Major genes and QTL influencing wool production and quality: a review

Whilst the genetic improvement of sheep bred primarily for wool production has been slow relative to other livestock species, this cannot be blamed on the tools available to the breeders and advisor geneticists. In most countries where wool sheep are grown, there is a quite sophisticated wool market and market intelligence, and the important price determinants are well quantified and communicated. This has facilitated the formal definition of breeding objectives for breeders. Of those traits that are important in an economic sense, most are either moderately or highly heritable, and are easy and inexpensive to measure to a level sufficiently precise for animal evaluation. For the few traits where measurement is difficult or expensive, such as staple strength, there are good indirect measures. For example, coefficient of variation of fibre diameter has been shown to deliver significant gains when used as a selection criterion in breeding programs focussed on apparel wool goals. Most countries have high quality performance measurement programs and well-developed tools for the use of index selection utilising BLUP methodology. So, why is there an intense and increasing interest in the study of genes of major effect on wool production and quality traits:

(i)   antagonistic correlations between two of the most important traits; clean fleece weight (CFW) and mean fibre diameter (MFD);

(ii)   finding ways of dealing with one of the major deficiencies of the wool fibre in the apparel processing system; that is, when compared to many of the synthetic fibres that are used for apparel wear production, wool is of significantly lower and more variable fibre strength. This translates into a more difficult and expensive processing system;

(iii)   wool currently comprises only 17% of the apparel processing system and this has been consistently decreasing over the recent decades. There is a clear need for the wool industry to deliver to the apparel wearer new and novel products. One way of achieving this goal is to produce wool with new and novel fibre properties.

Identifying genes of major effect offers the opportunity to improve production efficiency, product quality and product diversity, through utilising them in breeding programs, developing transgenic lines and by developing therapeutic agents that can be used to alter fibre attributes
by altering gene expression.

Examination of the underlying physiology that is integral to the production of a tissue product can be instrumental in identifying developmental steps under genetic control that are critical to the ultimate attributes of that tissue product. For example, in the production of meat there are many genes involved in the metabolic processes that control growth and differentiation of the composite cells and tissues, expression of the structural proteins that compose the tissues, and the timing or tissue specificity of gene expression and/or ligand – receptor systems that control cell function.

The biology of skin and wool growth in sheep has been extensively studied since the 1950's and the developmental processes at the cellular level are reasonably well understood. The basic units used in the study of biology of wool growth are the wool

follicle and the fibre growing from it. Although there is evidence for higher-level organisational mechanisms, such as the trio group of primary follicles and associated secondaries, it is at the level of the individual follicle that most studies have focussed.

There is clear evidence of a strong association between the developmental activities that occur during follicle initiation in the foetus and the fibre and fleece quality attributes that subsequently grow in the animal over its lifetime. The basis for the control of follicle initiation, follicle density and the consequent follicle and fibre attributes of the adult animals has been proposed to be due to (a) competition between wool follicles, (b) a biochemical pattern-forming mechanism (reaction-diffusion –RD- theory), and (c) competition for a limited pool of dermal pre-papilla stem cells. None of the above models adequately accounts for the observed variation. For example, the competition model does not easily accommodate the changes in follicle density that occur during foetal growth. Theories (b) and (c) each suggest that adult follicle density and MFD are co-determined at the time of follicle initiation. However, in an elegant examination of the relationship between foetal and adult follicle characteristics, Adelson *et al*. [1] have shown that control of follicle bulb size and fibre diameter occurs after follicle initiation.

Finally, the founder cell hypothesis proposes a fixed population of pre-papilla cells, and that this population of cells acts as a limiting resource for follicle initiation. Doubt has been cast over the validity of this model by the demonstration that the papilla cells divide during follicle development, and that the papilla can recruit dermal cells from the surrounding tissue. Hence, the explanation remains obscure. It may be that follicles are initiated according to a RD model, but the subsequent follicle size is influenced by competition, or lateral inhibition or by some other mechanism not realised until later in life.

Whatever the explanation, it is clear that an empirical functional relationship exists between follicle density and fibre diameter, and that the relationship changes as follicle density increases. Similarly, there is a well-documented relationship between length growth rate (L) and fibre diameter (D), such that L/D (or L/D2) for a given animal is approximately constant over a range of environmental conditions. The negative genetic relationship between L and D is counterbalanced, at the population level, by a positive association between L and D generated by changes in total nutrient availability, and a negative association between density and L (or D). Overall, we see that there are complex interactions between each of the important components of wool growth, and the correlations that we observe in a given population reflect an admixture of relationships generated by different developmental and physiological pathways.

The point that we wish to emphasise here is that we do not expect QTL (quantitative trait locus), when identified, to each reflect the genetic relationships seen at the population level. A locus involved in follicle initiation, for example, may influence both density and diameter, but have little effect on clean wool weight. Alternatively, a locus affecting voluntary feed intake, or nutrient flow to the skin, may influence both clean wool weight and fibre diameter, but have little or no effect on follicle density. These distinctions are important in assessing the value of various QTL in genetic evaluation, especially as we attempt to produce finer wools without adversely affecting other economically important fleece value attributes.