A review implicating a two compartment model for the processes of cell division and differentiation in the Wool Follicle

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ABSTRACT

The determinants of wool production per unit area of skin are reviewed, and found to be dominated by follicle volume. Evidence is presented to show that follicle cells destined to become fibre cells differentiate into a continuum of cell types rather than discrete populations of medullary, ortho- and paracortical cells as the literature suggests. Fibres of the same dimensions grown by a sheep at one point in time contain differing proportions of these cell types. It is hypothesised that there is a degree of independence between fibre volume and cell differentiation. Medulla formation is explained in terms of competition between follicles for keratin precursors, so that fibre volume exceeds the available volume of keratin. A similar mechanism is proposed for the cortex, where paracortex and mesocortex become less prevalent as total fibre volume increases. It is concluded that a model for fibre formation can be considered in two parts: one which generates fibre volume and another which determines cell type within that volume.

Keywords Wool production, wool follicles, follicle competition, fibre volume, orthocortex, paracortex, medulla, model.

INTRODUCTION

This review presents a model which Gandar *et al.*, (1989) refer to as an "inverse model", one which links observed phenomena back to the underlying processes. A number of models describing the formation of wool fibres have been proposed. Those which seek to explain the development of patterns in cell type and distribution in wool fibre cross-sections are especially relevant to the discussion. Aspects of these models are examined and found to suffer the deficiency of interpreting in two dimensions, the development of a fibre which occurs in three dimensions. The three dimensions of fibre development are examined below using some published and unpublished data from this laboratory. We propose an alternative inverse model for fibre formation, consisting of two compartments, and the elementary mathematical framework for a "forward" model is provided.

FIBRE VOLUME.

The following were outlined by Black and Reis (1979) as the determinants of the rate of production of fibre volume:

1) the rate of cell division in the follicle bulb,
2) the maximum number of cells in the proliferative zone,
3) the maximum size of cells in the proliferative zone,
4) the proportion of cells migrating from the follicle,
5) the proportion of migrating cells entering the fibre,
6) the maximum size of the cells in the fibre,
7) the total number of wool follicles.

The first six of these are characteristics of the individual follicles and are examined separately from the last which is a characteristic of the skin.

The rate of wool growth from an individual follicle.

The rate of wool growth is correlated with the rate of production of new cells from the bulb (Hynd *et al.*, 1986; Hynd, 1989a; 1991), and rate of cell division, is therefore an important determinant of wool growth rate. However, cell proliferation rate per bulb has been shown to be closely related to bulb volume (Hynd, 1989a; 1991), and Black (1987) also suggested that follicle size in sheep is controlled predominantly by cell number, rather than cell size. The rate of cell division and the number of cells in the proliferative zone, therefore appear to be dependent variables. Further support for this argument has been provided by Henderson (1965), who found that within populations of follicles from an individual animal, there was a consistent relationship between fibre diameter and follicle dimensions. Williams and Winston (1987) have also shown that mitotic density (mitoses per unit volume of follicle bulb tissue) was not significantly different between Merino sheep from lines selected for and against fleece weight, however the average cross sectional area of germinative tissue was 10% larger for the 'fleece plus' line and the proliferative region of the bulb therefore greater in volume. Holle *et al.*, (1992) have similarly found that a major difference between the Massey fleece weight selection lines is the size of the follicle bulbs. We can also extrapolate from these observations to say that if the proportion of cells migrating from the bulb changes whilst the rate of cell division remains constant, the size of the follicle bulb would fluctuate.

Another important factor which is not yet fully understood is that an inherently small proportion of cells leaving the bulb finally contribute to the fibre. Black (1987) reviewed evidence to suggest that as few as 10 to 25% of the cells leaving the bulb enter the fibre in Merinos. The follicles of a Lincoln on the other hand were found to be more efficient: 40 to 50% of the cells entering the fibre.

The sixth determinant of wool growth rate, the maximum size of cells in the wool fibre has also been reviewed by Black (1987), who concluded that one of the major factors limiting the rate of wool growth at a sub-optimal nutrient supply was a decrease in the final size of the cortical cells. Although estimates

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of the final size of the cortical cells show some variability, the different techniques used to measure the dimensions could lead to some misinterpretation. Complete three dimensional reconstruction of cells *in situ* from electron microscope or confocal laser scanning microscope images may help determine whether cell volumes measured by disruptive techniques are accurate.

