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Nutritional partitioning of growth for productive gain

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ABSTRACT

Various tissues in the sheep, because of their individual specialist roles, have very different nutrient requirements. These differences in metabolic behaviour provide a potential opportunity to manipulate biochemical pathways in specific peripheral tissues to enhance production characteristics and, consequently, commercial gain. Factors affecting such partitioning are discussed with particular reference to the sheep industry in New Zealand, which unlike most other international sheep systems, needs to produce meat and wool from the same animal. Because the relative returns from meat and wool vary from season to season there is a need to manipulate independently their relative production to achieve maximum economic return.

Keywords Growth, tissue requirements, protein regulation, wool, meat.

INTRODUCTION

New Zealand's temperate climate, and absence of very dry or very wet seasons for most of the country enables a high stocking rate (usually between 12 and 25 stock units/ha) and year round grazing. Pastures are predominantly grass, often perennial ryegrass (Grasslands Ruanui) or other cultivars of Lolium (e.g. Nui, Ellett, Manawa, Moata), in association with white clover. More recently a greater diversity of forage crops have been advocated, e.g. *Maruphalaris*, Grasslands Roa Tall Fescue, *Lotus pedunculatus*, and chicory, but the emphasis in choice of pasture species is based on agronomy. Cultivars are developed for specific climates and soils types, with resistance to disease and insects, and sometimes to suit particular grazing regimens. The same cultivars form the basis of all ruminant products, from the rapid daily conversion of pasture into milk, to slower rates of meat and wool production. However, cultivars are generally not bred with the requirements for milk, meat or wool synthesis in mind; in fact the optimal mix of nutrients for each of these products remains poorly defined and it is the difficulties associated with such definition which this paper aims to address.

There are significant differences between plant species (and cultivars) in the efficiency with which they are able to promote live weight gain in ruminants (Ulyatt, 1981). However, in the New Zealand pastoral system feed quality is often of less significance than gross nutrient supply. This is particularly so where the winter decline in feed availability coincides with high physiological demands such as foetal development and lactation. Nevertheless because of the unique dual purpose (meat/wool) sheep industry in New Zealand, interactions among individual peripheral tissues and the viscera in response to changing nutritional supply are of considerable commercial significance, and similar to the well documented demands of the foetus or mammary gland. In order to define these interactions in terms of potential manipulation for productive gain, it is necessary to understand some of the biochemical and physiological relationships within and among tissues.

In ruminants the carcass (muscle, bone and adipose tissue) and skin components together comprise 80-90% of body weight (Johnsson *et al.*, 1985) but require less than 50% of the energy at rest (Lobley, 1989). In contrast, the portal-drained viscera and liver demand half of the total energy supply (Huntington *et al.*, 1988) even though they constitute only 10% or less of body weight (Fig. 1). The output of commercial products (meat, wool, hide) by the peripheral tissues is therefore achieved after competing with the demands of the viscera. The peripheral tissues themselves have very

different requirements in the amount of energy (skin uses only about one sixth of the oxygen per unit weight than muscle; Harris *et al.*, 1989) and the preferred substrates for oxidation. Muscle energy is supplied predominantly by the TCA cycle while the skin acquires only a third of its energy from the TCA cycle depending instead on anaerobic oxidation of glucose and on the pentose phosphate pathway (Chapman and Ward, 1979). Such differences are a consequence of the drive within each tissue to provide specialist functions such as locomotion and thermoregulation. These differences in metabolic pathways also give potential to manipulate specific peripheral tissues in order to optimise individual pathways for production and, consequently, for commercial gain. This paper will discuss such potential with particular reference to the wool/meat production system.
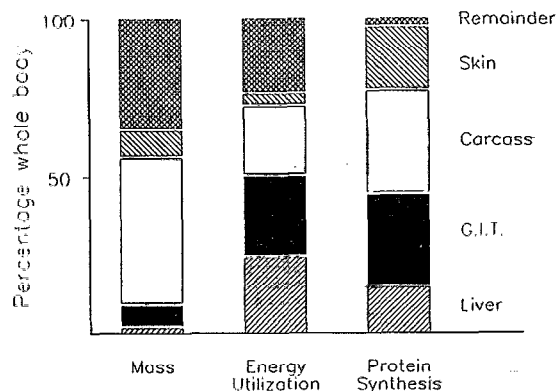

FIG 1 Contributions of the major body components to energy demands and protein synthesis in a 40 kg sheep.

