

Nutritional and Management Factors Affecting Marbling Deposition

Larry L. Berger, Ph.D.
Department of Animal Sciences
University of Illinois

Nathan A. Pyatt
Graduate Student

Introduction:

The future success of the beef industry will be largely determined by our ability to meet consumer demands. Consumers want beef to be safe, consistently tender, palatable, free of outside fat, easy to prepare, and reasonably priced compared to other proteins. The dramatic increase in the number of cattle marketed through grid pricing structures is an example of the beef industry rewarding cattle that meet consumer demands. Quality and yield grade are the major factors determining price in most grids. For young cattle, quality grade is determined primarily by marbling, the amount of intramuscular fat in the ribeye. Yield grade is greatly influenced by the amount of backfat on the carcass. Developing a system to produce high quality carcasses with minimal subcutaneous fat offers the opportunity for significant economic rewards.

The purpose of this paper is to review our current understanding of how nutritional and management factors affect marbling deposition while maintaining acceptable yield grades. Lipid deposition is believed to follow a set hierarchical pattern of omental, peripheral, subcutaneous, intermuscular, and intramuscular. However, this dogma may be a result of more controllable factors rather than biology alone. Certainly, genetics, sex, health, implantation program, environment, season of the year, etc. influence how cattle fatten, however, the potential impact of nutrition and management is often underestimated. In this paper we will first review recent research showing the impact of nutrition and management on quality grade, and secondly, evaluate possible modes of action at the tissue level.

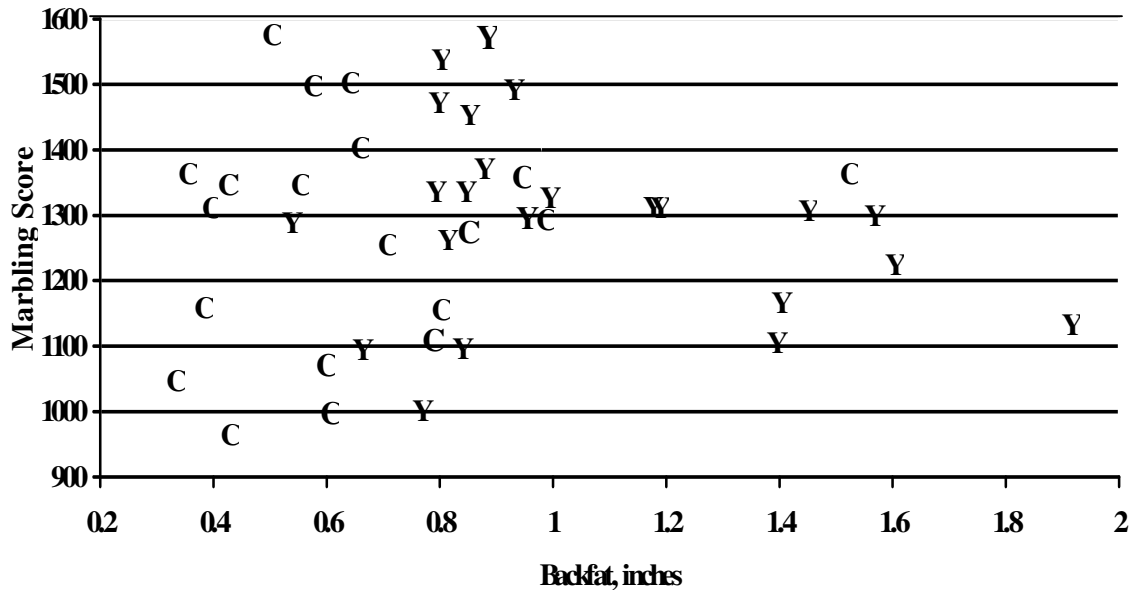
The perception in the feedlot industry has been that calf-feds won't grade. Many times large framed calves have entered the feedlot weighing 600 lbs after which they were grown for 60-90 days prior to being placed on the finishing diet. After 100 to 150 days on the finishing diet they were harvested and only 40-50% graded low Choice.