In summary, the balance of evidence suggests that the determinants of individual fibre volume are dominated by the volume of the germinative region of the follicle from which it arises, and the proportion of migrating cells entering the fibre. Of the first six determinants of wool growth, the first, second and fifth seem to be the most important. Indeed, Hynd (1989a) found that 96% of the variance in fibre output per follicle was accounted for by an equation incorporating mitotic rate and cellular efficiency (a measure of the proportion of cells which enter the fibre).

The volume of wool per unit area of skin.

As noted above, the constraints on fibre production outlined by Black and Reis (1979) include follicle density. Shrinkage of the skin after it has been removed from the animal is dependent on follicle density (Carter and Clarke, 1957) and the method of fixation and sectioning (Steinhagen and Bredenhahn, 1987). It is therefore difficult to measure the area of skin associated with a number of follicles to calculate density. The ratio of secondary to primary follicles (S/P ratio) is unaffected by shrinkage, and is used to define density since a high S/P ratio is generally associated with higher density (Nay 1973).

Williams (1987) proposed the volume of follicle tissue per unit area of skin as an alternative to follicle density, which would appear more suitable. Since follicle density determines the number of fibres per unit area of skin, and as shown above, bulb volume determines individual fibre volume, total volume of bulb tissue should therefore determine total fibre volume per unit area of skin (Williams, 1987; Hynd, 1991). However, this is not as simple as it would first appear, since there is evidence that a high follicle density is associated with a smaller volume per bulb (Hynd, 1991).

From a single base flock, selection for and against fibre diameter led to compensatory changes in follicle density, whereas selection for and against staple length resulted in a compensatory change in crimps per inch (Moore *et al.*, 1989). Fleece weight, (and presumably fleece volume) exhibited small differences between the groups, which led to the conclusion that the original flock had a maximum capacity to form follicle tissue, and therefore fibre. This fits the bulb volume per unit area of skin hypothesis of Williams (1987), and was further discussed by Hynd (1991).

THE FORMATION OF VARIOUS CELL TYPES IN THE WOOL FOLLICLE.

The cells that are derived from the germinative region of the wool follicle distribute themselves in an annular arrangement. From the outer ring these are the inner root sheath cell layers, the fibre cuticle, the fibre cortex, and in some cases the medulla (Auber, 1950). The cortex can be further divided into various cell types.

Inner root sheath.

Priestley (1967) examined seasonal changes in the area of inner root sheath in Herdwick sheep, and found that during the period of seasonal thinning there was a greater proportion of inner root sheath compared to fibre. Butler and Wilkinson (1979) used the term 'follicle production ratio' to describe the area of the fibre as a proportion of the total area of fibre and inner root sheath, and found that sheep which were more efficient at converting feed into wool generally exhibited a higher value for this ratio. Hynd (1989b) found that on a per follicle basis, the follicle production ratio accounts for very little of the variance in fibre production per follicle, and suggested that it may relate to other components in terms of output per unit area of skin. A mathematical analysis utilising data from various sources has been set out in Table 1, and lends some support to this hypothesis. These calculations seem to concur with the proportion of cells entering the fibre cited previously (Black, 1987), in that the Lincoln is apparently more efficient.

TABLE 1 The area of inner root sheath (IRS area) per follicle and per unit area of skin, calculated from fibre area, fibre density and production ratio for Lincoln, Corriedale and Merino sheep.