OPTIMISATION OF NUTRIENT REQUIREMENTS

Nutrient requirements for maintenance and growth of the sheep, together with additional requirements for growth, pregnancy and lactation have been well documented   (e.g., nitrogen and volatile fatty acids, Waghorn and Barry, 1987; macro, micro, trace elements, Grace, 1983). The unfulfilled demand for essential nutrients above maintenance requirements   (e.g. during pregnancy or lactation) will obviously place an

animal in overall deficit, the consequences which will depend on the ability of tissues to 'compete' with each other for the limited supply. For example, the demands of lactation in conjunction with limitations on magnesium absorption/transport frequently lower blood magnesium levels leading to hypomagnesaemia. Such demand for essential nutrients is merely additive with respect to maintenance requirements and can thus be readily identified and met. A more subtle problem is the requirement of individual tissues for essential nutrients, which may differ from those of the whole body. For example, if the essential amino acid composition of each tissue in the sheep is compared with that of the amino acids available from rumen microbial protein (Storm and Ørskov, 1983) then, on a simple factorial basis, the limiting amino acid for growth of the carcass is histidine while that for skin and wool is the combined S-amino acid (cystine and methionine) supply. If one tissue has a significant protein turnover and takes out large amounts of a single amino acid then the remaining amino acid flux may be imbalanced for other tissues. This imbalance results in low efficiencies for production and high amino acid oxidation. The demands of skin products for the S-amino acids (combined with the fractional protein synthesis rate of 10-20% for skin; Attaix *et al.* 1988) probably creates the greatest potential for such imbalances for other body components in the sheep; this would be exacerbated by any increase in wool production and potentially limit responses to exogenous stimulation of wool production. For example, exogenous growth hormone (GH) administration has been shown to increase both wool and muscle gain (Johnsson *et al.* 1985), increase wool alone (Johnsson *et al.*, 1987), or even depress wool growth (Wynne, 1982, Wynne *et al.*, 1988). This apparently contradictory data could be a consequence of the S-amino acid supply in each trial. If an excess supply is made available over that required for normal growth, then there is potential capacity for improved wool production and, in addition, carcass growth imbalances are not created. A smaller excess may only facilitate the promotion of wool growth while a balanced supply of amino acids for normal growth may mean that no wool stimulation is possible although other tissues with differing amino acid limitations may be able to respond. Such an interpretation of the GH trials assumes that the skin products dominate utilization of the S-amino acid supply. This has been

predicted theoretically by Black and Reis (1979), and is supported by the interactive nutrient/GH response found in a muscle growth trial by Pell *et al.* (1989).

Interactions between tissue requirements and whole body nutrient demand are demonstrated in other situations. The amount of copper required for maintenance and growth of the grazing sheep has been established (Grace, 1983). However, supply of Cu at well above predicted requirement levels results in significantly increased bone mineralization (Grace and Lee, 1990) and because of the interdependance of muscle and bone development if bone elongation can be demonstrated, then muscle growth may also be promoted. The reverse concept is also worth consideration, viz. exogenously promoted improvements in muscle growth (use of ß adrenergic agonists for example) may be restricted by bone development unless parallel stimulation of bone growth is achieved. This somewhat unexpected finding of Grace and Lee (1990) also raises a more general speculation that existing knowledge of whole body requirements does not adequately account for sub-optimal limitations on specialised, tissue specific, catalytic roles of certain essential nutrients (notably Cu, Zn, Se). Although adequate overall growth can be maintained, the potential exists for enhancing growth of specific tissues e.g. bone, wool, meat, through directing supply of limiting nutrients to these tissues.

Undoubtably, there are many other examples of differences in individual tissue requirements affecting not only their own ability to respond to production stimuli, but also in consequence affecting the response of other tissues. In some cases this flow-on effect may be a positive response (surplus nutrients passed in a cooperative way) but in many situations all tissues may be detrimentally affected. Clearly complex relationships exist among input nutrients and their metabolites: relative proportions may be more important than absolute amounts. The most notable example is the antagonistic/synergistic interrelationships which occur among elements such as Cu, Fe and Zn.

ADAPTATION OR ACCOMMODATION?

