



Growth, development and nutritional manipulation of marbling in cattle

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Abstract. This review discusses our current understanding of the growth and development of intramuscular fat and proposes a simple growth model to explain the accumulation of intramuscular fat in cattle. Potential effects of nutritional manipulation are discussed in relation to the proposed growth curve for intramuscular fat. The scope for nutritional control during both the pasture (or backgrounding) and intensive grain finishing phase are discussed. Additional discussion on nutritional triggers of the cellular and early life events associated with the development of the intramuscular fat are discussed in the companion paper by Harper and Pethick (2001).

Development of fat and muscle in cattle during growth

A common conclusion from animal developmental studies is that intramuscular fat is late developing (Vernon 1981). Indeed the usually quoted developmental order is abdominal, then intermuscular, then subcutaneous, then finally intramuscular. However, because fat is deposited at a greater rate than lean tissues later in life the concentration of fat in muscle will inevitably increase later in an animal's life. Therefore the commercial trait, marbling, visible intramuscular fat or simply % fat is late maturing. As we will show this does not mean that the rate of fat accretion in intramuscular adipocytes is also late maturing.

To determine if there is a difference in fat deposition over time, it is informative to express the data as proportions of total carcass fat that develop within various depots, because changes in these proportions would indicate if intramuscular fat develops at a different rate from other fat depots. When fat deposition have been described in this way (Johnson *et al.* 1972), the proportional distribution of fat between carcass pools is found to be constant over a wide range of carcass fat contents (in the range from 5 to over 150 kg total fat; Fig. 1). Other data (Cianzio *et al.* 1982 & 1985, Trenkle *et al.* 1978) are also consistent with this observation. There is substantial variation in intramuscular fat content between

different muscles of the carcass at the same carcass fatness (Johnson *et al.* 1973). However, it has become customary to assess intramuscular fat content in the *m. longissimus thoracis et lumborum* (striploin). On average the intramuscular fat content of the striploin is a little lower or about the same as the average carcass muscle intramuscular fat content. Importantly there is a high correlation between fat measured in the *m. longissimus thoracis et lumborum* and other muscles over a wide range of intramuscular fat content (Johnson *et al.* 1973; Brackebush *et al.* 1991).



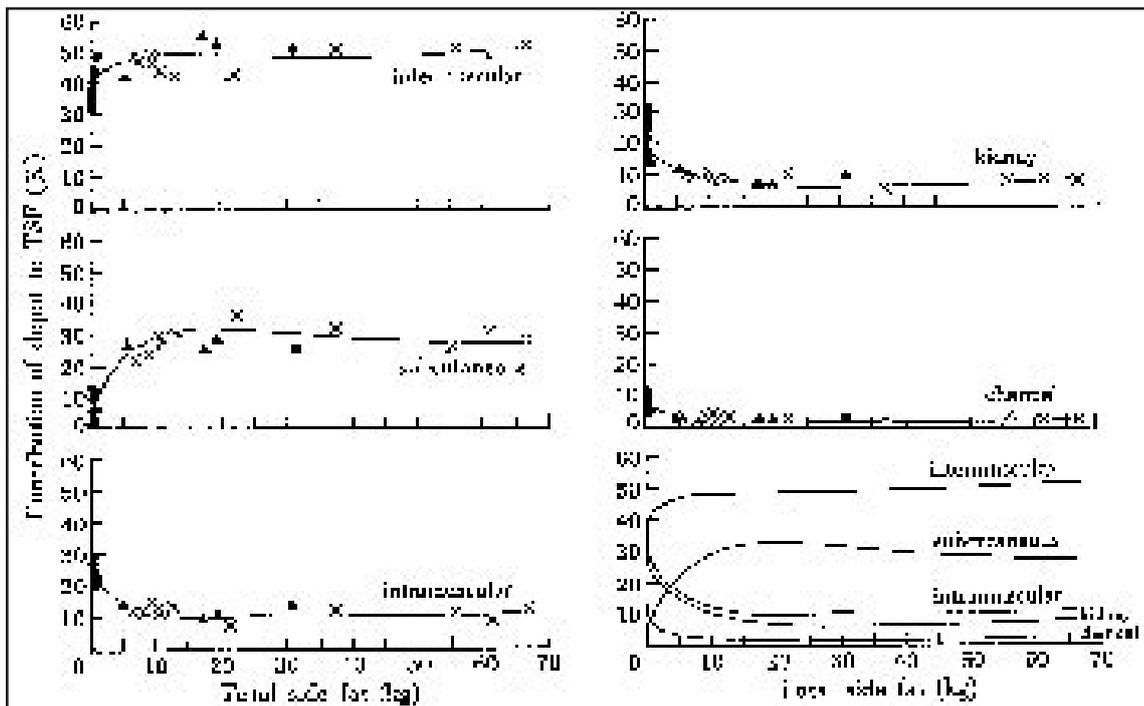


Figure 1. Contribution of individual fat depots to the total side fat. Adapted from Johnson *et al.*, 1972.

