

The partitioning of fat in ruminants—can nutrition be used as a tool to regulate marbling?

D.W. Pethick¹, L. McIntyre², G. Tudor³ and J.B. Rowe⁴

¹School of Veterinary Studies, Murdoch University, WA, 6150

²Agriculture Western Australia, South Perth, WA, 6151

³Agriculture Western Australia, Bunbury, WA, 6231

⁴Department Animal Science, University of New England, Armidale, NSW, 2351

Summary

In this paper we propose that regulation of the glucose/insulin axis by diet will result in increased fattening at the marbling (intramuscular) depot. The pattern of fat accretion in the whole carcass is first described to emphasise that the marbling depot is relatively late maturing. The pathways of fat metabolism are then discussed with the aim of examining the possibility of regulating fat partitioning between depots in ruminants. The importance of acetate versus glucose + lactate as substrates for lipogenesis differs between depots in the ruminant and it is proposed that this might allow for differential control of lipogenesis. The role of diet in the manipulation of pathways for lipogenesis in ruminants is then explored. Both glucose infusion and diets promoting starch digestion in the small intestine increase the activity of enzymes (ATP citrate lyase) associated with lipogenesis from glucose indicating a greater relative importance of glucose as a lipogenic substrate and this may have an impact on the relative growth of different fat depots via the glucose/insulin axis. Chromium supplementation to ruminants consuming a diet low in chromium also increases the relative importance of glucose as a precursor for lipogenesis and causes redistribution of fat away from the subcutaneous site. Finally the effects of feeding different cereal grains and chromium supplementation to 150 day fed steers on visual marbling score are discussed. It is concluded that starch digestion in the small intestine is associated with increased visual marbling score.

Introduction

Consumer preferences and the need to maximise profitability in the rural sector have resulted in an enormous research effort to maximise muscle and minimise fat in meat producing animals such as pigs, sheep and cattle. However, leanness at all sites is not always desirable and some markets will pay a premium

for beef meat containing extra levels of fat (marbling). In this review we first discuss the development of fat tissue during growth and how this relates to consumer preferences. We then examine the biochemical pathways for lipogenesis in ruminants and discuss dietary mechanisms for regulating these pathways. Finally, the possibility for altering the distribution of fat between depots in ruminants is explored with particular emphasis on marbling.

Growth of adipose tissue—practical aspects

Adipose tissue is deposited in specific depots which are similar for all mammals. The primary depots are within the abdominal cavity (perirenal, mesenteric and omental), intermuscular, subcutaneous and intramuscular. However, the proportions differ between the species and are influenced by age. Thus the pig has more subcutaneous fat (70% of total body fat) and less abdominal fat than sheep and beef cattle (Wood, 1984).

Adipose tissue depots are thought to develop in the order of abdominal, intermuscular, subcutaneous and finally intramuscular (Vernon, 1981). The progressive development of some fat depots in cattle is shown in Figure 1. The data suggest that abdominal fat changes largely in line with carcass (or body) weight while all other depots increase relative to carcass weight. Thompson *et al.* (1987) measured chemical fat content at all sites in mature Merino sheep and found intramuscular fat was 7% of total body fat. This compared with subcutaneous at 24%, intermuscular 20%, kidney fat 11%, omental fat 16% and mesenteric at 6%. Therefore the marbling depot is of moderate to small size.

Beef produced for the Australian domestic market originates from cattle yielding a carcass weight of about 200–220 kg and so this results in lean beef (Figure 1) with a muscle fat content of about 2.5–5% since the

subcutaneous and intermuscular fat can be trimmed leaving a low fat product. Alternatively some export markets are forced into producing excessive levels of subcutaneous and intermuscular fat to ensure the maximal development of marbling fat. Marbling is considered a key factor in determining the organoleptic properties for the consumers in these markets and accordingly there is a pricing structure which pays on marbling score. On the domestic market there is little scientific evidence that marbling plays an important role in palatability; however, the reader should be aware that this is a contentious issue within the Australian Beef Industry. When controlled studies are performed the influence of marbling on eating quality is relatively small when compared to the known effects of cold shortening and aging of meat (May et al. 1992).

