



Important genes affecting fibre production in animals: A review

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ABSTRACT

The realignment of the production profile to respond to demanding market signals is one of the most important challenges that an animal breeders face today. Animal fibre being a significant contributor to the agricultural economy needs special attention. This is especially true for sheep and goats where fibre production can account for as much as 20% of the total gross income. It is therefore necessary to gain a better insight into the genes governing wool traits. Gene mapping studies have identified some chromosomal regions influencing fibre quality and production. These may help in the selection of animals producing better quality wool. These are more efficient and accurate than the conventional techniques. This paper critically reviews various genes governing fibre growth in animals and their importance. Fibre quality and production genes may provide novel insights into our understanding of the science of genetics and breeding. The discovery of new fibre-related genes and their functions may also help in future studies related to fibre development and in the development of new and advanced techniques for the improvement of fibre production and quality.

Keywords: Animal fibre, Fibre, Genes, Keratin, Loci, Wool

Animals produce a variety of fibres some of which hold great significance for the economy. This is especially true for sheep and goats where fibre production can account for as much as 20% of the total gross income of livestock produce. Traits that most directly influence the value of fleece includes fleece weight, fibre diameter, and length of staple (Baba *et al.* 2019). The weight of the fleece, particularly clean fleece weight, is usually one of the most valuable traits. Fleece related traits are improved through scientific selection and breeding. Conventionally, selection for wool traits is based on phenotypic performance measurement programs utilizing well-developed tools like BLUP methodology (Best Linear Unbiased Prediction) (Hamadani *et al.* 2020). Despite best efforts, the demand and use of natural fibres have shown a declining trend (Hamadani *et al.* 2019, Baba *et al.* 2020, Rather *et al.* 2021). Therefore, there is a need to deliver only the best quality fibre to the apparel industry (Rather *et al.* 2019). Molecular approaches to selection offer an opportunity to exploit the genetic potential of fibre-producing species to the fullest. Traditional animal breeding programs can thus be augmented by the incorporation of genetic evaluation that has the potential to enhance selection accuracy, thereby expediting the genetic improvement of animal productivity. Identifying genes of major effect offers the opportunity to improve product

quality, production efficiency, and product diversity. It is of particular importance to study genes influencing oily fleece weight, clean yield, pigmentation, wool quality and keratin proteins, the latter of which are important for the morphology of the wool fibre. Furthermore, modern traits like fibre diameter, staple strength and staple length are of increasing importance in the fibre industry as well. This paper reviews the most important genes for wool quantity and quality in the animal industry.

Biology of fibre production

There are two main types of hair in the coat of mammals, long and coarse over-hairs, produced by pluripotent primary hair follicles (Yan *et al.* 2022), of the outer coat to provide mechanical protection, and short and fine under-hairs (produced by pluripotent secondary follicles appearing within the trio groups) of the inner coat for keeping the animal warm. There are two main types of commercial fibres comprising of ‘Double-coated’ (DC) species such as angora rabbit, cashmere goat, llama, vicuna, guanaco and primitive sheep having a coarse outer coat produced by the primary follicles, and a fine inner coat derived from secondary hair follicles and ‘Single-coated’ (SC) species such as angora goat, alpaca, camelids and modern woolled sheep in which all fibres are produced by both primary and secondary follicles (Sumner and Bigham 1993).

The cycle of hair growth in most fur mammals consists of three phases: growth (anagen), regression (catagen) and rest (telogen). The pattern of hair growth is different for different species. However, changes in the coat are

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generally due to seasonal variations in day length.

Molecular approaches

Candidate gene approach, transcriptome analysis (Yunxia *et al.* 2021, Liu *et al.* 2020), GWAS studies (Zhao *et al.* 2021) and other techniques have been used to study the effects of fibre related genes. Genes are identified, based on the differential and relative expression-based studies (Ma *et al.* 2022). Thus, the genes responsible for hair and fibre traits along with unique expression patterns can be elucidated. Over the last few decades, DNA-based marker technology has made it possible to identify genomic regions or quantitative trait loci (QTLs) underlying complex traits (Xiao *et al.* 2022), such as fibre diameter, crimp frequency, etc. Genome-wide panels of single nucleotide polymorphisms (SNPs) have used the approach of a genome-wide association study (GWAS). This has made it possible to identify and localized QTLs for complex traits in many livestock species including cattle (Daetwyler *et al.* 2008), swine (Zhao *et al.* 2021), sheep, and humans.

The next-generation sequencing (NGS) based digital gene expression (DGE) profiling technologies developed in recent years have brought about a revolution in traditional transcriptome technology (Wang *et al.* 2022). International Sheep Genomics Consortium (ISGC) has achieved initial success in assembling the reference sheep genome. The total length of the assembled genome, Sheep Genome v4.0, has reached a genome coverage of 166.0× with only 0% gaps between scaffolds.

