Genes with major effects on wool traits detected in Finn cross sheep

A. R. BRAY, D. O'CONNELL AND D.J. SAVILLE

AgResearch, P.O. Box 60, Lincoln 8152, New Zealand

ABSTRACT

Two Finn sires with short wool staple lengths (Finn-S1 91 mm, Finn-S2 107 mm) and two with long staple lengths (Finn-L1 147 mm, Finn-L2 133 mm) were joined with Dorset Down (staple length 37-120 mm) and Romney (staple length 105-166 mm) ewes. Over two years, each ram sired between 83 and 210 progeny. Wool characteristics of progeny were measured at 6 months of age. For all sire groups, distributions of fibre diameter, fibre curvature, fibre medullation and clean fleece weight were not significantly different from single normal distributions. Similarly the distributions of fibre diameter coefficient of variation (FDCV), staple-crimp frequency and staple length for progeny of Finn-S1, Finn-S2 and Finn-L1 were close to unimodal. In contrast, the same three traits for progeny of Finn-L2 fitted two normal distributions. For all three traits, the mean value of one of the distributions of Finn-L2 progeny was similar to the means of the other three sire groups, while the mean of the second distribution was 41% greater (FDCV), 65% greater (staple length) or 67% less (crimp frequency) than that of the first. These results suggest the presence of a gene or genes with major effects on fibre traits.

Keywords: fibre diameter variation; crimp frequency; staple length.

INTRODUCTION

Genes have been identified with major effects on sheep reproduction (e.g., Booroola, Inverdale)*,* muscle fibre development (callipyge, myostatin), wool fibre characteristics (Drysdale, lustre) and susceptibility to diseases (scrapie susceptibility, spider lamb syndrome). Such genes offer the prospect of rapid improvement in the affected trait through natural breeding, genetic engineering, or development of therapeutic agents that modify the expression of the gene.

Natural breeding can be highly effective in changing the frequency of a gene if a test or marker (phenotypic or genetic) is available to positively identify individuals carrying the gene. In the ideal situation, selection (or culling if the gene is deleterious) of carriers can be achieved with limited loss of selection pressure on other desirable traits. For instance, Booroola, Inverdale and callipyge genes have been introduced into new (recipient) breeds by crossbreeding then repeated backcrossing (with the recipient breed) of subsequent generations of the progeny carrying the desired gene.   In this way it is possible to return to near the genetic makeup of the recipient breed except for the presence of the desired gene and low frequencies of undesired genes from the donor breed.

The mutations responsible for scrapie susceptibility (Hunter, 1997), spider lamb syndrome (Cockett *et al.*, 1999), Inverdale (Galloway *et al.*, 2000), and Booroola (Wilson *et al.*, 2001) phenotypes have been identified. DNA tests for them are commercially available but, to date, this knowledge has not been used for genetic engineering or development of therapeutic agents in sheep.

Given the wide divergence in fleece types between sheep breeds the existence of genes with major effects on fibre characteristics is not surprising. Dry (1955) and Stephenson (1959) described genetic effects on the size of primary wool follicles, and consequently on the incidence of halo hairs in the birthcoat and medullation of the fleece of Romney sheep. The gene responsible, while often referred to as the N gene, was named *HH1* by COGNOSAG (Lauvergne *et al.*, 1996). Three alleles have been recognised - $HH1^N$ (Drysdale), $HH1^T$ (Tukidale), and $HH1^J$ (Carpetmaster). Two other genes affecting halo hairs are $HH2^{nr}$ and $HH3^{El}$ (Elliotdale) (Lauvergne *et al.*, 1996). Genes conveying unusually high wool lustre and low crimping listed by Lauvergne *et al*. (1996) are *LW* and *SW* in Merino, *LWM1* in Border Leicester x Romney and *LWM2* in Suffolk x Perendale sheep. Recent large-scale searches for other genes with major effects on wool characteristics within and between major wool-producing breeds (Crawford, 2001) have yielded small reward to date (Henry *et al*., 1998; Beh *et al*., 2001; Mackenzie *et al*., 2001).

This report presents preliminary evidence for genes with major effects on wool traits in Finn cross sheep.

