Questions regarding developmental control of fibre diameter and fibre length growth rate in sheep

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Contents

1   Introduction

This is not a research paper or a review. What we are trying to do is set down some ideas relevant to control of fibre diameter and fibre length growth rate in sheep.

The focus is on fibre diameter. We know that the number of papilla cells in a follicle bulb partly determines the diameter of the fibre grown. We want to underatand what else is involved so that we can understand how variation in fibre diameter between and along fibres arises.

Fibre length growth rate is included, because it is felt that understanding the relationship between diameter and length will help to unravel the diameter control issue.

2   The papilla cell model

The fleece of a Merino sheep consists of something of the order of 100 million wool follicles each growing a fibre of approximate circular cross section whose diameter may be anything from 10 to 50 microns, and may vary along the length of the fibre. The length growth rate of individual fibres may be between 100 and 1000 microns per day.

The determination of follicle number is understood. The work of Moore and Jackson(1984) [10], Moore, Jackson and Lax(1989) [11], and Moore, Jackson, Isaacs, and Brown (1998) [12] suggests that a population of cells known as pre-papilla cells is responsible for follicle initiation at sites at which these cells aggregate. These pre-papilla cells end up in the papilla cavity of the follicle bulb, and the number of papilla cells in a bulb tend to relate to the size of the follicle and the diameter of the fibre it grows.

We can calculate the consequences for follicle number from assuming various combinations of parameters of the papilla cell population and its dynamics and differentiation. There is a writeup and software for this calculation (Jackson and Moore (2018) [9]). There is also a writeup (Swan(1999) [19]) which tackles the algebra of pre-papilla cell population numbers. If we assume a relation between papila cell number and fibre diameter, we can even calculate mean fibre diameters.

We do have an empirical relationship between average no of papilla cells per follicle and mean fibre diameter. It is in Figure 4 of Jackson and Moore (2018) [9]. The correlation in Figure 4 is 0.81 - so only 67 percent of the variance in papilla cell number is explained by fibre diameter. There is room for some other effects to operate. Figure 4 is a mix of sheep from four selection lines. There is no evidence that any selection line deviates from the linear regression line.

However there is more to fibre diameter variation than the number of papilla cells can explain. Mean fibre diameter is a character with an enormous amount of phenotypic plasticity - it varies with seasonal conditions resulting in variation in diameter along the fibre. Papilla cells may be involved in controlling this

variation. In species which undergo a regular hair growth cycle, papilla cells direct the growth and decline of follicles as they go thru the various stages of the hair growth cycle, and fibre diameter varies with these stages. The physiological and hormonal signalling which affects follicles and fibre growth seems to operate via the papilla cells. In species like sheep in which follicles are almost permanently in Anagen phase, this effect is suppressed, but may not be entirely absent. One of the major modifications made to sheep in domestication is the shift from seasonal shedding to continuous fibre growth. There is also variation in fibre diameter (and in papilla cell number) between follicles on the one sheep. This variance of fibre diameter between fibres is unexplained by the papilla cell model, and it is not known to what extent it depends on the number of papilla cells which aggregate in the bulb of each follicle, or to what extent it depends on other factors such as variation in the density or sizes of follicles. It is known that the type of follicle has an effect on fibre diameter in some sheep - primary follicles sometimes grow fibres of a larger diameter than those grown by secondary follicles.

3 Competition between follicles

The classic paper on this is Fraser and Short(1951) [3]. In Fraser and Short(1952) [4] evidence is presented in the form of

> "..a negative correlation occurred between the size of a fibre and the number, size, and distance of fibres adjacent to it. "

It is suggested that there is a maximum distance over which this negative correlatin occurs. There is also an extensive discussion in Fraser and Short(1960) [6].

We focus here on the possibility of competition between adult follicles for some resource which is required to grow fibre. The issue of competition during follicle initiation and development is left aside.

3.1 The maths of competition and sharing

There are two possibilities. Organs can actively compete for a resource, of they can passiively share in it. Most organs seem to operate by passive sharing. In mammals, the circulation system is massively good at sharing nutritional resources around. The notable exceptions are the foetus, and cancer cells. These actively corner more than their share of everything. So, the big question, are follicles like most organs, or are they like cancer cells? We think the answer is obvious, the skin is like most other organs, it shares, both between the skin and other tissues, and between organelles within the skin.