As defined by Young (1989) 'adaptation' is the process that permits the organism to respond to change (e.g. sub-maintenance intakes) without adverse consequences while 'accommodation' is a response to dietary or other influences which favours survival but results in significant losses in some important functions (e.g. during fasting). While many of the metabolic studies comparing N or energy intake in non-ruminants have been based around fasting/maintenance/supra-maintenance comparisons, in the grazing sheep reduced levels of intake are generally only to sub-maintenance, and rarely fasting. Thus, 'adaptive' responses are more relevant to the grazing animal.

Whole body responses to changing nutrient supply have been reasonably well documented for many essential nutrients in the ruminant. For example, as energy and nitrogen intakes decrease from well above maintenance to below maintenance, there is an adaptive decrease in rates of both whole body protein synthesis and degradation (Fig. 2). Associated with this is a decreased rate of fractional oxidation of amino acids while the sheep moves from net protein gain to a small net protein loss. If intake stops completely i.e. the sheep is fasted, protein degradation and amino acid oxidation abruptly and rapidly increase to levels greater than those found above maintenance (Pell *et al.*, 1986). This suggests that over the whole body the sub-maintenance adaptive response has been to conserve the energy supply by reducing the metabolically expensive protein synthesis process. At the same time there is consideration of body protein by concomitantly reducing protein degradation, and reducing the oxidation of products from protein degradation to conserve essential amino acids (for essential protein production such as hepatic and renal functions). In contrast, the adaptation collapses in a fasting sheep, which accomodates the absence of feed by increasing tissue protein degradation to supply whole body energy needs from re-mobilised amino acids.

The ability to make adaptive responses in whole body protein metabolism is dependant on the rapid, and independantly regulated, fluxes of protein synthesis and degradation relative to the flux into protein gain or loss. Recent studies using arterio-venous catheterisation of the hind-limb suggest there are interactive and apparently cooperative changes in peripheral metabolism with changing intake. For instance, at an intake of 0.6 times maintenance (M), losses of amino acids from the peripheral tissues (hind limb) are significantly greater than those from the whole body and at an intake above maintenance (1.2 M), gains of amino acids to the

periphery are greater than the whole body (Fig. 2). During recovery from sub-maintenance intake (0.6M to 1.2M) this was achieved solely by an increase in protein synthesis, as hind limb protein degradation was unchanged i.e. all new peripheral protein synthesised was deposited giving 100% efficiency of protein gain (Fig. 2). Thus, as in the non-ruminant, the peripheral tissues cooperate by supplying essential amino acids during stress and conserve them efficiently, and then in excess as supply improves (Harris *et al.*, 1990).
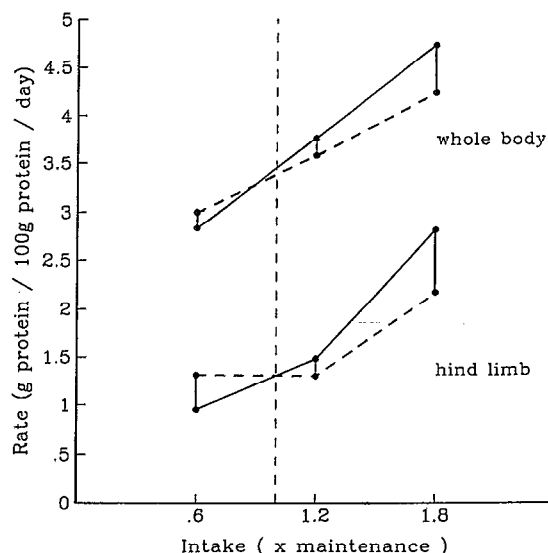

FIG 2 Fractional protein synthesis (-) and degradation (- - -) rates (4g protein synthesized/100g tissue protein/d) in the whole body and hind limb of 35 kg sheep at 3 different levels of intake (from Harris *et al.*, 1990).