MATERIALS AND METHODS

Two Finn sires with short wool staple lengths (Finn-S1 91 mm, Finn-S2 107 mm) and two with long staple lengths (Finn-L1 147 mm, Finn-L2 133 mm) in annual adult fleeces were joined with Dorset Down (annual adult staple length 37-120 mm) and Romney (annual adult staple length 105-166 mm) ewes. Over two years (1999 and 2000) each sired between 83 and 210 F1 progeny. The data in this report was obtained from the progeny at six months of age.   Staple length and crimp frequency were measured manually. Crimp frequency was measured separately on butt, mid and tip portions of staples but only the mean of the butt and mid-staple measurements is reported here. The crimp frequency of the tip portion was not included because it was consistently less than that in the other two portions, possibly because of different growth conditions during foetal life or because of postnatal environmental conditions affecting the exterior of the fleece. It is assumed that crimp frequency in the butt and mid regions is a more accurate reflection of follicle determinants of crimp acting after birth. Fibre diameter

(mean and standard deviation), curvature and medullation were measured by Optical Fibre Diameter Analyser (OFDA; Edmunds, 1995) after 24 hours conditioning of scoured wool samples at 65% humidity and 20°C for 24 hours.

Initial examination of the data indicated that the distribution patterns (unimodal or bimodal) of the main wool traits were consistent between years-of-birth and breeds-of-dam. The data for each trait from the four groups (two years-of-birth and two breeds-of-dam) of each sire's progeny were then standardised by subtracting the mean of each group from individual values and dividing the answer by the standard deviation of that group; the standardised values were then pooled. For each trait, the goodness of fit of the standard normal distribution was tested using a chi-squared test to compare the "observed" distribution of the standardised data values with the distribution "expected" under normality (with class intervals for the chi-squared test defined by subdividing a standard normal distribution into 10 equal parts). If a single normal distribution was a poor fit, two normal distributions were fitted using maximum likelihood methods, and the goodness of fit retested using a chi-squared test utilising the class intervals defined above. To determine which of the "bimodal" distributions matched the distributions of the three "unimodal" rams, the two normal distributions were then backtransformed to serve as an "average" of the four groups by multiplying means and standard deviations by the pooled standard deviation of the original data, then adding the overall mean of the original data to the mean of each normal distribution. The above fitting of a mixture of two normal distributions for each trait individually, was redone using a multivariate method, hierarchical cluster analysis, so that each individual was allocated to a single distribution for all (three) variables simultaneously. For this purpose a "similarity matrix" was calculated, using Pythagorean (or Euclidean) distance as a measure of the similarity of two individuals. Two clusters were then formed using the "group average" method of defining the position of

each cluster. For each trait, the mean and standard deviation was calculated for each of the clusters, and back transformed as described above.

RESULTS

The mean values and their standard deviations for mean fibre diameter, fibre curvature, fibre medullation and clean fleece weight were similar for the progeny of all four sires (Table 1a). This was not the case for values for fibre diameter variation (FDCV), staple length and crimp frequency. For each of these three traits, the standard deviation for sire Finn-L2 was higher than for the other three sires (P<0.01). Also, the differences in standard deviations were disproportionately greater than the differences in the sire-group means.

When standardised values for FDCV, crimp frequency and staple length were examined separately, the distributions of progeny Finn-S1 and Finn-L1 were not significantly different from single normal distributions. For the progeny of Finn-S2, FDCV and staple length were also unimodal but crimp frequency was bimodal due to the presence of four outliers among 83 observations. For the progeny of Finn-L2, a single normal distribution was a poor fit for all three variables (P<0.001). Two normal distributions were a good fit for all three variables, with chi-squared values of 7.52, 4.35 and 5.36 (9 d.f.; not significant) for FDCV, crimp frequency and staple length respectively; means and standard deviations are given in Table 1b.

When the three variables were treated simultaneously using cluster analysis and a "similarity threshold" of 90% was chosen, two clusters (C and D) were identified. Clusters C and D contained 127 and 83 individuals respectively, with means and standard deviations (Table 1c) similar to those obtained when the traits were treated separately (Table 1b). The resulting normal distributions (Figure 1) were a good fit for all three variables, with chi-squared values of 10.23, 8.47 and 8.78 (9 d.f.; not significant) for FDCV, crimp frequency and staple length respectively.