Partitioning between adipose tissue sites

Despite the enormous research effort directed at partitioning nutrients between fat and protein, selective regulation of fat depots has been given relatively little

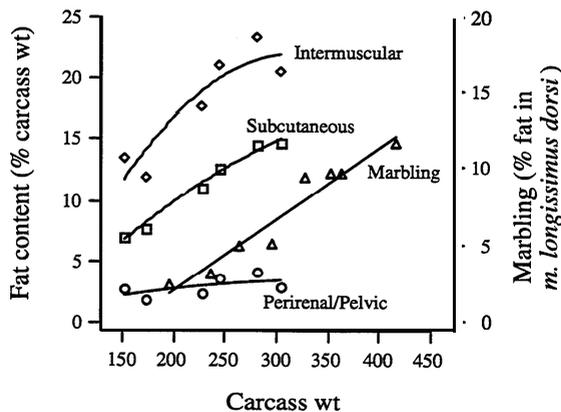


Figure 1 The changes in fat depots during growth in beef steers (data is from Hereford, Angus and Hereford X Angus cross steers, Duckett et al. 1993, Charles and Johnson, 1976)

attention in farm animals. Regulation of the economically important marbling depot is influenced by the genotype (heritability 0.37, Koots et al. 1994) and age (Figure 1). Apart from selecting cattle with a propensity for marbling the production system is based on lot-feeding cattle a high energy diet for some 200-300 days which results in high carcass weights (400 kg) and a proportion of animals with elevated marbling scores. With such an expensive production system it is of interest to know whether fat deposition at the marbling site can be

accelerated so as to reduce feeding time. The relatively small size of the marbling store suggests that small shifts in fat accretion to this depot would have a large impact on marbling score. However there is little information on the regulation of fat deposition at the marbling site.

Pathways of *de novo* lipogenesis

Pigs and 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. Ruminants represent a special case with respect to *de novo* lipogenesis since most dietary carbohydrate is extensively fermented in the rumen, and even when cereal grains such as wheat, barley and oats are fed there is little absorption of glucose from the small intestine (Rowe and Pethick, 1994). As a consequence acetate derived from fermentation in the rumen is thought to be the main source of carbon for fatty acid synthesis (Vernon, 1981). However there is also evidence for some synthesis from glucose, especially via lactate (Prior, 1978; Smith, 1995).

Studies by Smith and Crouse (1984) have shown that adipocytes associated with the marbling depot have a higher reliance on glucose and/or lactate as a substrate than acetate (Figure 2). Intramuscular adipocytes have lower rates of lipogenesis and associated smaller cell size than other depots (Vernon, 1981) but show an increased absolute and relative reliance on glucose for lipogenesis. Generally the marbling adipocytes were poorly responsive to increasing planes of nutrition when parameters of fat synthesis were measured (i.e. ^{14}C incorporation of substrates, enzyme levels); however, lipogenesis from glucose did respond to increasing

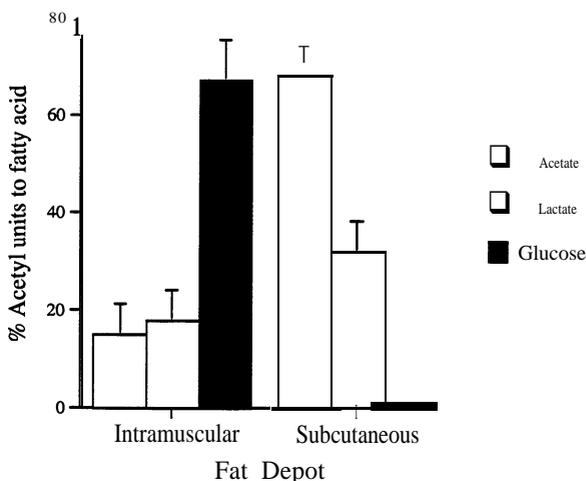


Figure 2 The relative contributions of carbon precursors to fatty acid synthesis in adipose tissue of 18 month old Angus steers (values are % \pm SD) (Smith and Crouse, 1984)