If, as the above data suggest, carcass fat depots develop at a constant rate, what does this mean for the pattern of intramuscular fat growth as the animal grows to maturity? Theoretically we might expect the relationship shown in Figure 2. The figure indicates that during the early post-natal developmental phase (around 50kg HCW) intramuscular fat content remains low and constant followed by a phase of more linear development as the carcass begins to fatten more rapidly (starting at around 200kg HCW). Finally it is assumed that as mature body size is reached (around 450 kg HCW) the increase in intramuscular fat is reduced as feed intake and growth rate decline. The actual weight ranges at which these 3 phases will occur would depend on the mature body size of the animal (Figure 2), and animal genotype (Wegner *et al.* 1996) and Figure 3 below.

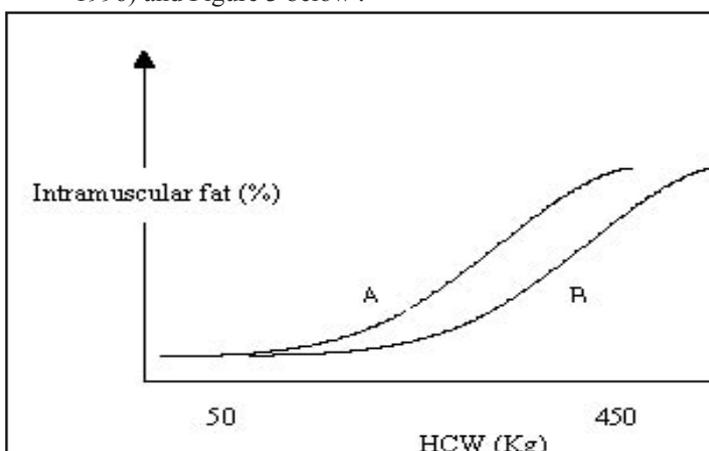


Figure 2. Hypothetical graph showing the development of intramuscular fat in cattle of different mature body weight (B>A).

is insufficient data at the lighter carcass weights (50-200kg) to understand the nature of the curve in this region. However the data shows that the intramuscular fat content, expressed as % fat, increases in a linear fashion between a carcass weight of about 200 - 400kg for British (Duckett *et al.* 1993) or Japanese Black x Holstein (Aoki *et al.* 2001) type cattle undergoing prolonged feedlotting. A further conclusion from Figure 3 is that over the 2 studies, which represent different countries, production systems (although both studies used concentrate feeding) and genotypes the rate of intramuscular fat (%) accretion is relatively similar such that for every 10kg of HCW intramuscular fat increases by 0.47% (Duckett *et al.* 1993) or 0.56% (Aoki *et al.* 2001) units between 200 and 400kg HCW. Similar rates of intramuscular fat increase have been shown by Zembayashi (1994). This suggests that an important determinant of the final level of intramuscular fat is the initial or pre-feeding level. This is an important concept because at the typical liveweight for Australian cattle entering 'marbling feedlots' (400kg) intramuscular fat content would need to be about 5% to achieve a final intramuscular fat content of 15% at 400kg HCW. This scenario should generate an AUSMEAT marble score 4.

In the study of Aoki *et al.* (2001) where the cattle were fed to heavier weights there is a suggestion that the intramuscular fat content does not increase beyond about a carcass weight of about 420 kg and this was a consistent finding for 4 different muscles. This concept of a 'maximum value' is most likely related to declining feed intake as the animals reach their mature body size and the composition of the carcass does not change (Aoki *et al.* 2001).

Recently Oddy *et al.* (2000) demonstrated that the level or



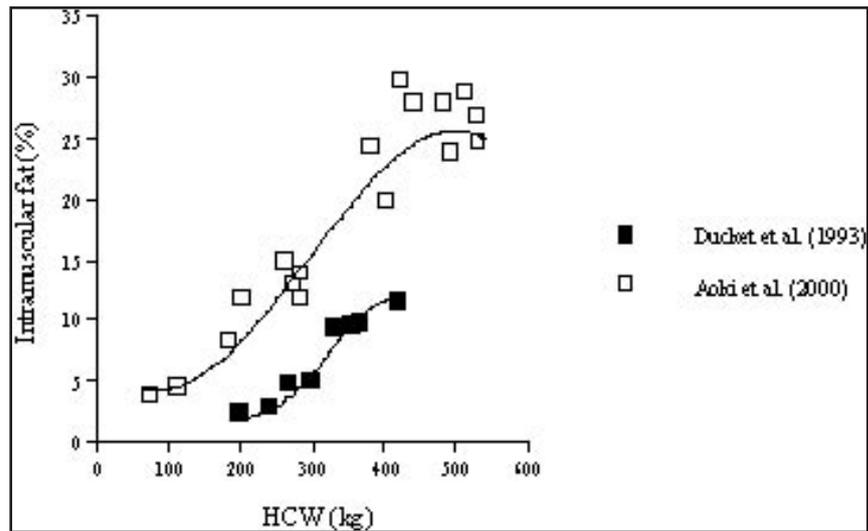


Figure 3. The relationship between carcass weight and intramuscular fat content of the *m. longissimus dorsi* of crossbred Angus x Hereford (Duckett *et al.* 1993) and Japanese Black x Holstein cross cattle (Aoki *et al.* 2000).

intramuscular fat % at the end of a 147 day feeding period was related to the ultrasound scanned intramuscular fat % at feedlot entry or 30 days after commencing feeding. The importance of the content of intramuscular fat at the time animals enter the feedlot is shown hypothetically in Figure 4. Factors affecting the initial level of intramuscular fat include (i) start weight relative to mature weight (ii) genetic propensity to marble, (iii) mature body size or maturity type and (iv) pre feedlot growth rate and pattern of growth. Some potential mechanisms for such effects are discussed in a companion paper in this proceedings (see Harper and Pethick 2001).

