cann, H.M., Kidd, K.K., Zhivotovsky, L.A. & Feldman, M.W., 2002. Genetic structure of human populations. Science 298, 2381-2385.

South African Studbook Association, 1971. South African Studbook Jubilee Edition. Dreyer Printers and Publishers, Bloemfontein, South Africa.

South African Hereford Cattle Breeder's Society, 2010. Hereford History, Origin of the Breed. http://www.hereford.co.za/

Sprague, G.F., 1962. "Hybrid Corn." In "After a Hundred Years - Yearbook of Agriculture". U.S. Department of Agriculture, 1962, pp. 106-107.

Tshipuliso, N.O.M., Alexander, L.J., Kotze, A., Ehlers, K., Reisenauer-Leesburg, V.L. & MacNeil, M.D., 2008. Structural assessment of backcrossing using microsatellite markers. S. Afr. J. Anim. Sci. 38, 290-292.

Winters, L.M., 1931. Inbreeding work under way with beef cattle. J. Anim. Sci. 1931, 114-117.

Wright, S., 1922. Coefficients of inbreeding and relationship. Amer. Nat. 56, 330-338.