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associated with wool follicles in the skin (Sumner and Craven, 2005).

A QTL for wool yellowing has been identified on chromosome 11 (McKenzie, 2002). A marker on chromosome 11, *OarFCB193* has been linked in a (Merino x Romney) x Merino backcross flock, with the development of wool yellowing in warm moist conditions. Subsequent half-sib analysis of this *OarFCB193* marker did not provide further support for the association (McKenzie, 2002).

#### **Where to from here?**

Many economically important wool traits are under the influence of multiple gene loci and are also influenced by environmental factors (Kendall *et al.*, 2006). Many of the traits also have been revealed to be interrelated, or to interact either positively or negatively, and many of the genes encoding the wool proteins are linked, as discussed above, making it difficult to dissect the influence of any one gene on fibre characteristics. What is more, extensive polymorphism has been found in many of the genes, which could also affect the wool fibre and wool traits by altering protein expression, structure or post-translational modifications.

Despite all these compounding and interacting effects, many wool traits show relatively high heritabilities and hence are relatively easy to breed for. This may be because the key wool genes are clustered; meaning that selection for one gene will result in indirect selection for a haplotype of alleles at the proximal or clustered loci. In this respect, further analysis of these clusters should enable us to advance breeding

for wool with more closely controlled specifications.

The potential impact of the gene-markers described here is difficult to evaluate. From the preliminary results described above, quite large differences in traits such as mean fibre diameter, fibre diameter variation and staple strength have been shown to be associated with variation in a number of genes and loci. The identified effects are of processing significance and may equate to price differences for raw wool, where that wool is purchased for a specific end-use.

To be of practical significance these gene-markers would need to reliably predict variation in these traits in different sheep breeding operations, and within and between breeds and to be cost-effective relative to other areas of activity. If they could achieve this consistently, with a minimal cost of measurement, the technology would assist growers in providing raw fibre to meet the specifications required by a particular processor to produce a specific product with reduced wastage.

Gene-marker-assisted selection techniques are currently utilised by ram breeders in New Zealand when breeding sheep for increased tolerance to footrot and rams to produce lambs with improved survival capabilities. Currently over 400 New Zealand sheep farmers use the footrot gene-marker test on a regular basis with independent surveys of the technology indicating multi-million dollar savings (Greer *et al.*, 2004). With confirmation of the location and identity of appropriate marker genes for important wool characteristics and demonstrations of their cost effectiveness, gene-marker-assisted selection techniques could assist ram breeders to select for particular wool characteristics.

### **Environmental and physiological mechanisms underlying wool growth rhythms in coarse wool sheep**

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#### **ABSTRACT**

Coarse-woolled sheep breeds such as the Romney exhibit a pronounced annual cycle of wool growth with concomitant changes in fibre length growth rate and mean fibre diameter with maxima in summer and minima in winter. This cycle, which is entrained by seasonal changes in daylength via changes in circulating prolactin, parallels wool growth rate in Romney sheep. The cycle is also influenced by complex interactions between nutrient supply and hormones associated with reproductive status. A marked depression in wool production occurs during early pregnancy, which cannot be completely ameliorated by supplementary feeding, and does not directly involve prolactin. Additionally, in ewes, experimental and pharmacological increases and decreases in the prolactin concentration at parturition and during lactation are associated with

increases and decreases, respectively, in spring and summer wool growth rate. A greater appreciation of the different mechanisms that temporally influence the wool growth cycle represents a potential means to change fleece characteristics. The development of sheep genotypes with a reduced amplitude of their wool growth cycle would significantly contribute to a reduction in fibre variability that can affect processing performance.

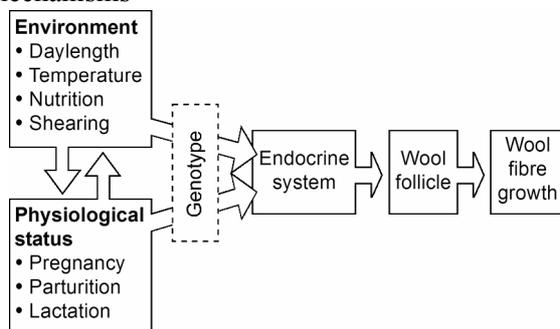
**Keywords:** coarse wool; rhythm; environment; physiology; endocrinology.