To understand the subtle difference look at the maths. Sharing is the easiest. We all learnt about sharing in primary school - it is called division. If there are 12 lollies and 4 kids we all learnt to do $12/4 = 3$, and work out that they each get 3 lollies. Division is equal sharing.

Now, what if the sharing is not equal? There has to be some reason for a recipient receiving an unequal share. It may be that the recipient is more actively competitive, or it may be that some external agent is supervising the sharing and imposes a rule. In either case the maths behind it is something we all learnt a little later in primary school - fractions or ratios. A fraction or proportion specifies a share. A ratio specifies a rule for sharing - one for me, two for you, etc. Fractions and ratios dont identify the reasons behind the unequal sharing, the just say it exists.

Conclusion. We can not distinguish between competition and unequal sharing for other reasons. Not by looking at the maths anyway - we might get somewhere by knowing about the biology. We can probably compute each follicle's share of resources, simply by calculating each follicle's fibre output as a fraction of the whole fibre output of the sheep. It would be a rather small fraction, of the order of 10^{-8}.

3.2   Follicle function

This is a huge topic. There are good reviews in .... What we are looking for here are things that might affect sharing. There are at least three levels

between follicles within a sheep some follicles might differ in a way which leads them to receive a greater or lesser share of nutritional resources than their neighbours. We know this is true of primary follicles. It may also operate within follicle groups or across the whole skin.

between different parts of the fleece bearing surface we know lots about this. Diameter and length growth rate variation over the body of the sheep has been extensively studied. Some key references are Chapman and Young(19..).... The issue of how this site variation relates to follicle structure and function is not well researched.

between sheep all the follicles on a sheep might be different in some way which leads the whole skin to receive a greater or a lesser share of nutritional resources

So lets make our tentative list of things that might affect sharing

follicle attributes this is actually quite difficult. Size apart, we can not imagine anything within a follicle that might cause it to consume more resources. So lets concentrate on size - if there are more bulb cells dividing to make fibre then we have a larger organ which might use more resources if they were available. It is another matter to say that if resources were limited a larger follicle might 'rob' its neighbours. If a follicle is simply 'more hungry' for resources, then, unless something actually supplies extra resources, it remains hungry. It can not go out and forage for extra on its own.

skin attributes outside the follicle the obvious issue here is blood supply to follicles. Studies of Ryder(1955) [17] show that follicle bulbs with a larger papilla cavity have more blood vessels inside the papilla. The work of Nay(1966) [13] shows that the arrangement of blood vessels in the papillary layer of sheep skin is different in sheep with tangled and straight follicles. This is a much more likely source of modifications to sharing. If follicles develop with different blood vessel supplies, then they may have different resource consuming abilities. This may be related to the number of papilla cells or it may be an independent issue.

whole sheep attributes some sheep simply make more resources available to all their tissues, wool follicles included. This would contribute to between sheep variation, but not to other levels within a sheep.

Tenatative conclusion. There is likely to be an unequal sharing of resources between follicles. The follicle attributes that seem to be correlated with growth of larger fibres (and therefore consumption of more resources) are likely to be developed in synchrony with skin atttributes such as blood supply so that enhance supply of resources. Biology works like that. So while it might seem that certain follicle types grab a larger share of resources, the truth is they are actually given a larger share. Follicle biology seems to be an 'old school tie' system, not a 'rat race'.

3.3   Closer look at Fraser and Short(1952) [4]

If we are going to deviate from Fraser and Short(1952) [4] we need to go back over that paper, and see exactly where it is we differ. Fraser and Short(1952) [4] is an amazing piece of work. It is only three sheep, a Ryland, a Lincoln, and a medium strong Merino. The samples came from Dr Carter's collection. The measurements were as follows - choose a fibre at random, draw a circle around it of radius 147 micron and measure the distance to every follicle within that circle, and its fibre diameter. Repeat for 173 and 293 micron. Repeat for around 70 randomly chosen fibres.

The analyses consisted of regressions of the diameter of the central randomly chosen fibre on a measure of the total cross sectional area of growing fibre in the surrounding circle. The measure was intended to describe the total fibre output of the surrounding follicles. The regressions were done with and without weighting according to the distance of each follicle from the centre of the circle. We reproduce their Figure 1 in Figure 1, so we can see how good a fit the regressions were.