TABLE 1: Wool characteristics at 6 months of age of progeny of (a) four Finn sires (mean ± SD; SD pooled over four year-of-birth and dam-breed groups), (b) of the progeny of Finn-L2 (mean ±SD for a mixture of two normal distributions), and (c) as in (b) except that two clusters were identified using cluster analysis. The values in (b) and (c) were obtained by back transforming the fitted normal distributions (c.f. Figure 1) as described in the Materials and Methods section. A hyphen (-) indicates the distribution was unimodal.

		Clean fleece weight (kg)	Fibre curvature (degree/mm)	Fibre medullation (%)	Fibre diameter (µm)	Fibre diameter coefficient of variation (%)	Crimp frequency (number/cm)	Staple length (mm)
(a) Sire groups (number of progeny)								
Finn-S1	(192)	0.94 ± 0.21	66.6 ± 8.9	57.9 ± 2.1	26.4 ± 1.6	22.6 ± 2.1	2.63 ± 0.63	79.5 ± 11.4
Finn-S2	(83)	0.93 ± 0.17	61.5 ± 10.4	56.7 ± 1.3	26.8 ± 1.5	25.7 ± 3.0	1.78 ± 0.76	91.8 ± 12.4
Finn-L1	(195)	0.97 ± 0.23	62.6 ± 9.4	58.2 ± 1.3	26.8 ± 1.7	24.9 ± 2.8	2.00 ± 0.66	90.6 ± 16.1
Finn-L2	(210)	1.01 ± 0.23	65.4 ± 10.8	57.5 ± 1.5	27.0 ± 2.2	29.8 ± 6.0	1.91 ± 1.06	107.6 ± 32.6
(b) Progeny of Finn-L2: Two normal distributions, A and B, fitted as a mixture of distributions (each variable fitted individually)								
Finn-L2A		-	-	-	-	24.8 ± 2.3	2.42 ± 0.86	82.1 ± 11.6
Finn-L2B		-	-	-	-	35.0 ± 3.8	0.80 ± 0.27	130.7 ± 27.3
Percentage in distribution A		-	-	-	-	51.3%	68.8%	47.5%
(c) Progeny of Finn-L2: Two normal distributions, C and D, fitted using cluster analysis (using multivariate methods)								
Finn-L2C		-	-	-	-	25.6 ± 2.9	2.60 ± 0.75	85.5 ± 14.3
Finn-L2D		-	-	-	-	36.2 ± 3.0	0.87 ± 0.34	141.4 ± 21.2
Percentage in distribution C		-	-	-	-	60.5%	60.5%	60.5%

FIGURE 1. Distributions of (a) fibre diameter coefficient of variation, (b) crimp frequency and (c) staple length in progeny of Finn-L2. Trait values from two years-of-birth and two dam breeds were standardised to have a common mean of zero and a common standard deviation of 1. Cluster analysis was then used to define two sub-groups. The standardised data values are presented in histograms along with fitted normal curves.
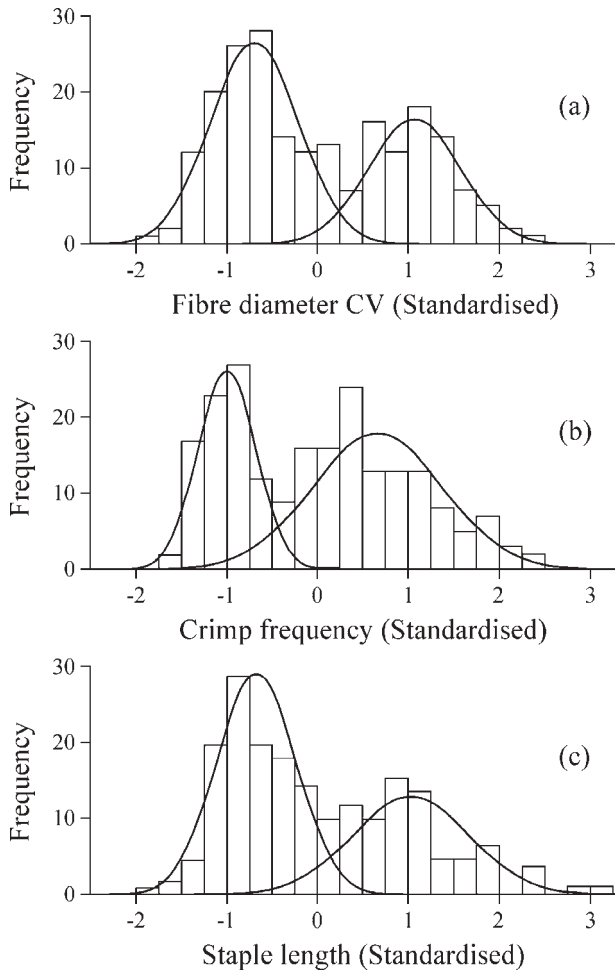
For each trait, its mean value in cluster C of Finn-L2 progeny was similar to the mean of the single normal distribution of Finn-S1, Finn-S2 and Finn-L1 (Table 1). The difference between the means for Finn-L2C and Finn-L2D, as a proportion of the mean of Finn-L2C, was +41% for FDCV, -67% for crimp frequency, and +65% for staple length.