	Lincoln	Corriedale	Merino
Average fibre area (μm^2)*	1122	406	129
Average production ratio (%)	54.5[a]	44[b]	46[c]
IRS area / follicle (μm^2)	936.3	516.7	151.4
Fibre density (No./mm^2)*	10.5	23.4	86.7
IRS area/unit skin area($\mu m^2/mm^2$)	9831.6	12091.4	13129.4

* Daly and Carter (1955)
[a] (Scobie and Woods, unpublished)
[b] Butler and Wilkinson (1979)
[c] Hynd (1989b)

An empirical examination in Table 2 and the following discussion lends further support to the hypothesis. Daly and Carter (1955) housed and individually fed sheep of four different breeds, and measured the production of wax, suint and clean wool and their data have been used to estimate yield in Table 2. Cellular debris in wool grease has been demonstrated, and protein content of wool washings found to be inversely related to yield (Orwin and Woods, 1985). This suggests that a lower yield of clean wool is associated with a greater number of cells from the inner root sheath and epidermis. In terms of 'waste products' of the skin, we could therefore rank the breeds; Lincoln, Corriedale, Polwarth and Merino in ascending order. The corresponding values for average fibre volume and total fibre density (Daly and Carter, 1955) have been used to calculate total volume of fibre per unit area of skin, on which basis the animals rank the same but in descending order (Table 2).

TABLE 2 Yield (%) calculated from wax, suint and wool production (g/28 days), and total fibre volume per unit area of skin ($x10^{-3}$ mm^3 .mm^{-2} .28 $days^{-1}$) calculated from individual fibre volume ($x10^{-3}$ mm^3 .28 $days^{-1}$) and density (fibres/mm^2).

	Lincoln	Corriedale	Polwarth	Merino
Wax (g/28 days)*	22	24	26	40
Suint (g/28 days)*	23	16	14	6
Wax + Suint + Wool (g/28days)*	267	158	141	129
Yield (%)	83	75	72	64
Individual fibre volume ($x10^{-3}$ .mm^3/28 days)*	15.27	4.31	2.81	0.93
Total density (fibres/mm^2)*	10.5	23.4	31.0	86.7
Total fibre vol. / skin area ($x10^{-3}$ mm^3 .mm^{-2} .28 $days^{-1}$)	160.34	100.85	87.11	80.63

* Daly and Carter (1955)

It is important to note that wool fibres ceased growing, and only inner root sheath was produced by the follicles of rapidly growing lambs fed spray dried cows milk (Chapman and Black, 1981). It seems therefore that inner root sheath can exist without the fibre, and we speculate that this cell type could be the cell type of highest priority for a follicle to form.

The proportion of cells which enter the inner root sheath is largely unresolved, and may be related to individual follicle volume in a linear manner as fibre production is, but not per unit area of skin. An accurate method of measuring the rate of migration of inner root sheath is therefore required to verify the relative numbers of cells entering the fibre, and inner root sheath.

Fibre Cells.

The phenomenon of bilateral segmentation of the cortex of wool fibres has attracted a great deal of research (reviewed by Chapman and Ward, 1979). Increased definition of bilateral segmentation of the wool fibre has been associated with increased crimp frequency and decreased fibre diameter, both between and within breeds. Yet the exact opposite relationship has been found within single wool fibres, where the regions of highest crimp frequency were associated with a lower proportion of paracortex (Campbell *et al.*, 1972; 1975). These workers concluded that both bilateral segmentation and crimp are a consequence of follicle shape and fibre length growth rate rather than concurring with the commonly held belief that they are associated in a cause and effect relationship.

Unfortunately examination of bilateral segmentation has been plagued by unreliability of the technique used to stain fibres (Kaplin and Whiteley, 1978). This is caused by subtle changes in the composition of the cells with the formation of an intermediate cell-type, the mesocortex (Bonés and Sikorski, 1967). A more satisfactory method of determining cortical cell type is correlative transmission electron microscopy and light microscopy. In fact, using transmission electron microscopy to study Romney wool fibres, Orwin *et al.*, (1984) showed up to five different types of cells namely para-, para-like-meso-, meso-, ortho-like-meso-, and orthocortex.

There are few references which provide information on cortical segmentation in medullated wool fibres, and some are conflicting. Ahmad and Lang (1956) observed an annular arrangement of the paracortex surrounding the orthocortex, which encompassed the medulla. Preistley (1967) presented evidence for bilateral segmentation of the cortex in the presence of a medulla during winter thinning of the fibre. Another form of cortical cell, the metacortex, has been shown to occupy the position of the medulla in fibres with a broken medulla (Brown and Onions, 1960). In terms of pattern formation, it is important to recognise that in crimped fibres, the medulla tends to be eccentrically placed, lying closer to the inside of the curve (Auber and Ryder, 1956). The limited evidence suggests that all types of cortical cells may exist in conjunction with a medulla, however closer examination under the electron microscope is required. Observations in this laboratory suggest an absence of paracortex in medullated Romney wool fibres (J.L.Woods unpublished).