Genes for wool production and quality

Gene mapping studies have identified some chromosomal regions associated with variation in wool quality and production traits which are essential for selection. Wool production and quality traits are polygenic and different interrelated (mostly pleiotropic) genes and pathways are thought to be responsible for different fibre characteristics like fibre yield, fineness, fibre diameter, staple length, fibre weight, colour and others. Major genes influencing wool production and quality traits are given in Table 1. Important wool production and quality traits are described below.

Fibre quality genes: The economic value of animal fibres is mainly determined by their intrinsic qualities which include mean fibre diameter, coefficient of variation, staple characteristics, comfort factor, spinning fineness, fibre curvature and clean fleece yield. Mean fibre diameter (MFD) is perhaps the most important wool characteristic and is often used in selection.

Fibre diameter genes: Merino is the most prized wool breed of sheep mainly because of its fibre diameter. It may therefore be concluded that wool fibre diameter (WFD) is the most important economic trait (Rowe 2010) of merino sheep and nearly 75% worth of wool fibres is determined by WFD (Mortimer *et al.* 2010). However, the genes specifically controlling WFD remain elusive. The WFD variation-induced profit accounts for 61% of the total profits

of wool. Wang *et al.* (2014) reported nine significant SNPs for fibre diameter distributed on seven autosomes. SNP markers have also been reported on *OAR1*, *OAR13*, *OAR25*, *OAR5* and *OAR6* in sheep. Bai *et al.* (2019) identified six variants (A-F) of KRTAP28-1 having eight SNPs and also detected TG dinucleotide repeat polymorphism.

Staple length genes: Staple length is the average length of a spinnable fibre. Seven QTLs were detected on chromosomes 3, 7, 14, 15, 18 and 25 for the staple length trait (Itenge-Mweza 2007). Three QTLs on chromosomes 3, 7 and 25 were detected related to staple and four putative QTLs for staple length on chromosomes 14, 15, 18 and 25. It was also seen that CRISPR/Cas9-mediated loss of FGF5 activity could promote wool growth and consequently, increase wool length and yield (Li *et al.* 2017).

Crimp frequency: 15 SNPs for crimp have been reported to be distributed on *OAR2*, *OAR3*, *OAR6*, *OAR9*, *OAR10*, *OAR11*, and *OAR23*, one on *EPHA5* gene, and 4 SNPs on chromosome 10. None of these genes plays an obvious role in the crimp trait. But the functions of all of the above genes are directly or indirectly related to epithelial cells or skin development, therefore it is presumed that such genes may be involved in determining the crimp trait. Variation in KRTAP8-2 was also found to affect crimping and growth rate of wool (Tao *et al.* 2017). Additionally, *DSG4* gene was also reported to be a likely candidate, or a major gene, influencing important wool traits including crimp frequency (Ling *et al.* 2014).

Fleece weight genes: Wool weight characters are known to be influenced by Leptin, *PIT1* also *IGF1* genes. However, little is known about their polymorphism. However, research indicates, that certain genes like *L4*, *P4*, and *I2* of Leptin, *PIT1* and also *IGF1* genes influence the wool mass which is the fleece mass at lifetime.

Keratin genes: Keratin proteins are a major component of animal fibres, and these are responsible for most of the structural properties of these fibres (Yan 2016). Some KAPs are rich in cysteine while others have a high content of glycine and tyrosine (Gong *et al.* 2019). Keratins may be grouped into types: the keratin intermediate proteins (IF) and the keratin associated proteins (KAP). The KAP proteins are constituted of three major groups based on their protein sequences, high glycine-tyrosine group, high sulphur group, and ultra-high sulphur group.

Two major multigene families of hair keratins are present, i.e. type I (acidic) and type II (basic) (Bragulla and Homberger 2009). They polymerize and form the 8-10 nm keratin intermediate filaments (KIF) of trichocytes. These are then differentially expressed throughout the fibre development. KIFs are proteins with less content of sulphur and are grouped into type I keratins which is acidic and type II which is non-acidic keratins. Three alleles at the KAP1.1 locus, five alleles at the KAP1.2 locus and nine alleles at the KAP1.3 locus were reported. Two alleles at KIF type I have been reported in Indian sheep breeds,