Although the cell biology behind these changes in lipid content of muscle are not known, at the macro level (muscle, fat depot) they are a result of differing rates of muscle and fat accretion as the carcass weight increases. As time on feed increases the rate of muscle gain declines while the rate of fat gain increases (Owens *et al.* 1995) but the relative growth of muscles and intramuscular fat content does not substantially change. This concept is supported by the results of Pethick *et al.* (2000) which show that the increase in intramuscular fat relative to total fat content in a five rib set remains constant

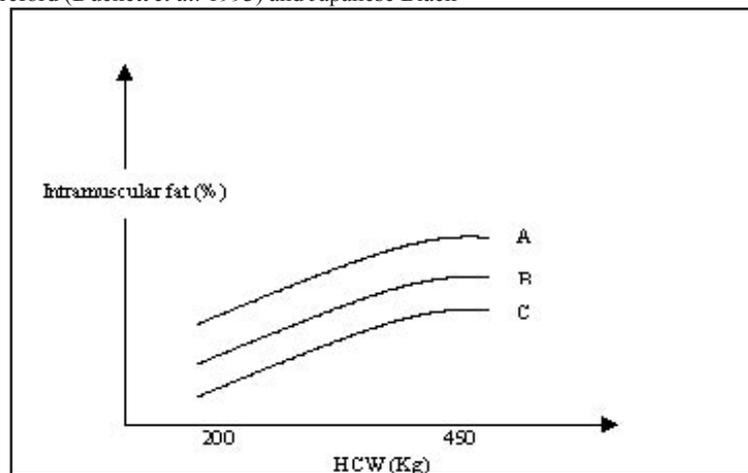


Figure 4. Theoretical pattern of intramuscular fat accretion in beef cattle - the effect of initial intramuscular fat (%) content (A>B>C) on final value in cattle of similar muscle growth potential.

despite substantial increases in total fat deposition (Table 1). These results suggest that increased intramuscular fat %, relies on continued fat synthesis within muscle combined with a decreasing rate of muscle growth (Table 1).

Table 1. Carcass composition data based on ribset dissection of Angus steers slaughtered at the beginning and end of a 150 day feedlotting period (mean \pm sem).

Carcass attribute	Initial slaughter	Final slaughter	Ratio of final/initial	Significance P
HCW (kg)	304 \pm 5.0	417 \pm 2.6	1.37	<0.001
Eye muscle area (cm ²)	671 \pm 1.6	773 \pm 0.7	1.15	<0.001
Intramuscular fat (%)	7.01 \pm 0.47	11.3 \pm 0.28	1.61	<0.001
Total Fat/Bone ratio†	2.65 \pm 0.14	4.19 \pm 0.08	1.58	<0.001
LI muscle/bone ratio†	0.72 \pm 0.03	0.78 \pm 0.01	1.08	0.082
gm fat in LI†	107 \pm 7	201 \pm 6	1.88	<0.001
LI fat/total fat ratio†	0.021 \pm 0.001	0.021 \pm 0.001	1	ns
LI fat/bone ratio†	0.05 \pm 0.004	0.09 \pm 0.003	1.80	<0.001

Growth history

The results from this study are consistent with the pattern of fat accretion described in Figure 1 in that fat accretion in the carcass depots (subcutaneous and intermuscular) and within muscles occur at the same rate through the 304 - 417kg carcass range. This data clearly indicate that intramuscular fat is not late maturing BUT the expression of marbling (% fat) is late maturing (see also Cianzio *et al.* 1982).

The implications for backgrounding and feedlotting are the sooner an animal reaches its near maximal potential for muscle and fat growth the sooner it would begin to commercially express intramuscular fat. That is fast growth throughout the animals life will result in marbling at an earlier age. A very long feeding period allows the cattle to obtain a high level of intramuscular fat since there is time for muscle maturity to be reached followed by time for the muscle to 'fill up' with fat. Shorter feeding periods will have a higher risk of failure particularly if there is a relatively short period of fattening after muscle maturity is reached. The data also infer that feeding diets with an increased energy density (maximised net energy for gain) will drive greater rates of fat synthesis. In addition factors affecting the potential for muscle growth will alter the marbling response. For example animals showing compensatory growth will need longer feeding periods. Metabolic modifiers which increase the potential for muscle growth such as hormonal growth promotants, β agonists (Hunter 2001) and organic chromium would be expected to reduce the rate of deposition of intramuscular fat.

There is limited published evidence that environmental and/or nutritional factors can alter the distribution of fat between muscle and other body depots (Trenkle *et al.* 1978, Zembayashi 1994) and the pattern of response may differ between breed types (Zembayashi 1994). Trenkle *et al.* (1978) showed that moderate growth to the same carcass weight lead to increased intramuscular lipid accumulation relative to rapid growth. However, this took approximately 300 days to develop because it was not apparent in the comparison at 150 d of feeding. This observation lead to suggestions that expression of marbling was greater in older than younger animals (Zembayashi 1994). However, Renk *et al.* (1986) explicitly tested this hypotheses and could not repeat the observations of Trenkle *et al.* (1978). Zembayashi (1994) showed that slower growth up to 450kg liveweight increased intramuscular fat at any given carcass weight for Japanese Black but not Japanese Shorthorn cattle.