DISCUSSION

The findings presented in this paper are evidence for a gene or genes with major effects on three wool traits. The existence of bimodal distributions of progeny of Finn-L2 clustered using FDCV, crimp frequency and staple length suggests that all three traits are influenced by the same gene or a closely associated set of genes. The genetic correlation between crimp frequency and staple length in Finn sheep was reported as -0.54 by Puntila *et al.* (1999) but no other relevant genetic correlation is available for Finn and Dorset Down breeds. Genetic correlations among FDCV or fibre diameter standard deviation, crimp

frequency and staple length for Romney (Morris *et al.*, 1996) and Merinos (Atkins, 1997; Smith *et al.*, 2001; Wuliji *et al.*, 2001) are generally below 0.2 indicating that in those populations the genetic associations are modest. More in line with Puntila *et al.*'s (1999) Finn data was that of Allain and colleagues (Allain *et al.*, 1998; Ponz *et al.*, 2001) who reported that genetic correlations among FDCV, crimp frequency and staple length were all about 0.5 in a study of INRA 401 sheep which are a cross between Romanov and Berrichon du cher breeds. Ponz *et al.* (2001) identified microsatellite markers affecting staple length and FDCV individually and others affecting both traits. Since, historically, Finn sheep come from the same geographic region as Romanovs and have at least two distinctive characteristics (high fecundity and short tails) in common with them (Maijala, 1996), the findings of Allain and colleagues may be relevant to the present study.

It is interesting to note that a further fleece trait, the incidence of halo hairs in the birthcoat, segregates in a similar manner to FDCV, crimp frequency and staple length in both the INRA 401 flock (D. Allain, personal communication) and our Finn crosses (A. R. Bray, unpublished data). Ponzoni *et al.* (1997) noted low to moderate genetic correlations (0.11 to 0.38) between hairiness of the birthcoat and the other three traits in Merino yearlings. We suggest that a gene or closely associated genes expressed during follicle development in the foetus influences all four traits.

REFERENCES

Allain, D.; Lantier, I.; Elsen, J.M.; Francois, D.; Brunel, J.C.; Weisbecker, J.L.; Schibler, L.; Vaiman, D.; Cribiu, E.; Gautier, A.; Berthon, P.; Lantier, F. 1998: A design aiming at detecting QTL controlling wool traits and other traits in the INRA401 sheep line. *Proceedings of the 6th world congress on genetics applied to animal production 27*: 51-54

Atkins, K.D. 1997: Genetic improvement of wool production. *In*: Piper, L.; Ruvinsky, A. *ed.* The Genetics of Sheep. CAB International. Pp 471-504

Beh, K. J.; Callaghan, M. J.; Leish, Z.; Hulme, D. J.; Lenane, I.; Maddox, J. F. 2001: A genome scan for QTL affecting fleece and wool traits in merino sheep. *Wool technology and sheep breeding 49*: 88-97

Cockett, N.E.; Shay, T.L.; Beever, J.E.; Nielsen, D.; Albretsen, J.; Georges, M.; Peterson, K.; Stephens, A.; Vernon, W.; Tomofeevshaia, O.; South, S.; Mork, J.; Maciulis, A.; Bunch, T.D. 1999: Localization of the locus causing Spider Lamb Syndrome to the distal end of ovine Chromosome 6. *Mammalian genome 10*: 35-38

Crawford, A. 2001: A review of QTL experiments in sheep. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics 14*: 33-38

Dry, F.W. 1955: The dominant N gene in New Zealand Romney sheep. *Australian journal of agricultural research 6*: 725-769