There is substantial variation around the regression line. This is not unexpected. Biological data are always noisy. This is the 'best' result - the Lincoln sample had the most significant regressions. We comment on this below. The weighting by distance did make some improvement. The regressions were better for the smaller diameter circle. That all makes sense.

What we now have to do is delineate our areas of concern. These are as follows

An infinite range of inverse functions of distance of separation could
be analysed, and it is intended in a later paper to detail the determination
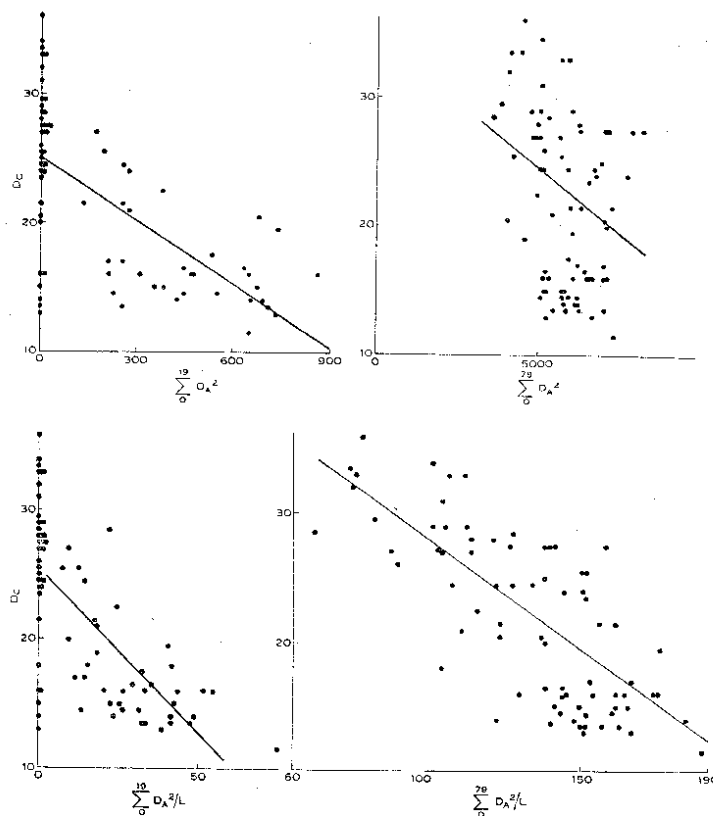of the function relating intensity of competition to distance of separation.

Fig. 1.—Scatter diagrams for the Lincoln sample of the diameters of the central
fibres plotted against the sum of the diameters squared of the adjacent fibres. This
summation is given from 0 to 79 and from 0 to 19. The two top diagrams are for
summation without correction for distance. The two bottom diagrams are for summation
after correction for distance.

Figure 1: Figure 1 from Fraser and Short(1952) [4]. These data are for the
Lincoln sheep only. The left side graphs are for the 147 micron circle, the right
graphs for the 173 micron circle. The lower graphs are weighted by distance
between follicles, the upper graphs are not weighted.

follicle positions these data came from horizontal sections of skin at sebaceous
gland level. What is sectioned at that level is the follicle shaft, not the

bulb. Bulbs deviate substantially from the position of the shaft, especially in sheep with high follicle curvature. This is why the Lincoln data have a better fit - the positional information reflects the bulb position more accurately in the Lincoln because they have straight follicles. The Ryland and Merino specimens would have some degree of follicle curvature. It is the position of the bulb which may matter in relation to competition, because the bulb is the active tissue involved in growing fibre.

length growth rate as a measure of fibre growth activity of the surrounding circle of skin, Fraser and Short used the sum of the squares of the diameters of all the follicles in the circle. This accounts for number of follicles, and fibre cross sectional area, but not fibre length growth rate. We do not know if diameter and length are correlated in this scenario. So one part of their measure of follicle output of fibre is missing.

confounding fibre growth and development we are going to take a punt and assert that most of the regression significance comes from follicle number, rather than from diameter. Follicle number is purely a development factor. It does not change as the follicles grow fibre in the adult. So the contribution of follicle number to the regression is not at all an indicator of competition between fibres while they are growing fibre. It may indicate competition during development, but more recent work (Moore etal (1998) [12]) indicates that it reflects variation in numbers of sites occupied by papilla cells, or, in the case of Merion sheep, follicles formed by branching from other follicles.