In contrast more recent studies conducted by the Beef CRC have shown that growth depression pre-finishing (before about 400kg liveweight) reduces intramuscular fat (%). Thus intramuscular fat content in *Bos taurus* cattle was reduced relative to fat thickness and carcass weight in steers that came from background growth patterns that resulted in lighter liveweights on entry to finishing (Table 2).

Cattle exposed to more extreme environments exhibit the same pattern. Figure. 4 shows data from *Bos indicus*, a *Bos*

Table 2. The effect of different growth pathways during backgrounding on carcass weight, rib fat thickness, intramuscular fat content of *m. longissimus dorsi* at the end of finishing of Angus, Hereford, Shorthorn and Murray Grey steers.

		Path3	Path2	Path1
Parameters at the start of finishing				
Liveweight (kg)		429	404	385
Rib fat thickness (mm)		5.4	4.3	4.1
Adjusted for liveweight				
Growth rate during backgrounding (kg/d)		0.89	0.76	0.67
Parameters at the end of finishing				
Carcass weight (kg)	Feedlot	328	321	314
	Pasture	304	297	294
Rib fat thickness (mm) (Adjusted for liveweight)	Feedlot	12.3	12.2	12.2
	Pasture	11.0	11.0	10.9
IM Fat (%) (Adjusted for carcass wt.)	Feedlot	7.4	7.1	7.1
	Pasture	6.2	5.7	5.5
Growth rate during finishing (kg/d)	Feedlot	1.14	1.22	1.28
	Pasture	0.65	0.68	0.72

indicus/Bos taurus composite and tropically-adapted *Bos taurus* steers finished in feedlots to carcass weights of > 300kg in two different environments (temperate northern NSW and the dry tropics of Central Queensland). The steers were grown out before feedlot entry in these two environments. The reason for the different patterns of fat distribution (reported here as fat thickness, fat trim as % carcass weight and intramuscular fat) is unclear. It may include growth pattern before feedlot entry, possible differences in feedlot diets (although evidence for an effect of feedlot diets on fat distribution is sparse) and thermal environment during finishing. Separate analysis of growth pattern of *Bos taurus* steers indicates that reduced growth rate during backgrounding tends to be associated with reduction in intramuscular fat content of steers, despite the steers exhibiting increased (compensatory) growth during finishing (M.J. McPhee unpublished observations).

However, the effect of growth rate during backgrounding is small compared to the effect of finishing system. In all the CRC 1 studies, intramuscular fat content is higher at the same carcass weight in steers finished in a feedlot rather than at pasture with a 40% reduction in intramuscular fat (%) for every 10kg HCW gained (Figure 5).

The difference in rate of increase in intramuscular fat % between pasture and grain finishing is associated with differences in deposition of fat (as assessed by change in back fat thickness). Dietary differences between feedlot and pasture finished animals include more net energy available for fat synthesis in the feedlot finished animals. Dietary induced differences in net energy availability include (i) greater total net intake per day in the feedlot, (ii) decreased relative intestinal size in feedlot animals - seen as increased

dressing percentage - which leads to reduced maintenance energy and thus higher net energy for gain compared with pasture fed animals and (iii) different pattern of energy substrates available to animal in feedlot compared with pasture diets (see below). Other non-nutritional factors such as less exercise in the feedlot animals resulting in a reduced basal energy expenditure and changed tissue biochemistry are also likely to be important. A further factor which might be responsible for inhibition of intramuscular fat accretion is conjugated linoleic acid (CLA). Conjugated linoleic acid is a mixture of positional and geometric isomers of linoleic acid (n-6C18:2) which are generated in the rumen particularly of pasture fed ruminants (Bauman *et al.* 1998). One effect of CLA relates to fat accretion and nutrient partitioning reduced body fat and increased lean body mass in laboratory rodents and pigs (reviewed by Dunshea and Ostrowska 1999). CLA content of fat from grass fed cattle is higher than in feedlot cattle. The development of marbling might therefore be reduced in pasture fed cattle, although given the complex effects on many enzymes of the fat biosynthetic pathways this conclusion cannot be certain. Clearly the role of CLA in the marbling response needs further investigation although given the reliance of pasture in the backgrounding phase of the Australian production system there maybe little scope for manipulation of CLA.

Environmental temperature and humidity

There is little information available on the effects of environmental temperature on fat development in ruminants.

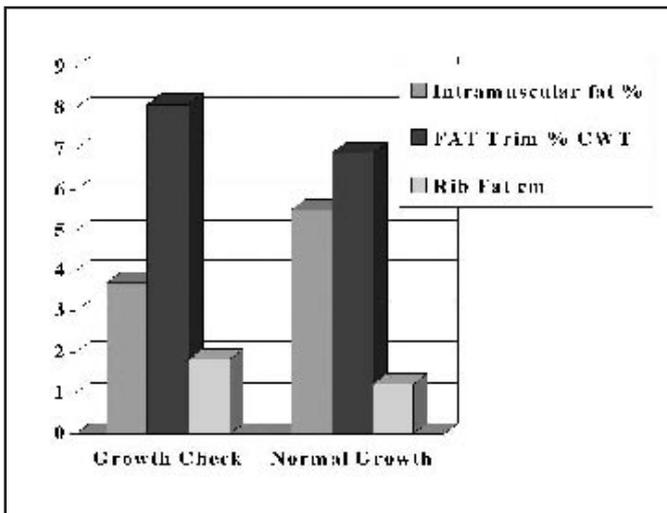


Figure 4. Fat content of the longissimus muscle (striploin), and carcass fat attributes in progeny of the same sires, grown out in central Queensland (Growth Check) and northern NSW (Normal Growth) and finished on a grain based feedlot diet for 150 days to Japanese specifications. Animals entered the feedlot at 400 kg and left at >600 kg. Carcass weights were the same in each group. (Unpublished data from CRC 1)