energy intake at the intramuscular site but not in subcutaneous fat (Smith and Crouse, 1984). These differences in the lipogenic pathways suggest the potential to manipulate fat depots since the pathways utilise different substrates and possibly have different hormonal sensitivity. In particular the role of the glucose/insulin axis should be critical and at least two questions seem obvious:

- 1 does upregulation of the glucose/insulin axis influence the pattern or absolute rate of lipogenesis and
- 2 can the glucose/insulin axis be regulated by diet in ruminants?

Effect of diet on pathways of *de novo* lipogenesis in ruminants

What practical scope is there to stimulate the glucose/insulin axis in ruminants? In recent studies in our laboratory we have used ATP citrate lyase as a marker of exogenous glucose supply. ATP citrate lyase is a key, inducible, enzyme of the citrate cleavage pathway which is necessary for fat synthesis from glucose. In addition it is assumed that the enzyme is a more general marker of the glucose/insulin axis since in laboratory rodents this enzyme is regulated by changes in transcription under the control of insulin and other hormones (Hillgartner *et al.* 1995). Initially we used glucose infusion in the same way as Ballard *et al.* (1972) to show that the activity of ATP citrate lyase was positively sensitive to exogenous glucose supply (Rowe and Pethick, 1994). Subsequently we fed sheep diets containing approximately 80% grain fed at 1.8x maintenance (i.e. isoenergetic) for 6 weeks to investigate the role of starch digestion in the small intestine on the expression of ATP citrate lyase (Pethick *et al.* 1995). Samples of subcutaneous adipose tissue were taken at

slaughter and the activity of ATP citrate lyase measured (Figure 3). The results were consistent with the hypothesis that the digestion of starch in the small intestine regulates the expression of ATP citrate lyase. Lupin contains virtually no starch for digestion and the starch of oats is known to be extensively fermented in the rumen. These grains have little or no effect on the activity of ATP citrate lyase. In contrast, some 30% of the starch from maize escapes fermentation (Huntington, 1994) and is absorbed from the small intestine (Janes *et al.* 1985a) which is consistent with the response of ATP citrate lyase activity in adipose tissue. Much of the starch in sorghum can escape fermentation (~40%) however it is also resistant to digestion in the small intestine (Huntington, 1994). To further investigate this hypothesis we repeated the experiment using steamed flaked sorghum as the dietary grain. Flaking the sorghum allowed for a similar expression of ATP citrate lyase in adipose tissue as seen for the feeding of maize, suggesting that the starch escaping fermentation was now being more effectively digested in the small intestine.

The mechanism for this powerful regulation of enzyme activity by diet is not clear from this work; however, it most likely involves the glucose/insulin axis. Most intriguing is the lack of enzyme response in the animals eating diets based on lupin and oats. The glucose entry rate in ruminants is determined primarily by the intake of metabolisable energy rather than by diet composition and so all diets would have allowed for similar glucose entry rates (Schmidt and Keith, 1983). There seems to be something special about the digestion of starch in the small intestine and we might hypothesise differences in the effectiveness of hormonal axes or possibly substrate (glucose or a metabolite) induced gene regulation. There is evidence in rats that several hormones are involved in the communication of nutritional state to adipose tissue and these include insulin, glucagon, thyroid hormones (T₄) and glucocorticoids (Hillgartner *et al.* 1995). Alternative and interacting regulatory candidates might be some of the hormonal or neural activities of the gut (Uvgus Moberg, 1992). There is also strong evidence, again in laboratory rodents, that glucose and/or a metabolite (glucose-6-phosphate) primarily controls expression of lipogenic enzymes and that insulin (and other hormones) have only a potentiating or indirect role (Foufelle *et al.* 1996). It is not obvious just how this proposition can be extrapolated to ruminants, since peripheral blood glucose does not undergo large changes in the post prandial period, even when diets which encourage the digestion of glucose in the small intestine are fed.