Table 1. Major genes influencing wool production and quality traits

Gene	Effect	Species/ Breed	More information	Reference
<i>4/HaeIII</i>	Fleece weight (FSFW)	Goat	The dominant genotype shows more expression	Karimi Kurdistani (2013)
<i>INRA 401, OARAE101, IDVGA8, IDVGA088</i>	Fibre diameter	INRA 401 sheep	Chromosome 6, Chromosome 25	Ponz <i>et al.</i> (2001)
<i>BMC1009 OARVH34 ILST005 IDGVA8 – IDVGA088</i>	Staple length	INRA 401 sheep	Chromosome 3, Chromosome 7, Chromosome 25	Pasons <i>et al.</i> (1999)
<i>Caspase-3</i>	Apoptosis of skin keratinocytes	Mouse	Catagen-associated apoptosis of hair follicle keratinocytes. Found in Skin Keratinocytes.	Lei <i>et al.</i> (2012)
<i>CCNA2</i>	Fibre diameter	Sheep	Upregulated expression. (NATs transcript)	Yue <i>et al.</i> (2015)
<i>DKK1</i>	Wool production and quality traits	Sheep	Regulates hair follicle morphogenesis and cycling	Mu <i>et al.</i> (2017)
Fibroblast growth factor 1	Wool fibre diameter	Sheep	Located on Chromosome 1	Robinson <i>et al.</i> (1995)
Fibroblast growth factor 5 (<i>FGF5</i>)	Regulates hair length	Human	FGF5 underlies trichomegaly and is a crucial regulator of hair growth in humans.	Higgins <i>et al.</i> (2014)
<i>Glu109His, Glu110ter, Glu206Glu, Arg213Lys and Arg218Lys</i>	Greasy fleece weight and fibre length	Makooei sheep	–	Lan <i>et al.</i> (2009)
Growth Hormone Gene exon-4	Fleece weight	Makooei sheep	20% elevation in raw and clean fleece weights	Santiago-Moreno <i>et al.</i> (2004)
<i>Gsdma3</i>	Skin keratinocyte apoptosis	Mouse	Catagen-associated apoptosis of hair follicle keratinocytes. Found in Skin Keratinocytes.	Lee <i>et al.</i> (2012)
<i>GSDMA3, HSPA2, RPS27A, PDCD6IP, DAP, CCNA2 and FOS</i>	Protects fibroblasts against apoptosis	Humans	Expressed in human somatic tissues	Filipczyk <i>et al.</i> (2012), Wang <i>et al.</i> (2014), Strappazzon <i>et al.</i> (2010), Levy-Strumpf and Kimchi (1998), Das <i>et al.</i> (2013), Reiner <i>et al.</i> (2000)
Halo- hair 2 (<i>HH2</i>)	Medullation	Sheep	Carpet wool production	Purvis and Franklin (2005)
Halo-hair 1 (<i>HH1</i>)	Medullation	Sheep (Romney Breed)	Carpet wool production	Purvis and Franklin (2005)
<i>Hr</i> gene	Hairlessness	Sheep (Valle del Belice Breed)	Mendelian recessive causes apoptosis of hair follicles and interfollicular epidermis.	Finocchiaro <i>et al.</i> (2003)
<i>IGF1, PIT-1, Leptin</i> genes	Wool weight	Makooei sheep	Fleece mass at lifetime	Negahdary <i>et al.</i> (2014)
<i>IGFBP-3</i> gene	Several wool traits	Chinese Merino and Kazakh sheep	Decreases staple length and increase fibre diameter.	Shen <i>et al.</i> (2013)
<i>K16 and K14</i>	Keratin protein	Goat	Clustered in two distinct regions of chromosome 17	Rosenberg <i>et al.</i> (1988)
<i>KAP</i>	Fibre diameter, staple strength, wool colour, and brightness		–	Beh <i>et al.</i> (2001)
<i>KAP 1.3</i>	Yield and staple length, Lustre	Sheep	Increased yield and staple length with whiter and brighter wool	Itenge-Mweza (2007)
<i>KAP1.1</i> (B2A), <i>KAP1.3</i> (B2C) and <i>KAP1.4</i> (B2D)	Keratin protein, staple length	Charon 4A breed of sheep and Merino, Romney sheep	Three B2 high-sulphur keratin genes (new name KAP1.n family)	Powell <i>et al.</i> (1983)

Continued...