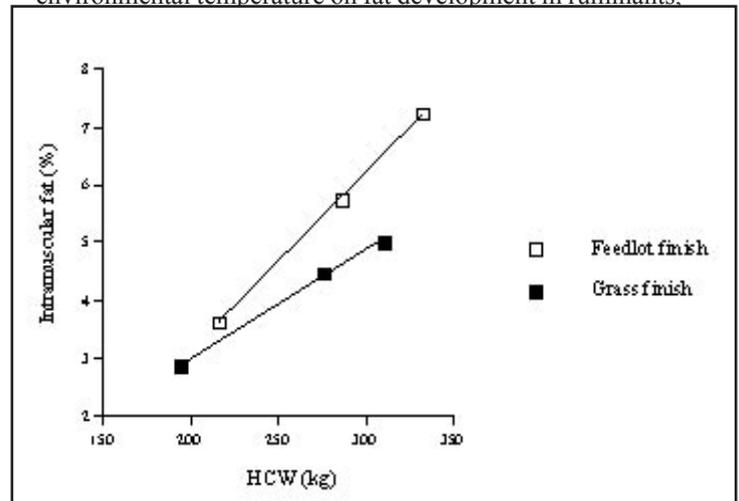


Figure 5. The relationship between HCW and intramuscular fat (%) in temperate breeds (Angus, Hereford, Shorthorn, Murray Grey) finished at 3 different market weights on either grass or in a feedlot. Analysis is based on simple regression of the least square means data generated by CRC 1 data.

Feedlot finished animals received a diet of 70% dry rolled barley with average M/D = 12.1MJ ME/kgDM, and grew at between 1 and 1.8 kg/d; pasture finished animals had access to pastures of variable composition and grew at between 0.4 and 0.75 kg/d. If y = intramuscular fat and x = HCW then the relation for grass finished animals is $y = 0.019x - 0.748$ and for feedlot finished animals is $y = 0.031x - 3.045$.

species. The effects of high ambient temperature on feed intake and growth in pigs are well documented with a reduced feed intake and growth the common finding (Verstegen and Close 1994). Associated changes include a shift of body fat toward internal sites which may reduce thermal insulation and so represent an adaptation to high ambient temperature (Le Dividich *et al.* 1998). Just how this hypothesis relates to the intramuscular fat depot is not known. However there is a strong beef industry feeling in Australia that high heat loads reduce the subsequent marbling response suggesting that fat turnover might result in relocation of intramuscular fat to another site, however there is no data to support this hypothesis (see below).

Metabolism of fat and nutritional implications

Biochemistry of fat synthesis

Finally we need to ask the question: can the rate of increase in intramuscular fat (%) be changed during the feedlotting phase? Thus far we have suggested the availability of net energy for fat synthesis as the key driver during the finishing phase. In the following sections we will explore the possibility for dietary formulation that will maximise both net energy and also possibility optimise the biochemical substrates and/or hormonal milieu that will increase lipid accretion. To discuss this question we need to understand the biochemistry of fat accretion. Fat accretion in any depot is the summation of triacylglycerol (TAG) synthesis and degradation. Synthesis of TAG requires both nonesterified fatty acids (NEFA) and glycerol. Glycerol is derived from glucose but the NEFA can be obtained from a variety of sources including (i) synthesis *de novo* from either glucose, lactate or acetate and (ii) they can be acquired as pre-formed fatty acids in the diet and delivered to the fat depot as lipoprotein TAG. Degradation of TAG within fat depots involves lipolysis and release of NEFA and glycerol into the circulation.

Dietary Protein/Energy ratio

Studies in rats (summarised by Webster 1993) indicate that animals eat to maintain lean body gain, and where diets contain relatively more energy than amino acids they will increase intake until their "needs" for lean tissue deposition are met, and become fatter in the process. This observation has been used in pigs to increase total body fatness and intramuscular fat content (Hays *et al.* 1969; Cromwell *et al.* 1971). More recently it has been shown that deficiency of an essential amino acid (lysine) is sufficient to increase intramuscular fat content in pigs (Essen-Gustavsson *et al.* 1994). In preliminary studies using sheep Oddy *et al.* (1998) have shown that the amount of feed energy required to increase intramuscular fat was less in sheep eating low protein diets (Beef CRC 1998). These studies suggested that an imbalance in amino acid supply relative to energy supply would be associated with changes in carcass fatness, and this will also impact on content of intramuscular fat.