Wertz et al. (2002) evaluated the effect of weaning calves and growing them on a high forage diet compared to early-weaning and placing the calves on a high-concentrate diet immediately. Consecutive calf crops were used so that differences in genetics were minimized. Twelve $\frac{3}{4}$ Angus and 12 Wagyu x Angus cross heifers were weaned at 180 days of age and grazed on endophyte-infected tall fescue for 16 months before entering the feedlot at 22 months of age. The following year's calves from the same cows and bulls were weaned at 142 day of age and immediately adjusted to an 80% concentrate-20% corn silage diet. Calves were fed 119 days prior to entering the feedlot at 9 months of age. All heifers were individually fed using Calan[®] gate-equipped bunks and ultrasound at ~60 d intervals to monitor intramuscular and subcutaneous fat. In order to maximize marbling, all heifers were implanted (Synovex[®] H) only

once at the beginning of the individual feeding period. Animals were harvested when heifers were estimated to grade 50% USDA Prime. The yearlings required 218 days on feed to reach the desire marbling endpoint, while calf-fed heifers needed 238 days on the finishing diet. Yearlings grew faster (2.62 vs. 2.27 lbs/d), but were less efficient (7.46 vs. 6.06 feed:gain) than calf-feds. By design, the two age groups achieved similar marbling endpoint, with 54% and 56% of the yearling and calf-feds grading prime, respectively. When marbling score was regressed against cumulative gain:feed, early-weaned calves were approximately 20% more efficient at any marbling endpoint compared to the yearling heifers.

Some interesting observations can be made as one examines the relationship between marbling and backfat within the two age groups (Figure 1). Most of the calf-fed were at 0.8 inches of backfat or less, while most of the yearlings were above 0.8 inches. In the yearling heifers there were eight carcasses that had an inch of backfat or more, but within that population, marbling score did not increase as backfat increased. It appears as if marbling had plateaued and additional fat deposition was primarily backfat. In contrast, 10 of the calf-fed heifers had 0.6 inches or less backfat and graded average choice or above. At the same marbling endpoint, yearling heifers averaged over 0.2 inches more backfat then the early-weaned calves. The yearlings had an average yield grade of 3.85, while the calf-fed averaged 3.35. On most grids, the premium/discounts would dramatically favor the calf-fed heifers. The fact that the two groups are of similar genetics suggests that the nutrition/management systems influenced the relationship of marbling and backfat deposition.

Figure 1. Relationship between marbling and backfat (Choice = 1000, Prime = 1300).



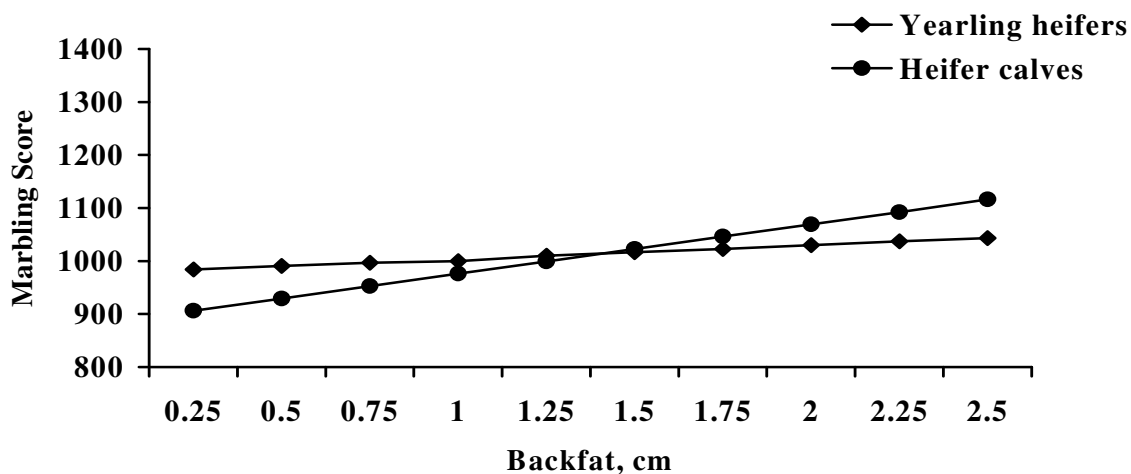
These data are interpreted to show that when calf-feds are managed so that they can express their genetic potential to marble, they will grade as well or better than yearlings. Obviously this trial

involved cattle with the genetic potential to marble, does the same relationship hold for Continental-cross cattle?