Table 1. (Concluded)

Gene	Effect	Species/ Breed	More information	Reference
<i>KAP1.1 C</i>	Wool brightness	Sheep	–	Itenge-Mweza (2007)
<i>KAP6.1, KAP8.1, KAP8.2, KRTAP9-2 KAP16.4 KAP16.4-1 and KAP16.4-2 KAP8.1 and KAP8.2</i>	Fibre diameter	Chinese Merino	A variant of the KAP gene	Sulayman <i>et al.</i> (2017)
	Cashmere weight, cashmere length, hair length, fibre diameter	Goats (cashmere)	A variant of the KAP gene	Lui <i>et al.</i> (2011), Itenge (2020)
<i>KIF</i> type I and II	Keratin protein	Bovine, Mouse, Human, Sheep	Inner root sheaths of the hair follicle in humans	Krieg <i>et al.</i> (1985), Johnson <i>et al.</i> (1985), Tyner <i>et al.</i> (1985)
<i>KRT1, KRT7, HSD11B1, S100A8, NT5C3 L and DNAJC12</i>	Promoting follicle cell proliferation and differentiation	Humans	Expressed in human somatic tissues	Fonseca <i>et al.</i> (2012), Glotzer <i>et al.</i> (2008), Sandilands <i>et al.</i> (2013), Smith <i>et al.</i> (2002), Tiganeşcu <i>et al.</i> (2011), Yang <i>et al.</i> (1992), Korndorfer <i>et al.</i> (2007), Nacken <i>et al.</i> (2003), De Bessa <i>et al.</i> (2006)
<i>KRT2.10 and KRT2.13 KRTAP6 and KRTAP8 KRTCAP3 gene</i>	Keratin protein Fibre diameter Keratin	Sheep Peppin Merino Chinese Merino	Located on chromosome 3 Located on chromosome 1 Expressed in skin keratinocytes.	McLaren <i>et al.</i> (1997) – Kang <i>et al.</i> (2008)
<i>L4, P4, I2 of Leptin, PIT1, IGF1, NT5C3L</i>	Wool weight Fibre diameter	Makoei sheep Sheep	Upregulation Downregulated expression. (DEGs transcript)	Negahdary <i>et al.</i> (2014) Yue <i>et al.</i> (2015)
<i>OAR1, OAR3, OAR4, OAR8, OAR9, OAR13 and OAR25,</i>	Fibre diameter	Chinese Merino	Significant SNP markers associated with the fibre diameter trait	Wang <i>et al.</i> (2014)
<i>OAR2, OAR3, OAR6, OAR9, OAR10, OAR11 and OAR23</i>	Crimp Frequency	Merino sheep	SNPs concentrated on chromosome 10.	Wang <i>et al.</i> (2014)
<i>POUIF1</i> locus	Greasy fleece weight and fibre length	Goats	<i>POUIF1</i> regulates PRL-associated with wool growth and wool traits in sheep and may cause the same effects in goats.	Dicks (1994)
<i>PTPN3</i> (Tyrosine-protein phosphatase non-receptor type 3), <i>TCF9</i> (GC-rich sequence DNA-binding factor 2), <i>GPRC5A</i> (G protein-coupled receptor, family C, group 5, member A), <i>DDX47</i> (DEAD (Asp-Glu-Ala-Asp) box polypeptide 47), <i>EPHA5</i> (EPH receptor A5), <i>TPTE2</i> (transmembrane phosphoinositide 3-phosphatase and tensin homolog) and <i>NBEA</i> (neurobeachin)	Crimp trait	Merino	The <i>GPRC5A</i> gene may be involved in modulating differentiation and maintaining homeostasis of epithelial cells.	Fujimoto <i>et al.</i> (2012)
<i>YWHAZ</i>	Fibre diameter trait	Sheep, Chinese merino, human	Overexpression of YWHAZ in HaCaT immortalized human skin keratinocytes promotes overgrowth, as well as morphological changes.	Wang <i>et al.</i> (2014)

whereas nine alleles are at KAP1.4.

Information on these genes in the goat genome is sparse. Three different alleles at KIF type I have been reported in Xinjiang breeds of goat. Also four KAPs 7.1, 8.1, 8.2 and 13.1 have been found in goats with polymorphisms of these genes associated with fibre diameter, combed fibre weight, fibre length and guard hair length traits.

Pigmentation genes: Pigmentation patterns of fleece and hair are influenced by multiple loci. Agouti is one of the most important loci for pigmentation and it codes a protein that binds to the melanocortin receptor (MC1R). If the gene is not present, melanocyte-stimulating hormone (α MSH) binds to MC1R and signals the production of eumelanin. The black colour in sheep is reported to be due to a 5 bp deletion in exon 2 (Zhang *et al.* 2017). Lateral symmetry in pigmentation patterns of fleece and hair may be due to badgerface (Ab) or reverse badgerface (At) alleles, which are both recessive. These two alleles are dominant to the self-colour black allele (Aa). The agouti locus (ASIP) is located on sheep chromosome 13 and except for the extension locus, other loci affecting colour patterns have not been identified.

Conclusion

This paper provides an overview of the important genes governing wool quantity and quality traits and their importance. It is concluded that fibre quality and production genes may provide novel insights into our understanding of the science of genetics and breeding. The discovery of new fibre-related genes and their functions may help in studies related to fibre development and in the improvement of fibre production and quality through technological advancement.

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