Diameter, on the other hand, could reflect either factors operating during development (such as the number of papilla cells that aggregate at sites) or factors that operate during fibre growth (such as the expansion and shrinkage of follicles that occurs over the hair growth cycle, or with nutritional and photoperiodic variations). So diameter mixes up developmental factors with adult growth factors. We suggest that the diameter effect on the regressions is likely to have been minimal - ie it is all about follicle number, which means it is all about development, not current growth.

Is there any way we can address these issues. Yes. The paper says

"The data from which the analysis detailed below was made are very bulky and have been lodged, with the accompanying statistical condensations and copes of the original drawings, with CSIRO Head Office Library, Melbourne, where they can be consulted. "

Maybe we should request access to these data, and see if we can redo the analyses separately for follicle number and fibre diameter. That would at least address the third point above.

3.4 Follicle groups

One of the messages from the classic papers of H.B. Carter (Carter(1943) [1] and Carter and Hardy (1947) [2]) is that the *trio group* of three primary follicles and numbers of associated secondary follicles is the *biological unit* of sheep skin. What happens inside one trio group is repeated all over the woolgrowing surface, with some variations according to body sites. Whan you switch to a different sheep, you may get a slightly differnet trio group, but it is again repeated all over the body.

So it has to be said that a large part of variation in fibre diameter between fibres within a fleece is due to variations in follicle and skin structure within the trio group. So studying trio groups is an important approach to trying to understand what controls fibre diameter variation.

Unfortunately data on trio groups, particularly with fibre diameters measured, is rather limited.

3.5 Where to ?

The mere idea of unequal sharing of some resource among follicles does not help much sort out why the shares are unequal. That is what we need to know - who or what is dealing out the resource unequally, and on what basis.

One thing is certain. We need to get quantitative. That is what the next section is about. We try to get some real data on length and diameter, and to write some equations.

4 Fibre length growth rate and fibre diameter

This is about quantifying individual fibre length growth rates and fibre diameters and trying to write some equations defining how length growth rate and diameter are related to each other and to other things. So we are putting explanations on hold and trying to establish some facts.

4.1 Understanding how one follicle functions

We need to tackle this before looking at variations between follicles. For the present purpose, one fibre grown over a nominal short time interval can be described as a cylinder of keratin with a length (L) and diameter(D). We are neglecting internal structure and shape (curvature and cross section) and are not allowing diameter to vary along the length of the cylinder.

The amount of keratin material in the cylinder can be described by its volume (V), which is related to length and diameter by an identity $V = \frac{\pi}{4}D^2L$. So we have 3 variables, V, D, and L. What the identity relationship says is that only 2 of the three could be under independent biological control. The third is automatically fixed by the other two.

So we already have a problem. Which 2 of the 3 are under biological control? There are three possibilites summarized in Figure 2.
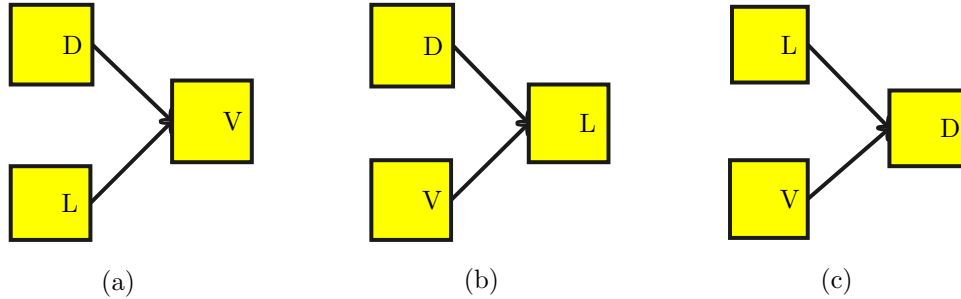
Figure 2: Path diagrams showing three possible causal relationships between fibre volume (V), fibre diameter (D) and fibre length (L).

We think the correct causal model is Figure 2(b). This corresponds to transforming the volume equation to

$$L = \frac{V}{\frac{\pi}{4}d^2}$$

So we are saying that D and V are what is biologically determined, and L is simply a consequence of setting D and V.