Given this background the Beef CRC and Meat and Livestock Australia undertook 2 linked experiments to test the effects of dietary protein and energy density on the marbling performance of cattle fed barely based diets (Oddy *et al.* 2000, Pethick *et al.* 2000). The conclusions were that diets which contain more or less protein than recommended amounts for feedlot animals do not lead to significant differences in marbling or intramuscular fat. However, there was a trend for high protein diets to produce less and low protein diets more marbling than control diets in both experiments. In the case of Oddy *et al.* (2000) the low protein diets in combination with added dietary fat (to decrease the P/E ratio) significantly decreased feed conversion ratio and cost of gain relative to control and high protein diets. However in the case of Pethick *et al.* (2000) the low protein diets did not change feed conversion ratio perhaps because in this case they did not include dietary fat. Certainly the data of Pethick *et al.* (2000) suggest that a simple diet based on barley and hay (with no additional protein source in the form of grain legumes or urea) fed to Angus steers at a starting live weight of 540kg (P8 back fat = 12mm) produced equal performance to more traditionally formulated rations containing extra protein sources at an extra cost.

Substrate availability and lipogenesis *de novo*

Ruminants (Bauman and Davis 1975) synthesise fat *de novo* in adipose tissue rather than the liver and so regulation of lipogenesis within adipose tissue is a key factor when considering fat accretion in the growing animal. The substrates for lipogenesis *de novo* in ruminants are acetate and glucose/lactate. Diets which are extensively fermented in the rumen (i.e. most diets) promote acetate as the major source of carbon and reducing power for lipogenesis with a smaller contribution from glucose for some of the reducing power and all of the glycerol (Vernon 1981). An alternative pathway for lipogenesis with glucose as the primary substrate is typically seen in monogastric animals when glucose is a major end product of digestion. Two key enzymes of the glucose lipogenic pathway are ATP citrate lyase and NADP malate dehydrogenase. In ruminants both of these enzymes are induced by intravenous glucose infusion, by an increased intake of metabolisable energy and by diets which promote direct glucose absorption from the small intestine (Ballard *et al.* 1972; Lindsay 1970, Pethick *et al.* 1995a,b, Smith *et al.* 1992). Regardless of the substrates used, the overall rate of lipogenesis is controlled by the activity of acetylCoA carboxylase which is under complex substrate, allosteric and hormonal control. Accordingly the activity of acetylCoA carboxylase is an indicator of the total capacity for lipogenesis and its activity is strongly correlated with changes in body composition in pigs (Harris *et al.* 1993).

Despite the reliance on acetate as a key lipogenic substrate the availability of glucose has long been thought a limiting factor for fat accretion in ruminants. Thus Preston and Leng (1987) speculated that diets high in roughage promote an excess of acetate with respect to glucose and so induce a reduced rate





of lipogenesis for a given intake of metabolisable energy. Few studies have critically tested this hypothesis. Two groups (Ballard *et al.* 1972; Prior & Jacobson 1979) have found an increased rate of lipogenesis *in vitro* when glucose was infused into sheep or cattle - the results are equivocal however since glucose was infused in addition to the basal diet and so the experimental design was not isoenergetic. Given a potential link between glucose availability and rate of lipogenesis can this be used as an axis to increase the rate of intramuscular fat accretion?

Glucose availability in ruminants is largely driven by the intake of metabolisable energy with higher ME intake promoting greater rates of gluconeogenesis (Lindsay 1970). One possible site of manipulation might be to use diets which promote both (i) maximal fermentation in the rumen to produce gluconeogenic precursors (propionate) and (ii) which maximise starch digestion in the small intestine. Such diets are usually associated with high levels of processing which increase the accessibility of the dietary starch granule to both microbial and animal amylases and so maximise the availability of glucose to the fattening animal (Rowe *et al.* 1999). Evidence for this comes from Lozano *et al.* (2000) who showed that decreasing the flake thickness of steam flaked sorghum resulted in greater hepatic release of glucose to the general circulation. Formulating rations with this concept in mind may increase lipogenesis at the intramuscular and other sites for several reasons:

- such diets would promote increased levels of anabolic hormones (insulin) which are known to stimulate lipogenesis.
- The logic parallels the observation in humans that diets with a high glycaemic index (i.e. diets that allow rapid glucose absorption and concomitant high insulin levels) promote obesity (Ludwig 2000).
- Such diets will also deliver increased levels of net energy for lipogenesis.
- There is evidence that marbling adipocytes show a preference for glucose/lactate carbon while subcutaneous adipose tissue uses mainly acetate as a source of acetyl units for

lipogenesis (Smith & Crouse 1984; Whitehurst *et al.* 1981). However this is by no means conclusive given that Lee *et al.* (2000) could not find such differences when comparing glucose versus acetate as a substrate. Comparisons of this work with others are difficult since the Lee *et al.* (2000) study used cattle of a different genotype, they did not use lactate as a substrate and the dietary scenario of the cattle was not stated. Clearly more work is needed to define the metabolic profile of the intramuscular adipocytes.

There is some evidence to support a link between the development of intramuscular fat and glucose supply (Figure 6). In the work of Pethick *et al.* (1997) the feeding of steam flaked maize or sorghum compared to dry rolled maize, sorghum or barley was associated with an increased content of intramuscular fat that was not simply related to changes in total body fatness alone. The steam flaked diets also induced a greater activity of ATP citrate lyase in subcutaneous adipose tissue indicating greater glucose supply since we have previously shown the activity of ATP citrate lyase in adipose tissue is an reliable marker for glucose availability in ruminants (Pethick *et al.* 1995). The best statistical model for explaining the data is shown in Figure 6 ($R^2=0.44$). The model implies that dry matter intake and the activity of the glucose insulin axis (as assessed by the ATP citrate lyase activity) where factors driving both total body fatness and the expression of marbling.