The anomaly within this scenario of self-sacrificing peripheral tissues is that of wool production. Wool, like lactation, is a one way production system with nutrients being irreversibly lost to the animal. Because there is little or no protein degradation then gain must equal protein synthesis. Wool production can not therefore be viewed as a substrate cycle (Crabtree and Newsholme, 1985) open to regulation in the same way as other tissue protein production. The classical work of Marston (1948) shows the consequences of this lack of sensitive control. Sheep fed at above maintenance intakes show a strong linear relationship between wool growth and intake, with deposition of N in the

wool about 30% of total N gain (Fig. 3). At intakes below maintenance, protein synthesis in the whole body and peripheral tissues generally continue to decline but wool growth plateaus at values of 0.2 to 0.3 g N/day - and 100% of retained N is associated with wool growth. This means that the demands of wool for both ATP energy and amino acids are of equal importance to those of the viscera during sub-maintenance intakes. It is still unclear at which stage wool growth ceases completely during periods of prolonged fasting. However complete shedding is not apparent even in extremely stressed animals although shedding may occur for other reasons e.g. deficiencies in specific nutrients such as Zn.
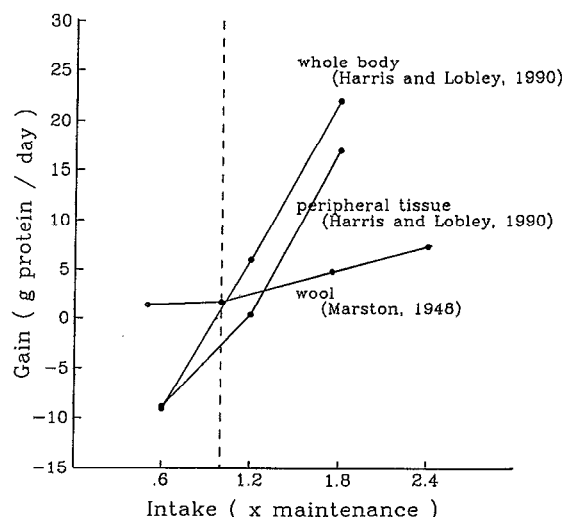

FIG 3 Variation in protein gain in the whole body, peripheral tissues or wool of sheep with varying levels of intake.

Although the continuing production of wool at sub-maintenance intakes suggests that it is a competitive (rather than cooperative) process acting against the demands of the whole body this may not be the case. At 0.6M intake the rate of whole body protein synthesis declined to 60% of that at 1.8M and the hind limb to 34% (Fig. 2), however the wool production at 0.5M intake was only 18% of that of 2M intake (Fig 3). Wool therefore has reduced the energy required for protein synthesis disproportionately compared to the conservation shown by other peripheral tissues, and also significantly reduced its demand for amino acids. It seems that for all tissues there is an obligatory level of protein

synthesis and while in most tissues this can be counter-balanced through changes in degradation, this is not possible for irreversible protein pools (such as wool), and the extreme reduction in their nutrient demand early in the adaptive process does not prevent them being a competitive drain in whole body terms. Inevitably the same must apply to other essential nutrients apart from amino acids. Certain essential trace elements such as Zn must also be incorporated into continuing wool growth, while other more labile tissues, perhaps muscle and bone, must be mobilised to meet this demand (Table 1).

TABLE 1 Differential distribution of Cu and Zn content in various tissues from sheep (Lee and Grace, unpublished data).

| | % Distribution | | Mobility |
	Cu	Zn	
Liver	64	1.8	(storage)
Bone	1	15.2	(labile?)
Skin	3	3.8	
Wool	0.5	27	(irreversible)
Muscle	13.6	45	(labile)

Bone is of interest as there is some evidence to show that nutrients are preferentially diverted to bone during periods of undernutrition. Most ruminant studies have considered the consequences of undernutrition on performance following realimentation. There is disagreement as to the effect of nutrition on changing skeletal size, and although Allden (1970) supports the view that body proportions were not affected by undernutrition, his review cites examples where some, but not all, animals appeared to change their proportions when subjected to extreme planes of undernutrition. Recently Searle *et al.* (1989) showed that sheep fed at 50% of *ad libitum* were only 44% of the body weight, but 90% of the body length and chest depth and 75% of hip and shoulder dimensions of animals fed *ad libitum* for 2 years. In the non-ruminant it has been suggested that it is the more advanced skeletal regions which are most affected by malnutrition and that available nutrients are taken up disproportionately by those bones with the greatest distance to grow in the future (e.g. radius relative to hand, tibia relative to foot). The

regulation of such proximodistal disproportion in limb bones is not understood (Burwell, 1986). Nevertheless, the indirect evidence for differential growth in bone suggests that macro and micro elements, together with amino acids essential for protein synthesis, are diverted to bone during nutritional stress while other tissues are undergoing compensatory catabolism.