Clearly, there is a continuum of cortical cell types rather than the two discrete forms as proposed initially. In order of increasing sulphur content these are medulla, metacortex, orthocortex, mesocortex and paracortex (Rogers, 1959; Campbell *et al.*, 1975; Black, 1987; Dowling *et al.*, 1990).

EXISTING MODELS.

The velocity field.

The concept of the velocity field in wool follicles was introduced by Gandar *et al.*, (1989) and deals specifically with the production of fibre volume, without touching on differentiation of cell types. The velocity field utilises the rate of change in the density of cell nuclei as they pass from the bulb to the skin surface, to produce a relationship for length and mass changes. Although this is a useful model, if the relationship between bulb volume and fibre volume is indeed constant as the present evidence suggests, then the final density of cell nuclei in the fibre is likely to be relatively constant. Furthermore, the density of nuclei cannot be determined in the medulla, and therefore the velocity field model can only be tested in non-medullated fibres.

The R/D theory

The mechanism by which the diffusion, reaction and resultant gradients of morphogens can specify the formation of para-, ortho-, mesocortical and medullary cell types has been described (Nagorcka and Mooney, 1982). Known as the reaction-diffusion theory, it appears to be able to explain the appearance of fibres observed by Priestley (1967), which were bilaterally segmented and also medullated.

The follicle competition theory.

The concept of competition between mature follicles on the other hand says that competition for a limited amount of fibre substrate can lead to the formation of a medulla (Fraser, 1951; Fraser and Short, 1952; 1960; Ryder and Stephenson, 1968). In the N-type Romney, fleece volume appears to have increased dramatically with either no change or only a small increase in fleece weight (Fraser, 1952; Wickham, 1990), evidence which has commonly been used to support this theory. This is outlined further in the following section.

AN ALTERNATIVE MODEL.

The modified competition theory.

Consider that a given volume of skin has a certain maximum potential for the production of keratins at one point in time. As the demand for keratin increases with an increase in the total number of fibre cells produced at that time, a simple law of diminishing returns (from Michaelis Mentin kinetics) would suggest that cells with higher sulphur content would become less prevalent until there was insufficient keratin to form any type of cortical cell, and a medulla would form.

Although medullated fibres tend to be the coarser fibres of a given fleece, there are often fibres with similar and greater diameter that show no medullation. In fact medullation can occur in a single fibre at one point and not at another, without a concurrent change in diameter of the fibre (Ryder and Stephenson, 1968). Similarly, the proportions of ortho- and para- cortices can change along very short lengths of fibres (Orwin *et al.*, 1984). Such variable characteristics of fibres with similar dimensions may be explained by the competition theory. Neighbouring follicles producing fibres similar in diameter and shape, may share keratin substrate and hence exhibit changes in cell proprotions along the length of the fibre.

Experimental evidence presented by Orwin *et al.*, (1984) can be used to modify the competition theory so that it can encompass the formation of the different cortical cell types as well as the medulla. Equations of the form y = alnx + b (& y = ax + b) were shown to satisfactorily describe the increase in the proportion of orthocortex with an increase in fibre diameter. For a given fibre diameter, seasonal shifts in the proportion of orthocortex were also noted, with an increase in the proportion of paracortex from July to December. Previously unpublished data revealed a simultaneous shift of the fibre diameter distribution between seasons, which lead to changes in the relative number of fibres of a given diameter. These data have been used to estimate the values presented in Table 3 by the following method. Both fibre diameter and medulla diameter at the point of measurement were recorded, which enables calculation of their cross sectional area (assuming a circular cross section). The area of para- plus mesocortex that would have been associated with each fibre from the diameter distribution was estimated using the equations provided by Orwin *et al.*, (1984) and assuming a constant thickness of 0.5μm for the cuticle.