However these studies do not conclusively show that the glucose/insulin axis can be used to specifically manipulate rates of intramuscular fat deposition. Firstly it is difficult to divorce glucose supply and starch digestion in the small intestine from changes in net energy. Thus the steam flaked maize based diets could well increase the net energy available for lipogenesis. Secondly Gilbert *et al.* (2000) showed that intramuscular fat deposition was not increased when 'protected starch and/or lipid' was fed to steers consuming a corn based diet. This was despite observed changes in other depots including greater rates of glucose metabolism in subcutaneous adipocytes.

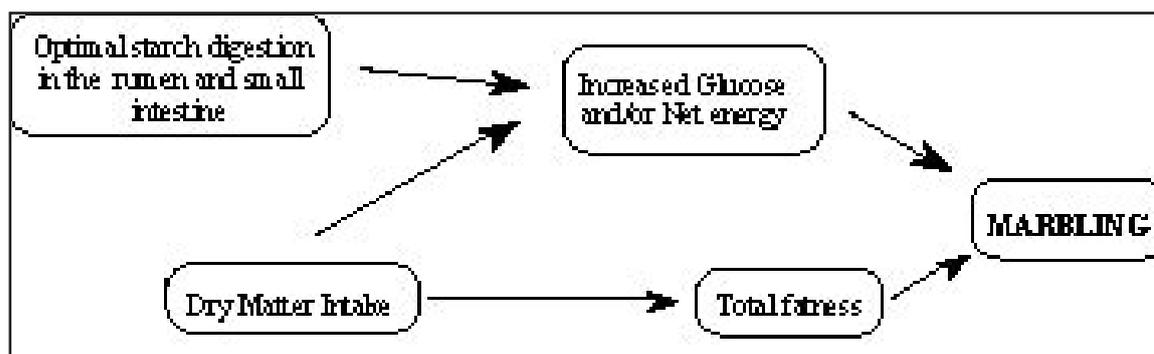


Figure 6. Statistical model to explain the influence of grain processing on glucose supply and the development of intramuscular fat (Pethick *et al.* 1995).



Preformed dietary fat

The other substrate for fat accretion is preformed fat from the diet. The literature reporting the effects of supplemental fat on marbling scores are mixed and are well discussed by Andrae *et al.* (2001). These authors argue that marbling responses to dietary fat have been more consistent when supplemental fat is added to diets based on grains that contain less fat than corn (i.e. wheat, barley) and this is supported by their study where high oil maize (7% fat in DM) was fed in comparison to traditional maize (4.7% fat in DM) to finishing cattle (final HCW = approx. 330kg). Simple measures of carcass fatness (fat thickness) and intramuscular fat (visual marbling score) were similar when cattle were fed isoenergetic diets. However when the high and low oil maize diets were formulated at the same inclusion level of maize the marbling score was higher for the high oil maize based ration. This is predictable since at equal inclusion in the ration along with equal dry matter intake, the high oil maize grain would supply more net energy for fat synthesis.

Lipolysis within adipose tissue

Traditionally the focus of fat accretion is on the rate of triacylglycerol synthesis from fatty acids synthesised *de novo* or obtained preformed in the diet. However for animals kept

out of doors there is considerable potential for lipolytic events associated with cold or hot weather, reduced feed intake and other stressful events. Indeed fat turnover as a contributor to fat accretion is suggested by the proposed mechanism for the antilipotropic effect of copper. Engle *et al.* (2000a,b) have shown that about 20ppm dietary copper reduces fat accretion in finishing cattle and a proposed mechanism is increased catecholamine activity with corresponding greater rates of lipolysis.

The potential for lipolytic events to elicit changes in the site of fat deposition is shown in Figure 7. Mobilised fat is presented to the plasma as non esterified fatty acids (NEFA) which in turn can be either oxidised or re-esterified. The liver is a major site of re-esterification and in this case the triacylglycerol (TAG) is presented back to the circulation as very low density lipoproteins (VLDL). The VLDL can be utilised by tissues which express lipoprotein lipase (LPL). LPL is expressed at different levels in the various tissues and furthermore there is evidence in the rat and human that LPL expression varies between different adipose tissue sites and here in lies a potential mechanism whereby fat turnover could alter the accretion of fat. The changes in fat deposition in the pig exposed to increased environmental temperature have been attributed to this mechanism, that is increased production of hepatic VLDL and increased LPL activity in particular adipose