## INTRODUCTION

British breeds of sheep that produce coarse wool, such as the New Zealand Romney, exhibit a pronounced annual cycle of wool growth with concomitant changes in fibre length growth rate and mean fibre diameter resulting in maximum mean fibre volume in summer and minimum mean fibre volume in winter (Bigham *et al.*, 1978). These changes in fibre dimensions influence fibre and staple tensile strength and the regularity of fibre crimping - characteristics that impact on processing performance (Hunter, 1980).

Research has shown these seasonal rhythms are largely controlled by the endocrine system in response to a range of interacting environmental and physiological factors to which different genotypes of sheep vary in their sensitivity. The key environmental and physiological factors known to influence wool growth are summarised in Figure 1 and will be discussed in the following review. Understanding the underlying endocrine mechanisms that regulate wool growth provides an opportunity to develop animal management practices or improved genotypes that modify fibre length growth rate and variation in mean fibre diameter. At present, the variability in key fibre properties, partly attributable to the high degree of polymorphism and variation in many of the genes affecting wool traits (Abbott *et al.*, 2006), is a significant impediment to direct wool supply chains (McDermott *et al.*, 2006). Genomic technologies can assist in identifying and modifying the genes that regulate the seasonality of wool growth, resulting in the production of wool with less variation in fibre characteristics within an individual fleece.

**FIGURE 1:** Overview of the regulatory factors that influence wool growth through endocrine mechanisms



## FACTORS KNOWN TO INFLUENCE WOOL GROWTH

### Season and photoperiod

The annual cyclical pattern of wool production is primarily entrained by photoperiod with the seasonal wool growth pattern being progressively abolished when sheep are kept in complete darkness by hooding (Hart, 1955). Reversing the normal photoperiodic rhythm causes a slow reversal of the wool growth pattern, with up to two years of exposure to the reversed rhythm being required before synchrony is achieved (Morris, 1961). Maintaining sheep under a constant short-day photoperiod (8 h light:16 h dark) results in increased winter and spring wool production with a decrease in the amplitude of the rhythm (Coop & Hart, 1953). Greater differences in seasonal daylength (Figure 2a) are likely to cause greater differences in the relative amplitude of wool growth rate, in combination with differences in seasonal pasture growth rate when the sheep are managed similarly (Figure 2b). A difference in latitude where daylength is one hour longer in summer and one hour shorter in winter, as in Southland compared to the Waikato, has been shown to result in a 40% greater amplitude of wool growth in Southland than in the Waikato for groups of genetically similar Romney sheep (Sumner *et al.*, 1998). Nevertheless, sheep at both sites still grew the same total amount of wool over the whole year.

A relationship between seasonal changes in circulating prolactin concentration induced by photoperiod and wool growth has been established in shedding breeds of sheep (Lincoln, 1990; Pearson *et al.*, 1996) and coarse-woolled breeds like the Romney (Kendall, 1999). In contrast, Merino sheep do not exhibit a pronounced photo-dependent seasonal wool growth cycle (Sumner *et al.*, 1994) and are not responsive to seasonal changes in prolactin concentration (Lincoln, 1990). Prolactin receptors identified in the wool follicle of sheep with seasonal wool growth (Choy *et al.*, 1997) provide a biochemical mechanism whereby perturbations in circulating prolactin influence wool growth cycles. In non-pregnant Romney sheep, the seasonal profile in prolactin concentration parallels changes in daylength