4.1.1 Glass beads in a cylinder model

How do we justify saying that L is not determined? Lets start with an analogy. Take a beaker of glass beads and pour them into a measuring cylinder. The beads form a stack of diameter equal to the diameter of the mesuring cylinder, and the height of the stack corresponds to L. Put a larger beaker of beads into the cylinder and the diameter stays the same, but L increases. Use a smaller cylinder with the same volume of beads and diameter of the stack will be less, but L will be greater.

So, to what extent is the growth of a wool fibre like making a cylindrical stack of glass beads? We suggest it is exactly like it mathematically, but not , of course, physically. To justify that we need to identify the biological factors which correspond to the volume of beads and the setting of the diameter of the cylinder. Here is our best guess

V volume is an easy guess. Each glass bead corresponds to a cortical cell. So V is the total volume of cortical cells (per unit time). That in turn depends on the number of cells (per unit time) and the average cell volume. That in turn depends on the number of basal cells in the bulb (the cells which divide to form the cortical cells) and their mitotic rate, and certain cortical cell differentiation processes which determine their average volume. V is also at least proportional to the amount of resources used to grow the fibre. We come to that later.

D diameter is more difficult. Some of the basal bulb cells divide to form cortical cells which migrate up to form fibre. Some of the basal cells divide to form cells which migrate up to form the inner root sheath, which is not part of the fibre, and is eventually resorbed. It would seem that follicles which produce larger fibres have larger bulbs, larger stems, larger papilla cavities, and more papilla cells in the papilla cavity. It is also known that larger papilla cavities have more blood vessels inside the cavity. We might guess that the papilla cells influence the size of the array of basal cells which become fibre, (they probably influence more than that - the whole follicle seems to get bigger). The only thing we know is that size can vary with time (eg nutritional changes, photoperiod effects, hair growth cycle effects) in an adult follicle and that the diameter of the fibre varies with it. There are also genetic differences in average follicle size between animals. There are also developmental differences in average size between P, So, and Sd follicles. There is also variation in size within each of these follicle types.

We also need to identify any biological factors which correspond to differences in fibre length growth rate, beacause if these exist our 'glas bead' model is inadequate. Here is our best efffort to understand length growth rate ofa fibre.

L length growth rate of a fibre is affected by one factor apart from V and D. As the bulb cells migrate upwards from the bulb into the follicle shaft they continue to differentiate. Some become inner root sheath cells. Some become fibre cortex, and as this occurs the cells lengthen and grow microfibrils of protein which eventually grow out of the cell ends and join up to form a fibril matrix which is the fibre cortex. Because the differentiating cortical cells elongate they contribute to fibre length growth rate.

So, we have identified two biological factors which invalidate the 'glass beads in a cylinder' model.

inner root sheath bulb cells are partitined into inner root sheath and fibre. Estimates of the proportion which become fibre (....) are around 50 percent. So not all of the bulb cells contribute to fibre diameter, or to fibre volume.

cortical cell differentiation those cells which do become cortical cells continue to differentiate, and this involves increase in length. So L is under some biological control because the amount of cell lengthening could be varied independently of D or V.

We need to make another attempt to find an adequate abstraction.

4.1.2   Modified glass beads in a cylinder model

Lets stick with our beaker of glass beads, and measuring cylinder, but let us now have some very special beads which behave as follows

- after the beads enter the cylinder, a proportion (γ) stick to the wall of the cylinder and are not further involved in forming the fibre, except that they reduce the diameter of the fibre below that of the cylinder, and they reduce the volume of bulb cells which become fibre.

- those beads which become part of the fibre expand lengthwise by an amount (λ), but do not change in width. This lengthwise expansion contributes to fibre length growth rate.

Under these modifications, our original $V = \frac{\pi}{4}D^2 L$ identity no longer applies. We will rewrite it

$$V_0 = \frac{\pi}{4}D^2 L_0$$

where V_0 and L_0 refer to the volume and length of a *virtual* fibre which would contain all the bulb cells and have no cell length expansion.