To answer that question, a similar trial was designed using British X Continental cross heifers. Sixteen Angus x Simmental cross heifers were weaned at 73 days of age and grazed on endophyte-infected tall fescue for 18 months before entering the feedlot at 22 months of age. The following year's calves were weaned at 71 days of age and immediately adjusted to a high concentrate diet. Calves were fed 119 days prior to entering the feedlot at 7 months of age. During the finishing period ultrasound measurement were taken at ~60 day intervals to monitor backfat and intramuscular fat. The yearlings were harvested after 218 days at 0.64 inches of backfat, while calf-fed heifers needed 258 days on the finishing diet to reach 0.63 inches of backfat.

Similar results were observed with Angus x Simmental heifers as reported previously (Wertz et al., 2001). In this study, when marbling was regressed against backfat (both determined by ultrasound) the slope of the line differed ($P < 0.01$) due to age (Figure 2). Calves that were fed-high energy diets, deposited more marbling relative to backfat than heifers of the same genetics that were finished as long yearlings.

Figure 2. Regression of marbling score on 12th-rib fat thickness (both determined by ultrasound) for early-weaned heifers finished as long yearlings or finished as calves (Wertz et al., 2001)



An obvious question one could pose is whether feeding high-concentrate diets early in life only improves carcass quality in cattle that have the genetics to achieve high levels of marbling (i.e., Angus and Angus crosses), or does it also benefit cattle that are predominately Continental breeding? To answer this question, a four-year study was conducted utilizing 192 Simmental steers (mostly 7/8 or greater) from sires with known marbling EPD's. Steers were weaned at 88 days of age and immediately adjusted to a 90% concentrate diet based on whole shelled corn (Pyatt et al., 2004). Animals were individually fed (48 steers/year) using Calan[®] electronic gate system. Steers were implanted with Synovex[®] C at weaning and successively with Synovex[®] S and Revalor[®] S (approximately 120 days prior to harvest). Marbling EPD's of the sires ranged from -0.24 to 0.51 and averaged near breed average at 0.057. Steers were harvested at 14

months of age and averaged nearly 1400 lbs after a 4% shrink. All steers were harvested at the IBP plants in Iowa or Illinois and quality and yield grades determined by USDA graders. Quality grades were: 14.5% Select, 46.2% low Choice, 36.6% average or high Choice and 2.7% Prime. Yield grades were: 17.7% YG 1, 59.7% YG 2, 21.5% YG 3 and 1.1% YG 4. Steers were fed to heavier weights than would be typical to evaluate changes in gain, feed efficiency, and carcass value over time. Approximately 26% of the cattle had carcasses that weighed more than 950 lbs. Although one could argue that the quality grades would be reduced if the cattle were marketed at an optimum carcass weight, very few of the heavy cattle were near the break in Select-low Choice marbling. Although it is impossible to make direct comparisons with traditionally managed cattle, steers with similar breeding in the American Simmental Association database average less than 55% Choice.

It is also interesting to compare this data set with cattle that have been genetically selected, managed and sorted to achieve high quality grades. The Angus Best of the Breed Feeding Contest results are a good example (Table 4).

Table 4. Angus Best of the Breed Feeding Contest Results for 2002.

Choice Range	No. Head	% Choice	% Yield Grade 1 & 2
100	325	100.0	17.6
90-99	2,436	94.9	20.6
80-89	2,217	85.6	19.1
70-79	2,298	75.5	20.6
60-69	2,295	64.9	27.7
50-59	732	56.7	41.7
40-49	800	42.9	43.9
30-39	159	34.1	49.4

These cattle are selected, often using ultrasound, to identify cattle with the genetic potential to grade. Certainly, the numbers are impressive and demonstrate the genetic potential of Angus cattle to achieve high marbling levels. However, as one studies these data it becomes obvious that the outstanding quality comes with a price in terms of cutability (yield grade). The Angus cattle (2,217 head) that average 85.6% Choice had 19.1% yield grade 1 and 2 cattle. Our early-weaned Simmental steers averaged 85.5% Choice with over 77% yield grade 1 and 2 carcasses. It is well documented that breed average Angus have greater marbling potential than breed average Simmentals, as used in our study. We would propose that feeding of high concentrate diets early in life allowed for the initiation of marbling deposition earlier than what would have occurred with more traditional management.