Adaptive responses by individual tissues to either productive or catabolic change are therefore limited in at least two ways; firstly tissues such as wool, which are irreversible protein sinks, have limited potential for change through substrate cycles and, secondly, tissues of fundamental importance to body structure, such as bone, appear best able to compete for changing nutrient supply (or benefit from cooperative changes in other tissues). It is the regulation among such demands which thus becomes important.

REGULATION OF INTER-ORGAN COOPERATION

While the overall regulation of tissue growth is mediated by hormonal signals, different tissues can produce very different metabolic responses to the same hormones and cell receptors. This suggests that the individual tissue response is affected by other metabolites providing signals and/or acting as modulators. It is these signals which have the potential to be manipulated in order to modify production differentially within the animal for commercial gain. Substrate cycles provide a sensitive mechanism by which tissue growth can be regulated (Crabtree and Newsholme, 1985). It is becoming increasingly clear that it is the activation, by changes in the phosphorylation state of key enzymes within the substrate cycles, which facilitates their individual modulation without necessitating further *de novo* enzyme synthesis (which would be slow). The question remains as to what are the signals which modify the phosphorylation state within individual tissues.

Within the area of peripheral protein metabolism a candidate regulatory signal may be the catabolism of essential branch chain amino acids (BCAA) valine, isoleucine and leucine. Leucine itself has been implicated in the control of protein metabolism in the non-ruminant with an inhibitory effect on deprivation induced levels of hepatic protein degradation (Mortimore, 1986) and enhancing the responsiveness

of muscle protein synthesis to insulin (Garlick and Grant, 1988). However, the first irreversible step in leucine degradation is the decarboxylation of the branch chain oxo-acid (BCOA) catalysed by the branch-chain oxo-acid dehydrogenase (BCOD). This enzyme exists in both an inactive, phosphorylated, and active, dephosphorylated form and the forms are regulated by competing actions of a protein kinase and protein phosphatase. There are multiple regulators of the kinase activity (see Lobley, 1988) and some, such as glucocorticoids and leucine, have been implicated as regulators of protein synthesis. Others, such as ATP, BCOA and acetoacetate, have not. Thus, control of protein synthesis and amino acid catabolism can be performed independantly or sychronously depending on physiological conditions.

Phosphorylation pathways of enzymes may be one key component of growth regulation, but other pathways may be involved in equally fundamental areas such as the regulation of cell replication itself. In a production system such as wool growth it is probably "cell birth rate" which is the major determinant of fibre growth rather than production of keratin protein (Hynd and Everett, 1990).

Of particular significance is the fundamental role of zinc, not only in association with both the degradation and synthesis of enzymes, but in growth itself. Its association with DNA-motifs (Klug and Rhodes, 1987), the reproductive system, as a structural component of insulin, in enzymes involved in collagen hydrolysis and in metallothionein induction, all indicate a multiplicity of functional involvement in growth. It is now recognised that zinc, as well as copper, is interactive with intracellular components and is influenced by the endocrine system in a similar way as the metabolism of major nutrients (Cousins, 1985). The hormonal regulation of Cu metabolism has aspects that are markedly similar to mechanisms that influence transport of amino acids. Many facets of these pathways may well be of productive significance, especially in the changing rate of wool growth associated with changing intake.

A great deal of interest has recently focussed on transgenic animals where the use of the metallothionein promoter region linked to the coding sequence of 'foreign' inserted genes allows their expression in response to changes in dietary zinc. For example it has been used to regulate expression of the growth hormone gene in transgenic sheep (Pursel *et al.*, 1987). However the GH effect has been mainly studied with respect to muscle/fat interactions and as yet the effects of increased growth hormone on other tissues, such as wool, are unclear.

It is possible that animals may be selected for elevated levels of metallothionein and bred for increased metallothionein synthesis in response to dietary Cu or Zn levels. For instance, genetic selection techniques have been successfully employed to produce populations of sheep with altered Cu retention characteristics (Wiener *et al.*, 1985). These sheep had improved liveweight gain and wool production when subjected to naturally Cu-deficient pastures.