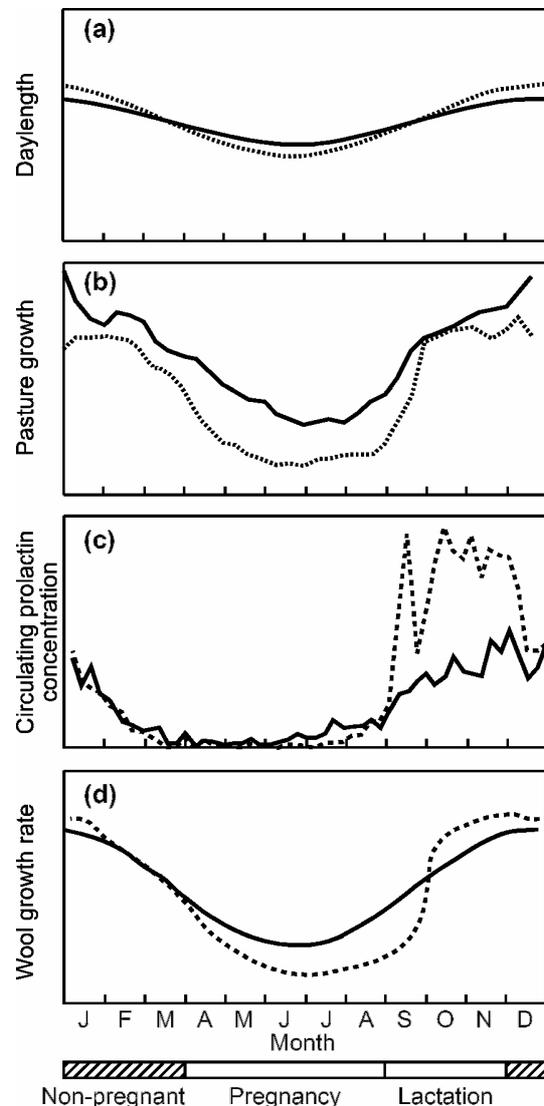
(Figure 2a and c). Using artificially regulated photoperiod it has been possible to modify the profile of plasma prolactin concentration in Romney ewes (Kendall, 1999), which was associated with concomitant alterations in the annual wool growth cycle. Exposure of non-pregnant ewes to a long-day photoperiod (16 h light:8 h dark) for four months commencing between the autumnal equinox and winter solstice induced a four-fold increase in winter prolactin concentrations relative to control sheep exposed to a natural autumn and winter photoperiod. This prolactin surge was associated with a marked increase in both fibre length growth rate and mean fibre diameter during the winter and spring, leading to 27% more clean fleece wool being grown over this period. Continuous exposure of non-pregnant ewes to a long-day photoperiod, beginning at the autumnal equinox, increased circulating prolactin concentration during the winter months, and ameliorated the seasonal decline in wool growth in the winter. Winter and spring clean wool growth rate was 37% higher in these animals resulting in an 18% increase in annual fleece weight.

A feature of both studies has been the muted initial prolactin response over several months following the imposition of the long-day photoperiod treatment in autumn, indicating secretory refraction to long-day photoperiod during this season. The decreased autumn sensitivity of prolactin secretion in response to experimentally-increased photoperiod may be a consequence of maintenance of high circulating prolactin levels over the preceding summer.

While it is clear there are endocrinological constraints in achieving a sustained elevation in the concentration of prolactin and potentially long-term increases in wool growth, the evidence suggests that a prolactin stimulus over a few months will reset the wool growth cycle resulting in a medium-term increase in wool growth. This net increase in wool production is a consequence of a shift in the timing of peak wool growth rate with the seasonal maxima occurring earlier. However, as New Zealand sheep are not housed during the winter, sheep farms do not have facilities where an artificial photoperiod could be imposed on a large group of sheep for a sufficient period of time to induce a significant response.

Although ambient temperature *per se* does not influence fleece wool growth rate (Bottomley, 1979), sustained high temperatures can induce elevated prolactin concentrations (Walker *et al.*, 1990), which could potentially influence wool growth rate.

**FIGURE 2:** Mean annual (a) daylength and (b) pasture growth in northern regions (—) and southern regions (----) of New Zealand, and (c) circulating prolactin concentration and (d) wool growth rate for non-breeding (—) and breeding (- - -) coarse-woolled ewes.