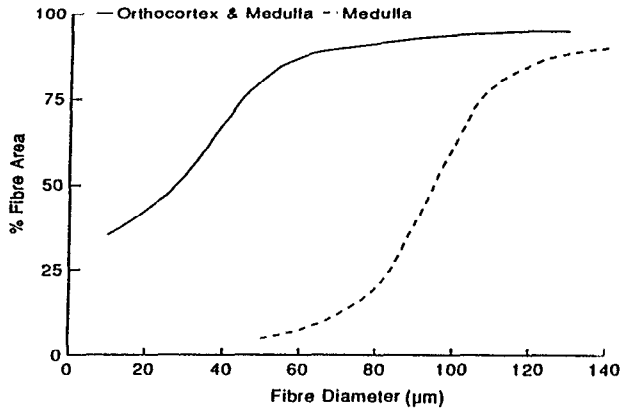
TABLE 3 Total area ($x10^3\mu m^2$) of 500 fibres and the estimated area occupied by paracortex ($x10^3\mu m^2$) and medulla ($x10^3\mu m^2$). The percentage of total area occupied by paracortex and medulla are displayed in parentheses.

Sheep	Month	Total area $x10^3\mu m^2$	Paracortex area $x10^3\mu m^2$	(%)	Medulla area $x10^3\mu m^2$	(%)
R111	July	430	130	(30.2)	0.6	(0.1)
	Dec.	785	280	(35.7)	5.8	(0.7)
R148	July	195	39	(20.2)	0	(0.0)
	Dec.	623	112	(18.0)	6.7	(1.1)
R327	July	473	48	(10.2)	2.0	(0.4)
	Dec.	880	151	(17.1)	21.8	(2.5)
R381	July	268	26	(9.8)	0	(0.0)
	Dec.	736	28	(3.9)	1.1	(0.1)

The area of paracortical and medullary cells varied considerably between sheep and between seasons. In some instances the proportions changed in similar directions, yet opposing directions in others. This reflects shifts in both the average fibre diameter and in the shape of the fibre diameter distribution. Most notably, fibres of a diameter that carried no medulla in winter began to contain one in summer, which suggests competition between fibres.

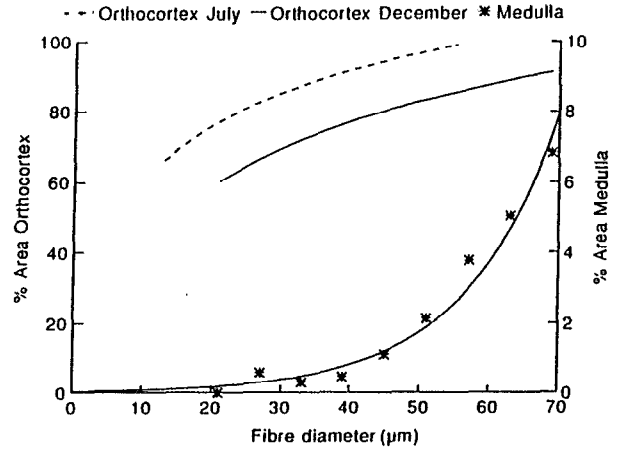
Ross (1990) showed that across the broad range of fibre diameters produced by the N-type Romney, the percent area occupied by the medulla could be represented by a sigmoid curve. Given that the N-type is essentially a Romney, this picture may be expanded upon. Of the four sheep in Table 3, R111 was found to exhibit a linear relation between diameter and percent orthocortex, while the other animals exhibited a log-linear relationship. These relationships may represent a small portion of a sigmoid curve similar to that for percent medulla in the N-type. Portrayed in Figure 1 is a hypothetical relationship between fibre diameter and percent cross sectional area of medulla, and medulla plus orthocortex for the Romney. The area of the cuticle and paracortex represent the remainder, paracortex disappearing with increasing diameter. The curve commences at about 8 to 10μm, below which no fibres were observed from any animal and perhaps represents the diameter at which only inner root sheath would be formed by the follicle.

FIGURE 1 Hypothetical relationship between fibre diameter and percent area occupied by the medulla and by the medulla and orthocortex.