Other researchers have also shown that feeding high-starch diets early in life can improve the quality grades of other classes of cattle. Angus x Simmental calves were allotted to a bull or steer group based on sire, birth date and birth weight (Schoonmaker et al., 2002). At 75 day of age, calves in the steer group were castrated. All calves were weaned at 115 days of age with no exposure to creep feeding. Beginning at weaning and continuing until the calves averaged 200 days of age, animals were fed a 70% concentrate and 30% corn silage diet. For the first two weeks after weaning the diet contained 17.3% crude protein and was then reduced to 15%. From day 201 to harvest all calves were fed a 14% crude protein diet that was 85% concentrate and

15% corn silage on a dry matter basis. Ultrasound was used to monitor backfat thickness, and cattle were harvested at a common backfat endpoint (0.45 inches).

No differences in the quality grade were detected between bulls and implanted steers (Table 5). Although there are no comparisons with more traditional management systems, most researchers who have fed young bulls would admit that quality grades over 80% Choice, including over 50% with average Choice or greater at less than a year of age, is a result of early-weaning on high-energy diets.

Table 5. Carcass characteristics of Early-weaned Angus-Simmental bulls and steers^a.

Item	Bulls	Steers
Hot carcass wt. lbs	744	719
Fat Thickness, in.	0.48	0.50
Yield Grade	3.2	3.4
Quality Grade, %		
Select	15.8	15.0
Low Choice	26.3	50.0
Ave. Choice	36.8	30.0
High Choice	21.1	5.0

^aSchoonmaker et al., 2002.

Creep Feeding:

Previous research by Faulkner et al. (1994) indicated that creep feed energy source could affect carcass quality. Calves creep fed a corn-based diet had much higher marbling scores ($P < 0.05$) when compared to calves fed a soyhull-based creep, even though pre-weaning ADG was similar and identical diets were fed from weaning to harvest. In another trial 168 Angus x Simmental steers from the University of Illinois beef herd were randomly allotted to 24 pens to compare the effects of early-weaning on a high-concentrate diet with creep feeding on carcass quality (Shike et al., 2003). Four treatments compared were: 1) early-weaned with a programmed intake of a whole corn diet; 2) normal-weaned after being fed a 25% corn creep feed; 3) normal-weaned after being fed a high-fiber creep feed; and 4) normal-weaned with no creep feed. Creep feeders were placed in pastures when steers were early-weaned (63 days of age). The experimental growing period was from day 63 to the time of normal weaning at day 189. After a 23-day adaptation, all steers were placed on a common finishing diet for an average of 185 days.

By design, there were no differences in gain, resulting in similar days to slaughter between early-weaned and creep-fed steers, or among creep-fed steers (Table 6). The normal-weaned steers without creep feed gained 0.26 lb/day less ($P < 0.01$) and were 12 days older ($P < 0.01$) at slaughter compared to the other treatments.

Table 6. Carcass characteristics of early-weaned, normal-weaned creep-fed, and normal-weaned steers without creep^a.

Item	Early Wean (1)	Corn Creep (2)	Fiber Creep (3)	No Creep (4)	1 vs. 2&3	2 vs. 3	1&2&3 vs. 4
Yield							

HCW, lbs.	757	774	757	724	0.53	0.23	<0.01
Backfat, inches	0.50	0.44	0.47	0.47	0.09	0.40	0.77
KPH	2.24	2.45	2.23	2.62	0.40	0.13	<0.01
REA, inches ²	12.87	12.99	13.22	12.58	0.31	0.39	0.04
Yield Grade	2.98	2.90	2.77	2.92	0.17	0.28	0.74
Quality							
Marbling Score ^b	663	588	608	615	<0.01	0.43	0.79
% ≥Choice ^c	90	79	80	73	0.15	0.91	0.14
% ≥Choice ^o	73	33	44	46	<0.001	0.33	0.68

^aShike et al., 2003.