Edmunds, A.R. 1995: OFDA measurements of additional fibre parameters; some preliminary results. *International Wool Textile Organisation Technical Committee. Report Number 19, June 1995*

Galloway, S.M.; McNatty, K.P.; Cambridge, L.M.; Laitenen, M.P.; Juengel, J.L.; Jokiranta, T.S.; McLaren, R.J.; Dodds, K.G.; Montgomery, G.W.; Beattie, A.E.; Davis, G.H.; Ritvos, O. 2000: Mutations in an oocyte-derived growth factor gene (BMP15) cause increased ovulation rate and infertility in a dosage-dependant manner. *Nature genetics 25*: 279-283

Henry, H.M.; Dodds, K.G.; Wuliji, T.; Jenkins, Z.A.; Beattie, A.E.; Montgomery, G.W. 1998: A genome screen for the QTL for wool traits in a Merino x Romney backcross flock. *Proceedings of the 6th world congress on genetics applied to animal production 26*: 433-436

Hunter, N. 1997: PrP genetics in sheep and the implications for scrapie and BSE. *Trends in microbiology 5*: 331-334

Lauvergne, J.J.; Dolling, C.H.S.; Renieri, C. 1996: Mendelian inheritance in sheep 1996 (Mis 96). COGOVICA/COGNOSAG, Clamart France – University of Camerino, Camerino, Italy.

Maijala, K. 1996: The Finnsheep. *In*: Fahmy, M.H. *ed*. Prolific Sheep. CAB International.

McKenzie, G.W.; Maher, A.P.; Dodds, K.G.; Beattie, A.E.; Henry, A.E.; Hickford, J.G.H.; Montgomery, G.W. 2001: The search for quantitative trait loci affecting wool colour. *Proceedings of the New Zealand Society of Animal Production 81*: 104-108

Morris, C.A.; Johnson, D.L; Sumner, R.M.W., Hight, G.K.; Dobbie, J.L.; Jones, K.R.; Wrigglesworth, A.L.; Hickey, S.M. 1996: Single trait selection for yearling fleece weight or liveweight in Romney sheep – correlated responses in liveweight, fleece traits and ewe reproduction. *New Zealand journal of agricultural research 39*: 95-106

Ponz, R.; Moreno, C.; Allain, D.; Elsen, J.M.; Lantier, F.; Lantier, I.; Brunel, J.C.; Perez-Enciso, M. 2001: Assessment of genetic variation explained by markers for wool traits in sheep via a segment mapping approach. *Mammalian genomics 12:* 569-572

Ponzoni, R.W.; Grimson, R.J.; Jaensch, K.S.; Smith, D.H.; Hynd, P.I. 1997: Birthcoat: Is it worth taking into consideration in Merino sheep genetic improvement programmes. *Wool technology and sheep breeding 45*: 12-26

Puntila, M.-L.; Nylander, A.; Nuutila, E.M. 1999: Genetic parameters for wool traits in Finnsheep lambs. *50th Annual Meeting of the European Association for Animal Production*, Zurich, Switzerland, August 22-26, p. 264

Smith, J.L.; Swan, A.A.; Purvis, I.W. 2001: Genetic variation in crimp frequency and the implications for breeding fine wool Merinos. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics 14*: 297-300

Stephenson, S.K. 1959: Wool follicle development in the New Zealand Romney and N-type sheep. III. The diameters of follicles and fibres. *Australian journal of agricultural research 10*: 108-120

Wilson, T.; Wu, X., Juengel, J.L.; Ross, I.K.; Lumsden, J.M.; Lord, E.A.; Dodds, K.G.; Walling, G.A.; McEwan, J.C.; O'Connell, A.R.; McNatty, K.P.; Montgomery, G.W. 2001: Highly prolific Booroola sheep have a mutation in the intracellular kinase domain of bone morphogenetic protein IB receptor (ALK-6) which is expressed in both oocytes and granulosa cells. *Biology of reproduction 64*: 1225-1235

Wuliji, T.; Dodds, K.G.; Land, J.T.J.; Andrews, R.N.; Turner, P.T. 2001: Selection for ultrafine Merino sheep in New Zealand: heritability, phenotypic and genetic correlations of live weight, fleece weight and wool characteristics in yearlings. *Animal science 72*: 241-250