### Pregnancy and parturition

Wool growth rate of breeding Romney ewes declines by between 10% and 20% during pregnancy (Figure 2d) (Kendall, 1999; Reid & Sumner, 1991; Sumner & McCall, 1989). The concomitant reduction in mean fibre diameter and fibre tensile strength diminishes the economic value of the fibre for producing a range of wool products. Although this depression in wool growth during pregnancy has been attributed to competitive demands for available nutrients by the developing foetus, the extent of the depression can only be reduced and not prevented by supplemental feeding during late gestation (Fitzgerald *et al.*, 1984; Hawker & Thompson, 1987). A depression in wool growth rate associated with pregnancy has been detected as a reduced fibre length growth rate

as early as day 21 of gestation (Pearson *et al.*, 1999). This depression in wool growth occurs too early in pregnancy to be the result of competition for available nutrients between the ewe and the foetus, so it is thought to be under endocrine control.

Prolactin secretion is suppressed during pregnancy before increasing sharply just prior to parturition (Figure 2c). As reductions in circulating prolactin concentration do not exert short-term effects on wool production (Pearson *et al.*, 1996) it is unlikely that the depression in wool growth associated with pregnancy is mediated via prolactin. However, the prolactin surge prior to parturition appears to be important in re-setting the inherent wool growth cycle and reinforcing the spring surge in wool growth rate.

The concentration of circulating progesterone has been shown to increase following uterine implantation of the foetus. The timing of the rise in circulating progesterone corresponds with the timing of the pregnancy-induced decline in wool growth (Kendall, 1999). Although there are reports of progesterone having no direct effect on wool growth (Slen & Connell, 1958), specific progesterone receptors have been identified in human skin and hair follicles (Wallace & Smoller, 1998).

Another potential candidate hormone that may depress wool growth rate during pregnancy is placental lactogen. This hormone signals through both growth hormone and prolactin receptors (Herman *et al.*, 2000) and has been implicated in the development of wool follicle populations in foetal lambs (Wickham *et al.*, 1992). It may also play a regulatory role in the pregnancy-induced depression in wool growth. While the decline in wool follicle output occurs before any appreciable increase in placental lactogen concentration (Chan *et al.*, 1978), placental lactogen disappears from the circulation at parturition, coinciding with a marked increase in wool growth rate.

### Timing of lambing

Birth season influences the seasonal pattern of wool growth. When ewes lamb in spring the decrease in winter wool growth rate coincides with the pregnancy-induced decline in follicle output and reduced pasture growth. When ewes lamb in autumn or winter the winter decline in wool growth is less pronounced and the ewes can produce up to 33% more greasy wool at annual shearing than spring-lambing ewes (Morris *et al.*, 1993; Reid & Sumner, 1991). Wool grown by ewes lambing in autumn or winter has less variation in fibre diameter and hence a higher staple tensile strength (Morris *et al.*, 1994), leading to improved

processing performance. The underlying explanation has been attributed to interactions between pregnancy and lactational influences on prolactin secretion with photoperiod (Kendall, 1999). While peak circulating prolactin concentrations at parturition were similar in winter- and spring-lambing ewes, elevated prolactin concentration during the winter in lactating autumn/winter-lambing ewes provides a stimulatory effect on winter wool production. In contrast, prolactin levels remain low in spring-lambing ewes during winter (corresponding to pregnancy), and wool growth continues to decline until lambing (Figure 2c and d).

### Lactation

Wool growth of coarse-woolled sheep increases during lactation (Figure 2d) with the magnitude of the increase being influenced by feed quantity and quality, and the number of lambs being reared (Hawker *et al.*, 1982), as absorbed nutrients are preferentially used for milk production at the expense of wool growth.

Lactation is associated with a period of continual high concentrations of circulating prolactin (Figure 2c) with levels able to be modified by photoperiod or pharmacological treatment. It appears that the prolactin profile during lactation, in combination with the extent of the prolactin surge at parturition, is important in stimulating wool growth post-lambing. On average, increases in annual fleece weights of 18% have been observed in autumn/winter-lambing ewes exposed to a long-day photoperiod (Kendall, 1999) compared with control ewes. The fibre grown was also coarser by approximately 5  $\mu\text{m}$ . This marked increase in wool production may be associated with an up-regulation of prolactin receptor populations in skin during the pre-partum period, hence, enhancing prolactin signalling capacity (Montenegro, 2003), in combination with higher circulating prolactin concentrations at parturition and the subsequent lactation.