OPPORTUNITIES FOR MANIPULATION THROUGH THE DIET

Both the efficiency and absolute productivity of ruminants are open to manipulation by normal farm management procedures, such as herbage allowance, rotational grazing, use of improved cultivars and supplements etc. These procedures generally only address the welfare of the whole animal, and only occasionally are specific tissues targetted (e.g. flushing ewes prior to mating). However, given that individual tissues are subject to regulation it should be possible to predict an optimal nutrient flux for differential growth of tissues; i.e. meat in preference to wool (or fat), wool in preference to meat, or both optimally. The challenge then is to modify either the pasture or animal to generate the predicted flux.

Both plant and animal modification may be undertaken by either traditional (e.g. selective breeding for desirable characteristics) or novel biotechnological (sustained release technology, transgenic engineering) means. In the case of the animal manipulations they can be further supported by feed based supplementation such as the inclusion of antibiotics, ionophores, anthelmintics or, with gene modified animals, the inclusion of gene promotors or suppressors that may be activated by signals in the pasture, such as Zn in the GH/metallothionein gene modification. However, it is outside the scope of this paper to discuss in any detail the many possibilities that exist in both pasture and animal modification. Therefore, this section is limited

to possible pasture and animal manipulations which may differentially improve wool growth and outline the difficulties associated with a single target. This is an apparently simple target open to differential improvement through gross and specific nutrient supply.

Diet Manipulation

Nutrient manipulation via the diet may include changes in absolute quantities of nutrient available, but changes in the relative amounts, or quality of nutrients available to the tissues are more important. These changes can be effected in several ways including supplementation with readily fermentable carbohydrate, protecting plant proteins from degradation in the rumen, feeding cultivars containing condensed tannins, altering the proportions of legume to grass in the diet, affecting the rate with which forage passes through the rumen and selecting feeds which differ from most others in their content or proportions of limiting nutrients.

Addition of readily fermentable carbohydrate to roughage diets, at levels up to 25% of dry matter intake, can have a synergistic effect with regard to nutrient availability. Readily fermentable carbohydrate enables an increased incorporation of rumen ammonia into microbial protein. The flow of non-ammonia N to the intestine is increased as a consequence of improved microbial growth, and thus can substantially increase N retention (Obara *et al.*, 1989). There is a direct relationship between dietary intake (available protein) and wool production, however this relationship is confounded by effects of protein intake on weight gain (Allden, 1979) and although readily fermentable carbohydrate will improve N retention, it does not differentially target wool (or meat) production.

The current interests in condensed tannins (CT) is a consequence of improved N retention and leaner carcasses produced by lambs grazing forages with CT (Purchas and Keogh, 1984; Waghorn *et al.*, 1990). Condensed tannins affect nutrient availability by increasing the flow of non-ammonia N to the intestine, but the mode of action is different to that of readily fermentable carbohydrate supplementation. Condensed tannins bind with plant proteins and reduce their degradation in the rumen. Digesta flowing to the intestine contains more plant protein than when equivalent CT-free forages are given. The amount of protein reaching the small intestine is higher when forages containing low concentration of CT (under 4% of DM) are given, but high concentrations of CT bind proteins to an excessive degree and microbial growth is reduced. Fibre breakdown is diminished and intakes fall (Waghorn *et al.* 1990).

An important aspect of CT and digestion is that there appears to be a preferential protection of essential amino acids (EAA) in the rumen. Waghorn *et al.* (1987) reported a 50% increase in EAA flux including branch chain amino acids and a 14% increase in (NEAA) non-essential amino acid flux to the intestine of sheep given *Lotus corniculatus* with 2.2% CT in the DM. Recently the net absorption of S-containing amino acids was shown to increase by about 30% with CT (McNabb, pers. comm.). In other words, supplementation of the diet with CT improves the flux of leucine - a possible regulator of protein synthesis -while also improving the supply of the first-limiting amino acids for wool growth.

One of the appealing aspects of CT for protecting protein from degradation in the rumen is the range of possibilities for inclusion in the diet. All species consumed need not include CT as the inclusion of only one tannin containing plant (e.g. *Lotus* or *Rumex* (dock)) has the desired effect in mixed pasture. Modification of more common pasture species, such as ryegrass and clover, to include CT producing genes is now possible with genetic engineering.