The extent to which changes in the glucose/insulin axis or the feeding of different cereal grains influence body fat deposition has not been fully tested. However there are studies in sheep to suggest that alterations in insulin action can cause significant partitioning between fat depots (Walkden-Brown *et al.* 1994). Rams

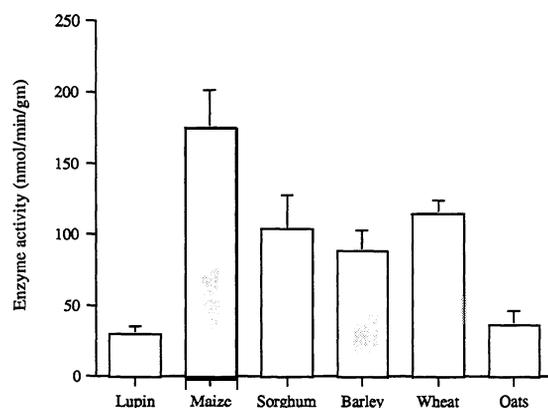


Figure 3 The effect of cereal grain type on the activity of ATP citrate lyase in subcutaneous adipose tissue of Merino sheep (Pethick *et al.* 1995).

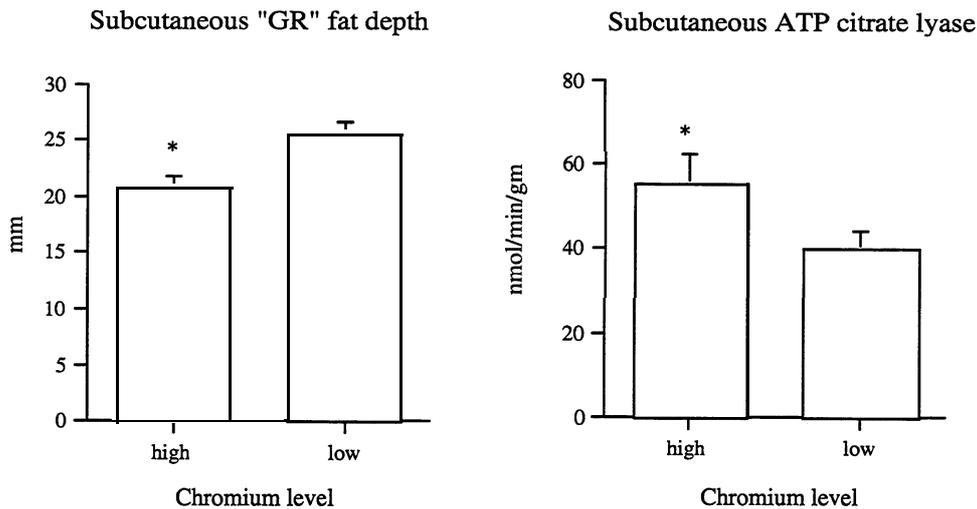


Figure 4 The effects of chromium supplementation on subcutaneous fat depth and ATP citrate lyase activity in subcutaneous fat of mature Merino sheep (Gardner et al. 1997).

immunised against growth hormone releasing factor had increased abdominal and pelvic fat with no change in subcutaneous fat depth or body weight and this might be explained by reduced levels of growth hormone being associated with increased insulin sensitivity (Pethick and Dunshea, 1996). Further evidence is available to suggest that body fatness and marbling is stimulated by diets promoting starch digestion in the small intestine. Reddy et al. (1975) compared maize, triticale and wheat in feedlot rations given to cattle fed for 107 days before being slaughtered at about 420 kg live weight. The level of intramuscular and subcutaneous fat was significantly increased on the maize ration.