Pharmacological treatments can eliminate the high circulating prolactin concentration during lactation and suppress the seasonal spring rise (Kendall, 1999). Although such treatments do not have an immediate effect on wool growth rate during early lactation, chronic suppression of prolactin suppresses wool growth in summer by an average of 13% with a further 20% reduction in wool growth rate if the prolactin surge at parturition is also abolished. The long-term depression in wool growth rate, as reflected in final fleece weight, is mainly due to a decline in length growth rate with little change in mean fibre diameter.

### **Nutrition**

The level of nutrition can greatly affect the productivity of sheep. Both wool growth rate and the associated fibre characteristics can be influenced directly by variations in pasture quantity (Figure 2b) and quality through their associated effect on voluntary feed intake (Hawker *et al.*, 1984). Wool growth is also influenced by individual dietary components but is outside the scope of this review. While most studies have shown there is a direct increase in wool growth as feed intake increases, the response is seasonally dependent with the absolute response in coarse-woolled breeds in summer being approximately twice that in winter (Hawker & Crosbie, 1985). The relative response of wool growth rate to changes in feeding level is essentially similar across seasons.

### **Shearing**

Frequency of shearing influences the length of fibre available for processing. Time of shearing, on the other hand, influences the position of the region of minimal fibre diameter along the staple. This in turn affects the length of fibres in a yarn and thereby yarn strength. As a consequence, the tensile strength of a staple of wool and the position of tensile weakness within the staple influences the economic value of that parcel of wool. Most coarse wool flocks in New Zealand are typically shorn between November and January, and sometimes “second shorn” in May after mating. The thinnest part of the fibre is then midway between the tip and base of the staple – a worst case scenario from a processor’s point of view. Although wool may grow faster in the six weeks or so following shearing when the sheep have access to adequate amounts of green pasture, the effect is the result of an increase in the sheep’s voluntary feed intake in an attempt to maintain their body temperature (Elvidge & Coop, 1974), not an effect of cutting the fibre *per se*.

### **PRACTICAL IMPLICATIONS**

As the price for wool has continued to decline over some decades, sheep farmers have

been forced to adapt to the changing global market to remain profitable. For many this has included a change in the management of their farm with the adoption of new technologies to improve productivity. The ability to optimise the processing performance of the shorn fleece wool by reducing the variation in key wool characteristics, such as mean fibre diameter during the year should potentially increase the price received by the grower. However, as the price differentials applying across the range of coarse wools are relatively small, the economic returns from producing coarse wool are principally related to fleece weight rather than the characteristics of the fleece.

Feed quality and quantity, photoperiod and the reproductive cycle are all affected by season and collectively reinforce the inherent annual wool growth pattern seen in grazing sheep (Figure 2). Manipulation of the time of lambing with its associated endocrine profile, in combination with improved nutrition, provides an opportunity to capitalise on the respective influences of these different factors throughout the year. Despite marked increases in seasonal wool growth in ewes manipulated in an indoor environment, endocrine treatments do not currently offer a cost-effective technique to stimulate wool growth rates in sheep managed under New Zealand pastoral farming systems on account of the cost of the treatment relative to the returns from wool. However, there is clearly potential to develop sheep genotypes whose follicles are insensitive to seasonal changes in circulating prolactin, as in modern Merino strains. Wool follicles in these sheep would also need to be less responsive to reproductive hormones that depress wool growth during pregnancy. Such sheep would be characterised by increased wool growth productivity, producing fibre with less variable fibre diameter profiles and higher staple strength. In the meantime, farmers should continue to maximise wool production in their flock when feed availability is high and to shear their flock when the rates of wool growth are lowest, while taking into the account the welfare of the animal.