Protection of plant protein from rumen degradation is one possible target for pasture plant gene modification: protection will provide ruminants with an improved supply of limiting amino acids in a form that is available for hydrolysis and absorption from the small intestine. About 70% of pasture protein is degraded in the rumen, with methionine being more extensively degraded than most other amino acids (Susmel *et al.* 1989). However it appears that some plants may contain a higher proportion of EAA than others. Kaldy *et al.* (1979) compared sainfoin with lucerne and report an EAA:NEAA ratio of 1.10 and 0.99 for the respective species. If the protein in sainfoin were protected from degradation in the rumen, then the gains would be two fold: increased protein flow to the intestine, and an improved protein composition. A similar concept has been taken with expression of the seed coat protein, pea albumin 1, in lucerne leaves (Higgins *et al.* 1989). Pea albumin 1 is high in S-amino acids and has been shown

'in vitro' to be resistant to rumen degradation.

It is clear that a number of methods are available by which nutrient supply may be manipulated via the feed. In general any manipulation of feed composition must be secondary to the requirement that feed plants grow vigorously and competitively in pasture, and that high levels of intake be achieved. However there is a niche for specialised feeds that could be used for specific purposes e.g. forages with aromatic oils capable of modifying meat flavour that could be fed for 2-3 weeks prior to slaughter, or feeds with a high concentration of branched chain amino acids that could be fed for a week prior to mating with a view to stimulating ovulation rate (Waghorn and Smith, 1990).

Animal Manipulation

It has been generally accepted that supplementation of the S-amino acid supply to the sheep will improve wool growth in the grazing sheep. Consequently a great deal of research has been directed towards protection of high S-amino acid protein from rumen microbial degradation through both traditional and biotechnological means, including gene transfer into appropriate plant species. Genetic engineering approaches to improve S-amino acid supply also include manipulation of ruminal flora (Brooker *et al.*, 1989), and expression of microbial genes in the epithelial tissues of the sheep (D'Andrea *et al.*, 1989). The problem of targetting wool growth can be solved with a variety of approaches. However some caution should be observed on the basic premise on which the work is founded: more S-amino acid will give more wool.

The available data on S-amino acid supplementation was reviewed by Reis (1979, 1989) and several points are noteworthy in translation to the New Zealand grazing system. Firstly, the effectiveness of abomasal, duodenal or parenteral supplements of sulphur amino acids is diet dependent, and in some cases is entirely ineffective (Reis, 1979). Secondly, surprisingly, methionine has been found to be a more potent stimulant than cysteine under the same dietary conditions, suggesting a signalling rather than simple requirement response (Reis, 1989). Such signalling mechanisms may be related to levels of the methyl donor S-adenosyl methionine which is also involved in nucleic acid and protein synthesis pathways. The third

and probably most significant feature of S-amino acid supplementation trials is that merino sheep with a high genetic potential for wool growth respond to supplementation to a greater extent to these with a low genetic potential (Williams *et al.*, 1972). In our own studies with Romney sheep selected for high fleece weight, the uptake of ^{35}S-cysteine into the skin was 28% compared with 11% in the control line. This suggests that dietary manipulation may be irrelevant if the capacity of the skin to transport S-amino acids is the main limitation to wool growth. Which means that further research is needed to define the signals affecting individual cell transport processes. Although methionine is transported by a hormonally regulated and extracellular amino acid concentration-dependant system, cysteine is transported differently. The cysteine transport system is not hormonally sensitive nor is it sensitive to extracellular amino acid concentration but it is stimulated by changes in intracellular concentration (Shotwell *et al.*, 1983). The use of animals with quite different wool production potential which is linked to significant differences in cysteine uptake gives potential for defining these signal mechanisms.

Undoubtedly there is potential for genetic engineering to manipulate skin metabolism to improve the uptake of S-amino acids and their incorporation into the follicle itself. The skin has particular appeal as tissue specific promotors are already available based around the 'hard' keratin promotor genes. However, as with all plant and animal based transgenic research, an understanding of the pathways to be modified is essential if successful enhancement of wool production is to be achieved.

CONCLUSION

The partitioning of growth between tissues is affected by nutrient availability and regulated by endocrine and biochemical mechanisms at the tissue level, so that the most promising approaches for manipulation of meat and wool production are through animal, rather than pasture, manipulation. However manipulations are dependent on an appropriate nutrient supply (pasture composition) to support any stimulated, differential, growth. Because of the differences between tissues arising from their individual specialised roles, nutrients are partitioned differently. Therefore promotion of

an individual tissue in a modified animal will require revision of current estimates of nutrient requirements for whole body maintenance and growth.

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