The percentage of total area occupied by medulla has been plotted against fibre diameter for one animal in Figure 2 (R327 December sample, r^2=0.992). Included in Figure 2 are the July and December relationships between fibre diameter and the percentage of total area occupied by orthocortex. The curves for percent orthocortex were generated from the equations provided by Orwin *et al.*, (1984) for the range of fibre diameters observed in the relevant sample. Limited by the expression of fibre diameter, this animal could satisfactorily represent a small portion of the hypothetical relationship in Figure 1. The December samples for R148 and R111 exhibited similar and significant relationships between fibre diameter and medulla area (r^2=0.991 and 0.996 respectively). All samples exhibited a similar relationship when medullation was present, although as the number of medullated fibres declined to less than 5% of all fibres, the relationships were not significant.

FIGURE 2 Relationship between fibre diameter and the percentage area of fibre occupied by medulla for R327 Dec. sample. (Including the relationship between fibre diameter and orthocortex from Orwin *et al.*, (1984)).



Fibre Length: The missing link.

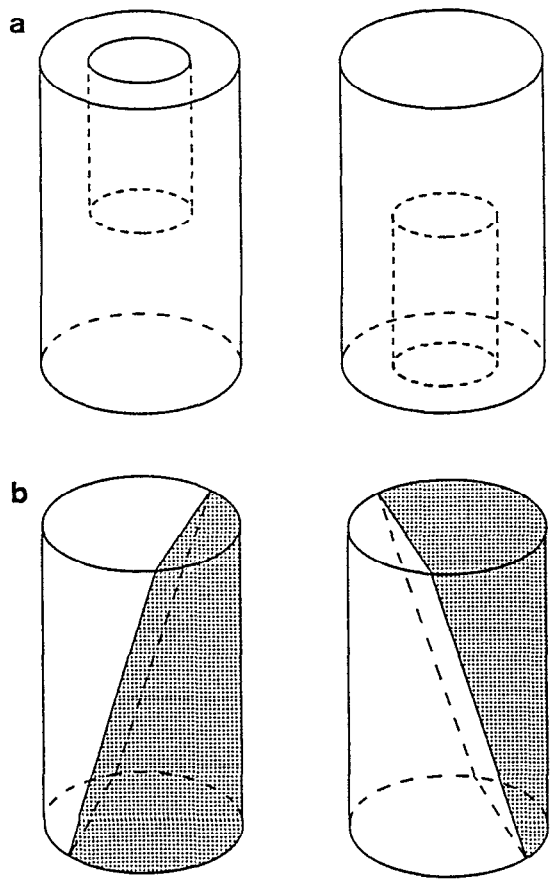
Various ratios involving the length and diameter of the fibre (L/D and L/D^2 ratios) have long been touted as a constant for an individual animal. However, Woods and Orwin (1988) showed that for single fibres taken from Romneys, the L:D ratio fluctuated seasonally with an amplitude of about 10%. This suggests that length and diameter are often closely related but may vary independently.

Although it has been suggested that a sequence of cross sections provides a chronological record of cellular activity (Gandar, 1991), the rate at which cross-sections are formed must vary with the rate of change in length of the fibre. For example, changes in length growth rate make the interpretation of the data for cross-sectional area presented in Table 3 even more complicated. If the finer fibres, which carry a greater proportion of paracortex in cross sectional area, also tend to be shorter, the proportional volume of paracortex would be reduced. Rather than limiting observations to just two dimensions, we propose that changes in volume should be used in future, in the manner briefly outlined below.

The three dimensional approach.

Aspects of the modified competition theory, incorporating fibre length have been portrayed diagrammatically in Figures 3a and b. In Figure 3a, the volume of medulla and the total volume of wool remain constant during the period of growth, however the medulla is carried in one fibre in the first half of the period and the other in the second. A classical bilaterally symmetrical pattern of two cortical cell types has been demonstrated in Figure 3b. Although there is a shift in the proportions of cortex between the two fibres, overall there is no change in the amount of either cortex present. Of course a much more complex picture than just two fibres would be observed in the skin of the sheep, where a range of diameters are produced in space and time.