We have recently used chromium supplementation (1 ppm chromium as an amino chelate; Gardner et al. 1997) to a basal diet low in chromium (0.05 ppm) to alter fat deposition in mature sheep (Figure 4). Chromium supplementation reduced subcutaneous fat depth ($P < 0.05$) yet increased the activity of ATP citrate lyase when expressed per g of tissue ($P < 0.05$), indicating increased insulin sensitivity which is the known primary effect of chromium (Anderson, 1991). The age (2.5 years) and fat score (3-4) of the sheep would suggest little ability for partitioning the nutrients associated with reduced fat growth into muscle growth—a response more generally found in the growing pig after chromium supplementation (Dunshea and Walton, 1995). Consequently it is tempting to suggest that fat was partitioned to more insulin sensitive fat depots.

Nutritional regulation of marbling via manipulation of glucose/insulin axis

Recently we have completed a trial where steers were fed various diets for 154 days in an effort to further understand the nutritional regulation of marbling. Angus steers were obtained at 324 kg (fat depth: P8 = 4.6 mm,

12th rib = 3.4 mm) and backgrounded on a diet of hammered milled hay/lupin grain (50:50) for 205 days at a mean daily gain of 0.55 ± 0.04 kg/day. The steers entered the feedlot at an initial body weight of 442 kg (fat depth: P8 = 7.5 mm, 12th rib = 5.6 mm) and after acclimation were fed different diets for 154 days. There were 6 diets based on barley, barley plus 1 ppm trivalent chromium as an amino chelate (Chelavite™), dry rolled maize, steam flaked maize, dry rolled sorghum and steam flaked sorghum. The diets contained 72–75% cereal grain, 15% hay and 7–10% lupin grain and 0.5–1% urea with a metabolisable energy value of 11.4 MJ/kg and protein content of 13.5–14.5%. The aim of the experiment was to determine the effects of different cereal grains, grain processing and chromium (chelavite™) supplementation on feedlot performance and various parameters of fat metabolism including the deposition of marbling fat.

Preliminary performance data and fat parameters measured to date are shown in Table 1. At this stage only visual marbling scores of the *m. longissimus dorsi* are available for analysis. It is extremely important to remember that chemical fat is a far more reliable indicator of muscle fat content since marbling score can be affected by quartering site, assessor, chiller (carcass) temperature and fatty acid composition of the fat (Tume et al. 1997). Measurements of chemical fat content and distribution of dissectable fat were not available at the time of writing the paper.

Despite the reservations about visual marbling score discussed above there were significant effects of cereal grain with maize and steam flaking of maize and sorghum associated with higher marbling scores. These effects were not related to changes in fat depth at either the P8 or 12th rib site, although maize and barley resulted in a greater fat depth than sorghum. Certainly subcutaneous fat depth was not correlated with marbling score. Animal performance as judged by carcass weight and daily live weight gain tended to be higher for the maize versus sorghum based diets. Feed

Table 1 Performance and fat parameters of steers fed different cereal grains and a chromium supplement

Parameter	Barley		Maize		Sorghum		Standard error of difference	Significance of effect (<i>P</i>)			
	Dryrolled	Dry rolled Chromium ⁱ	Dry rolled	Steam flaked	Dry rolled	Steam flaked		Cereal grain ^h	maize vs sorghum ⁱ	Dry rolled vs steam flaking ⁱ	Chromium
Visual marbling ^a	1.20	1.10	1.60	2.00	0.90	1.60	0.40	0.03	0.004	0.006	NS
Fat depth P8 (mm) ^b	17.30	15.70	16.30	16.70	14.90	15.30	1.70	NS	0.021	NS	0.076
Fat depth 12th rib (mm) ^b	16.50	14.80	15.70	14.90	13.10	14.10	1.70	0.011	0.033	NS	NS
Carcass weight (kg) ^c	358.00	367.00	354.00	381.00	338.00	348.00	12.00	0.055	0.055	NS	NS
Liveweight gain (kg/day) ^d	1.33	1.41	1.16	1.53	1.13	1.37	0.16	0.08	0.075	<0.0001	NS
Dry matter intake (kg) ^e	12.90	13.50	13.10	14.30	12.70	13.60	1.00	NS	NS	0.032	NS
Feed/Gain ^f	9.90	9.60	11.10	9.10	13.10	10.50	1.10	0.009	0.003	0.0002	NS