If only a fraction γ of bulb cells enter the fibre, we have $V_f = \gamma V_0$, and the diameter will be reduced to $D_f =$. So we have another *virtual* fibre which contain a fraction γ of the bulb cells, but with no cell expansion. For this *virtual* fibre we have $V_f = \frac{\pi}{4}D_f^2 L_0$. The subscript f refers to this *virtual* fibre.

If we now expand the length of the cortical cells by λ, we have $L_d = \lambda L_0$, and diameter will stay the same at $D_{fd} = D_f$, so for the real fibre we have

$$V_{fd} = \frac{\pi}{4}D_{fd}^2 L_d$$

The subscript d refers to this *differentiated* fibre, that is to the actual fibre. So this is just the equation for the volume of the real fibre, as a cylinder. We can substitute for L_d and D_{fd} and get

$$V_{fd} = \frac{\pi}{4}\gamma D_0^2 \lambda L_0$$

This ties together 5 parameters ($V_{fd}, D_0^2, \gamma, L_0, and\lambda$) , but it is not quite the form we want. (V_{fd} is a result, L_0 is an intermediate, and only $D_0^2, \gamma, and\lambda$ are biological variables. We need to get the right hand side of the equations purely in terms of biological variables, and we need equations for 3 results, V_{fd}, D_{fd}, and L_d. Getting that is a fairly simple transformation which leads to

$$
\begin{align}
V_{fd} &= \gamma\lambda V_0 \tag{1} \\
D_{fd}^2 &= \gamma D_0^2 \tag{2} \\
L_d &= \lambda\left[\frac{V_0}{\frac{\pi}{4}D_0^2}\right] \tag{3}
\end{align}
$$

Equations 1, 2, and 3 are our equations of fibre growth, given the modified glass beads in a cylinder model. They predict the volume growth rate, diameter, and length growth rate of a fibre given the biological parameters D_0, γ, λ, and V_0. We summarize these 4 biological parameters and their meaning in Table 1

We see in Table 1 that parameter V_0 is complex. It is meant to sum up all the output of the follicle bulb, that is the bulb produces a certain volume of

Table 1: Definition and interpretation of the 4 biologically determined parametrs used in equations 1, 2, and 3

Parameter	Model Description	Biological Interpretation
D_0	Diameter of the cylinder	Internal diameter of the follicle wall or outer root sheath
γ	Proportion of the glass beads which do not adhere to the wall of the cylinder	Proportion of the cortical cells which form the fibre, rather than the inner root sheath
λ	Degree to which glass beads expand lengthwise	degree to which cortical cells which enter the fibre cortex expand in length during differentiation
V_0	Volume of glass beads poured into the cylinder	Volume of cells produced by mitoses in the follicle bulb per unit time. Involves the number of basal cells in the bulb, the mitotic rate, and the average cell size before differentiation.

cells per unit time. If we delve into how the bulb does this we can break V_0 up into a number of subparameters. We are going to try and get away with just havin one parameter for bulb function.

We also see something important in equation 2. Fibre diameter depends only on two things - the diameter of the follicle wall (D_0) and the proportion of bulb cells that go into fibre (γ). In particular it does not depend on the bulb activity. We interpret (D_0) as a general follicle size parameter - large follicles are large all over - ie in diameter and length and bulb size and papilla size. There are only two ways a follicle can alter the diameter of its fibre - get bigger overall, or alter the proportion of cells going into fibre.

In contrast, length growth rate is far more complicated. It depends on bulb cell volume per unit time, it depends inversely on how much of that volume is required to form the diameter, and it depends in cortical cell length expansion during differentiation. So a follicle can alter its length growth rate output by churning out more bulb cells, by changing fibre diameter, or by changing the cortex structure formed during differentiation so that length expansion is changed.

Volume growth rate (equation 1), which is the same thing as fibre weight if there is no medullation, does not depend on (D_0). It cancels out in doing the substitutions to get equation 1. That is a little strange. What it is saying is that it doesnt matter whether you spread a certain volume of cells over a large or a small diameter cylinder, the volume stays the same. It is all about the volume of material the bulb produces in the first place (modified by γ and λ). Wool production is basically follicle bulb output. Diameter is something else.

We need to look at some data to see if our 3 equations stand up to scrutiny.

4.2 Data on length growth rate and diameter for individual fibres

4.3 Quantitative genetic data on fibre diameter

4.4 Cell model for fibre growth

5 Discussion

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