FIGURE 3 (a) Schematic representation of medullae formed by competition between neighbouring fibres of identical dimensions, in which the total volume of fibre and medulla within the fibre would remain constant. (b) Schematic representation of shifts in the amount of paracortex through competition; the amount in each fibre changes but total volume and the total volume of paracortex remains constant.



Woods and Orwin (1988) found a large range of fibre volumes were expressed throughout the year by individual animals. Accompanying this, there was a seasonal change in the amount of medullation. The minimum fibre volume was expressed in winter samples collected from all animals, when there was no medulla (Woods and Orwin, unpublished), and medullation and fibre volume peaked during the summer months. It was apparent that fibre volume may reach some threshold, where once a certain volume of fibre was produced, medullation became apparent, but disappeared completely when fibre production was below this level.

The two compartment model.

The evidence presented in the preceding sections has led the authors to propose the following hypothesis: The volume of wool produced per unit area of skin is a function of bulb volume per unit area of skin, (as intially proposed by Williams (1987)) but the weight of that wool is determined by the capacity of the individual animal for forming keratin at that time. This leads us to a model with two compartments: one which generates volume and the other which determines the differentiation of cell types through competition.

The formation of cortical cell patterns is considered by Campbell *et al.*, (1972; 1975) to be governed primarily by the shape of the follicle and the length growth rate of the fibre. This should perhaps be modified to include the volume growth rate, since the proportions of various cell types from inner root sheath through to medulla appear to be dependent on the rate at which a certain volume of cells passes through the keratinisation zone, and the keratin-forming potential of the skin at that time.

To provide the framework for a forward model, we could say that in mathematical terms the volume of fibre produced at a certain time is a function of bulb volume at that time:

$$FV = a_1BV + a_2IRSV \quad (1)$$

Where FV = fibre volume, BV = bulb volume, IRSV = inner root sheath volume and a_1 and a_2 are constants.

For keratinisation on the other hand, a law of diminishing returns is likely to be operating in the skin. The volume of keratin is dependent upon the maximum potential of the skin to form keratin and the volume of wool being produced at that time, which can be expressed as:

$$PKV = (K_{max} - k) - [(K_{max} - k)^{(b/FV)}] + k$$

or

$$PKV = K_{max} - [(K_{max} - k)^{(b/FV)}] \quad (2)$$

Where PKV = potential keratin volume, Kmax = maximum keratin forming capability, FV = fibre volume, b = a constant, k = the volume of keratin which could be formed, at the point at which fibres cease to form (Chapman and Black, 1981) (which is also the point where b = FV).

When FV > PKV a medulla will form, and when PKV > FV paracortical cells will become evident.

CONCLUSIONS AND IMPLICATIONS

It seems that research into the histology of wool production has become hung up on the use of ratios (L/D, O/P, S/P and production ratio). However, none of these measures have dimension. In future we should strive to measure the volume of wool, skin and follicle tissue and the volume of the various cell types of the fibre and inner root sheath. To accomplish this, new

measures of follicle productivity must be developed, some of which have been outlined in this review. For example a method of determining the rate of migration of the inner root sheath is required to replace production ratio.

It would seem that the volume of the proliferative region of the follicle bulb and cell division rate are intimately related. Therefore, a major determinant of fibre volume per follicle seems to be germinative tissue volume per follicle. As a direct consequence, the major determinant of fibre volume per unit area of skin would appear to be the total volume of germinative tissue per unit area of skin. Follicle density determines the number of fibres per unit area and therefore how a given total volume of fibre is partitioned.

Clearly, the production of keratin is a rate limited process, and the production of cells by division can exceed the capacity for keratinsation and result in the production of medulla. Alternatively, the rate of protein synthesis may exceed the rate of cell division with a resultant oversupply of keratin substrate and the formation of paracortical cells. The proportions of inner root sheath, cuticle, cortical and medullary cell types are dependent on the rate of production of cells and on the keratin forming potential of the skin at that time.

The production of the continuum of fibre cell types and the volume of fibre produced are apparently separable. The two compartment model we have provided is the simplest model based on experimental observations. It is perceived that more of the determinants of fibre volume provided by Black and Reis (1979) may be incorporated into the equation for the first compartment. Similarly the second compartment may require some expression to quantify competition between neighbouring follicles of varying sizes as the model develops further.

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