a Visual marbling score (mean of 2 assessors) of the *m. longissimus dorsi* at the 12th rib was estimated at a carcass temperature of 12°C.

b Ultrasound fat depth determined on day 142 of feed-lotting; Body weight at 142 days used as covariate for statistical analysis.

c Body weight upon entry into the feedlot was used as a covariate for statistical analysis.

d Calculated from the linear regression of 9 body weight determinations over days 19–149 of the feedlot period.

e Measured while steers were in individual pens from days 50–100. Values are the mean of 43 days from day 57–100 of feed-lotting.

f Calculated from live weight gain from Day 19–149 and feed intake from day 57–100.

g Measured on samples taken by biopsy at day 97 of feed-lotting.

h One way ANOVA on dry rolled grains.

i Two way ANOVA on maize/sorghum & dry rolled/steam flaking.

j Students 't' test on barley ± chromium supplementation as Chelavite™

intake and liveweight gain were significantly increased by steam flaking of sorghum and maize. However feed intake, carcass weight and liveweight gain were not correlated with marbling score.

The activity of ATP citrate lyase was measured in the subcutaneous fat of the steers at day 97 of feed-lotting. The enzyme activity was significantly increased by both the addition of chromium and by steam flaking of maize and sorghum (Figure 5). The mechanism for the increase in the activity of ATP citrate lyase is likely to be different for these treatments. Chromium's primary known mode of action is to increase insulin sensitivity which presumably has increased the expression of ATP citrate lyase. This change in enzyme activity was associated with a trend toward decreased fat thickness at the P8 site (a similar response to the sheep) and no change in visual marbling score. This suggests that an increased insulin sensitivity alone is insufficient for increased lipogenesis at the marbling site. The conclusions for the chromium supplement are confounded however since there was a trend ($P = 0.057$ using repeated measures ANOVA on live weight) for chromium to increase liveweight during the last 90 days of feed-lotting suggesting a greater rate of protein accretion. Consequently it is possible that extra energy was required for the additional protein accretion, thus drawing substrate away from lipogenesis.

The increases in the activity of ATP citrate lyase due to the steam flaking of maize and sorghum must have arisen due to changes in glucose availability. This is partly explained by the significant increase in dry matter intake due to steam flaking. In addition we suggest that steam flaking results in increased digestion of starch and associated absorption of glucose in the small

intestine. Steam flaking of maize and sorghum is known to increase the digestibility of starch both in the rumen and post ruminally (Huntington, 1994). Janes et al. (1985b) compared insulin level in the blood, and insulin responsiveness and sensitivity in sheep fed dried grass and maize based diets. The maize based diet resulted in an increased glucose turnover and more importantly 6.1% of the glucose turnover in the blood was derived from glucose absorption in the small intestine (Janes et al. 1985a). These changes in glucose metabolism were associated with no increase in blood insulin concentration, no change in insulin sensitivity and a slight increase in insulin responsiveness. Despite the lack of changes in insulin metabolism (at least in sheep), the metabolic pathways within adipose tissue have responded to the altered source of glucose (intestinal versus hepatic) within the animal suggesting precise regulation at a level which is not yet understood. Given that the marbling depot is relatively slow to develop, small increases in blood glucose over a longer period (which would be difficult to detect experimentally) might contribute to the regulation of lipogenesis when starch is digested in the small intestine.