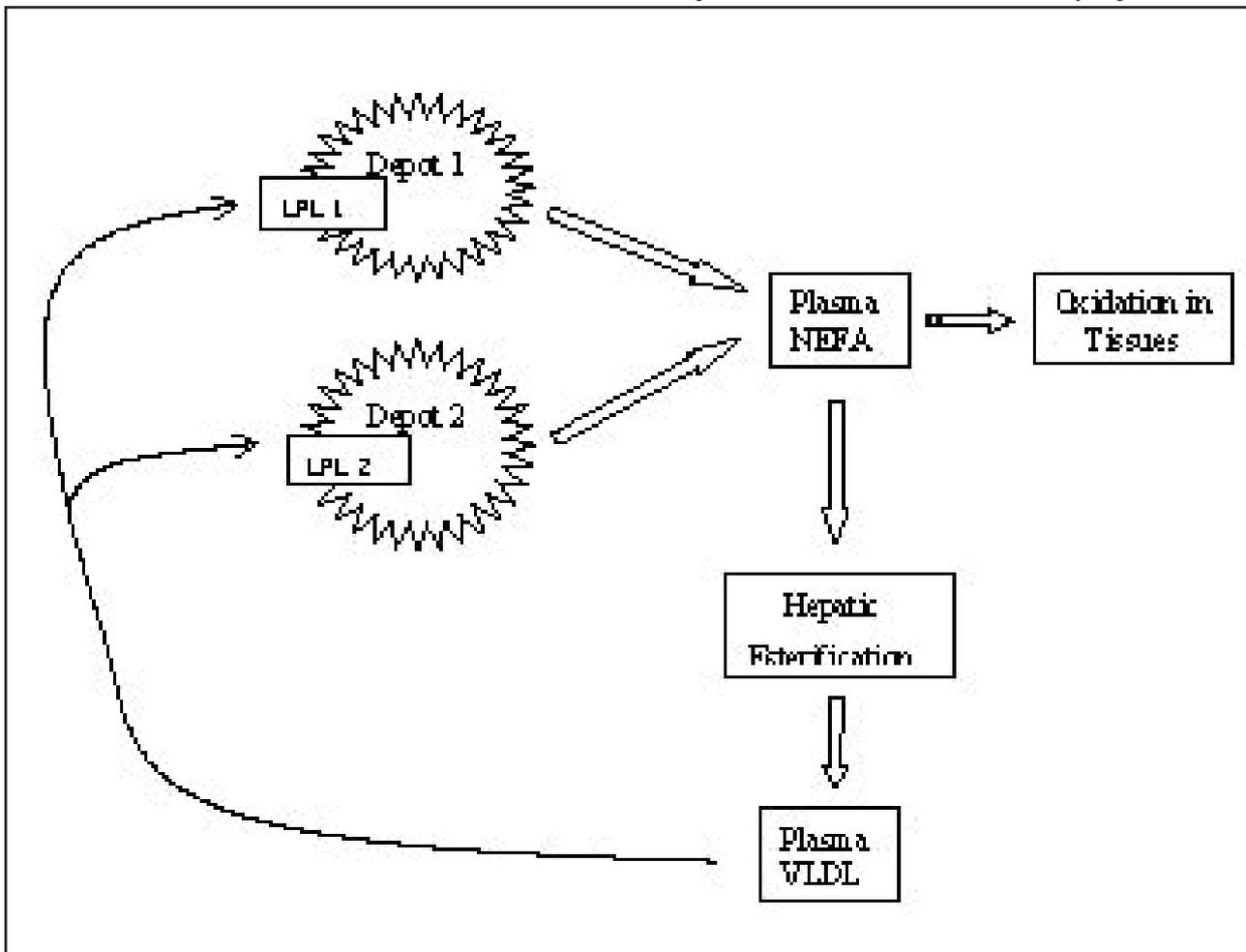


Figure 7. NEFA turnover and how it might effect adipose tissue distribution with time (LPL = Lipoprotein lipase; VLDL = Very low density lipoproteins) .





showed there is some evidence that changes in the activity of thyroid hormone might in part regulate these changes.

Lipolysis in ruminants is very sensitive to catecholamine with sensitivities in cattle some 100x greater than for pigs (Pethick and Dunshea 1996) suggesting that managing fat turnover in ruminants might be very important. Management attributes that minimise fat turnover will in part be associated with optimising the climatic conditions for cattle. Indeed fat turnover might explain the Industry observation that marbling scores of finished cattle tend to be lower in the summer months despite maintained growth and fat depth estimates. An alternative possibility for manipulation might be to use feed additives such as niacin which reduce lipolysis at least in dairy cattle (Harmeyer and Grabe 1981).

Conclusion

This review proposes a simple growth model to explain the accumulation of intramuscular fat in cattle. Potential effects of nutritional manipulation are discussed in relation to the proposed growth curve for intramuscular fat. The scope for nutritional control during both the pasture (or backgrounding) and intensive grain finishing phases are discussed. A key conclusion is that the final level of intramuscular fat after finishing is determined to a large extent by the pre-feedlotting level established in the pasture or backgrounding phase of the Australian production system where the feedlot entry live weight is around 400+kg. Several determinants of initial or pre-feedlotting intramuscular fat % were highlighted and they include (i) start weight relative to mature weight, (ii) genetic propensity to marble, (iii) mature body size or maturity type and (iv) growth path/pattern during the pre and post weaning backgrounding phases with faster growth associated with increased intramuscular fat. The scope for manipulation of intramuscular fat accretion during the feedlotting phase (growing animals from 200 - 400+kg HCW) is also discussed. A key factor highlighted is the net energy available for fat synthesis. In addition it is proposed that the substrate supply and/or hormonal milieu can also be optimised along with the availability of net energy to maximise fat accretion. Finally the possibility of fat turnover affecting the accumulation of intramuscular fat is also discussed.

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