Associated with the increased activity of ATP citrate lyase in subcutaneous adipose tissue due to steam flaking was a similar increase in the visual marbling score (Figure 5). Indeed there was a significant correlation between the activity of ATP citrate lyase in subcutaneous adipose tissue and visual marbling score over all treatments ($r^2 = 0.35$). On the basis that the dietary regulation of ATP citrate lyase activity in adipose tissue was via a different mechanism for the chromium

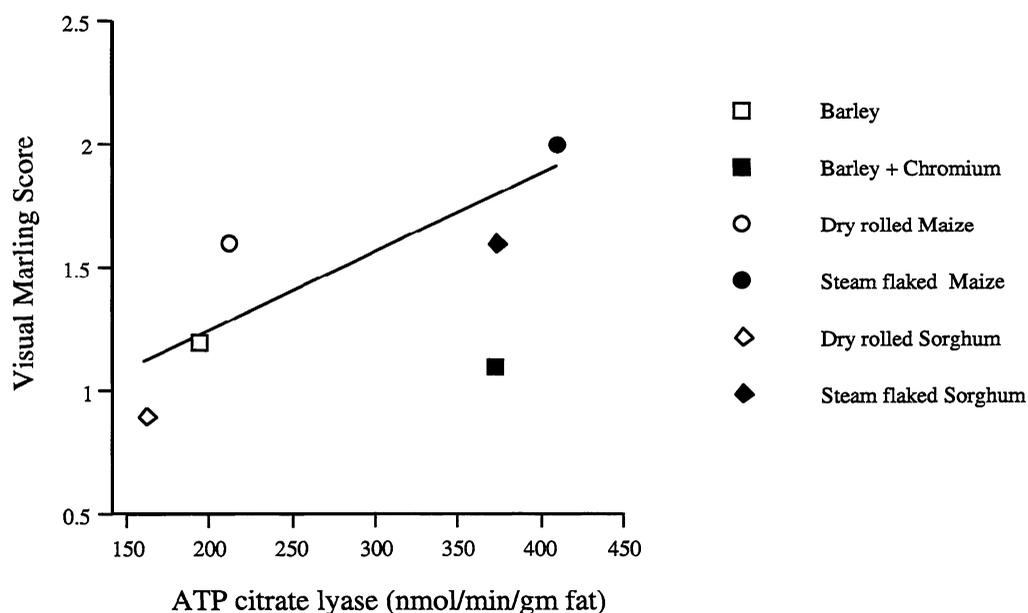


Figure 5 The relationship between ATP citrate lyase activity in subcutaneous fat and visual marbling score, $r^2 = 0.72$ (The linear regression was fitted excluding the Barley + Chromium treatment; see text).

supplemented and cereal grain treatments, a separate correlation was calculated for the treatment groups not involving chromium supplementation. The correlation was further improved ($r^2 = 0.72$) when the chromium supplemented treatment was not included. This suggests that altering the pathways of lipogenesis within adipose tissue by formulating diets which provide for increased digestion of starch in the small intestine promote lipogenesis at the marbling site.

Conclusions

It is concluded that fat depots in the ruminant can respond to diet by changes in expression of the lipogenic pathways using glucose as a precursor. The potential for biosynthesis of fat from glucose, as estimated by the activity of ATP citrate lyase activity, is influenced by chromium supplementation and the digestion of starch in the small intestine. However the visual marbling score was more closely associated with increases in ATP citrate lyase activity in adipose tissue as a result of changes in starch digestion in the small intestine. The reasons for the different response to visual marbling are not clear, but they are related to glucose being derived from the gut rather than from hepatic gluconeogenesis alone. A deeper understanding of the mechanisms which regulate compartmentation of fat in ruminants awaits further research.

Acknowledgments

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