^bMarbling Score: 500 = Small^o, 600=Modest^o, 700=Moderate^o.

When comparing carcass traits, the normal-weaned steers without creep had lighter carcasses ($P < 0.01$) than the average of the other treatments (Table 6). There was a trend ($P = 0.09$) for the early-weaned steers to have more backfat than the average of the creep-fed steers. Marbling score was greater ($P < 0.01$) for early-weaned steers compared to those receiving creep feed. By industry standards all treatments graded very well with between 73 and 90% Choice. However, early-weaned steers had a greater ($P < 0.01$) percentage of average Choice or higher carcasses compared to the average of the creep-fed steers.

Mode of Action:

After reviewing these data, a logical question to ask is whether there is a metabolic or hormonal explanation for an apparent increase in marbling deposition in early-weaned cattle fed high-concentrate diets? Obviously, intramuscular fat and hence carcass quality can be influenced by numerous factors including nutritional management and breed. Myers et al. (1999b) reported that early-weaned calves immediately placed on a grain diet had higher marbling scores at lower backfat endpoints than normally weaned calves. Additionally, Myers et al. (1999) reported an increased percent of early-weaned, grain-fed steers graded USDA Choice relative to early-weaned steers grown on pasture and then fed grain. These data suggest that marbling deposition may be affected early in development, and furthermore that diet composition during the growing period may influence marbling deposition.

The literature indicates several mechanisms by which nutrition can affect composition of gain in ruminants. Diet composition influences volatile fatty acid profile, which has been attributed to differences in composition of gain. Prior (1983) indicated that nutritional factors in hay-fed cattle yielded adipocyte hypertrophy (increased cell size) without increased adipose tissue mass in subcutaneous depots. In contrast, cattle fed grain-based diets had smaller adipocytes and equal subcutaneous mass due to increased adipocyte hyperplasia (cell number; Prior, 1983). Furthermore, Cianzio et al. (1985) reported that the number of adipocytes was more closely related to marbling score than was cell diameter. Additionally, Hood and Allen (1978) reported the ribeye contained a greater proportion of these small adipocytes. The combination of these reported findings might suggest that adipocytes in the ribeye prefer available substrates resulting from the fermentation of grains compared to forage. In addition, Cianzio et al. (1985) reported an increased hyperplasia between 11-15 months of age in steers creep-fed and immediately placed on high concentrate diets. Exactly which nutritional factors caused differences in

lipogenesis were not delineated, however the interactions of volatile fatty acids and hormones have been implicated as the mechanism. Etherton and Ewcock (1986) reported lipogenesis to be stimulated by the presence of insulin and to a lesser extent by insulin-like growth factor-I in vitro.

Several researchers have attempted to address the question of whether lipogenesis simply result from differences in caloric density or dietary substrates. Smith and Crouse (1984) demonstrated no difference in the marbling scores of steers weaned at eight months and fed *ad libitum* corn silage or *ad libitum* corn to 16 or 18 months of age. Likewise, no differences were observed in enzyme activity, adipocyte diameter or cells per gram as a result of diet or age. However, Smith and Crouse (1984) did report that while acetate provided 70-80% of the acetyl units for lipogenesis in subcutaneous adipocytes, it only supplied 10-25% in intramuscular adipocytes. Meanwhile, the majority (50-60%) of the acetyl units for lipogenesis in intramuscular adipocytes came from glucose. High-grain diets yield a greater proportion of propionate than forage-based diets. Propionate, a gluconeogenic precursor, may lead to greater glucose and hence greater marbling deposition. The negative correlation between the number of adipocytes per gram of ribeye tissue and the incorporation of acetate into that tissue reported by Hood and Allen (1978) supported the hypothesis that acetate was not the preferred carbon source for intramuscular fat deposition. Research conducted by Okine et al. (1997) supported the theory that glucose was the preferred substrate. The authors reported a 52% increase in the enzyme acetyl-CoA carboxylase and a 38% increase in the fatty acid synthase enzyme when isoenergetic diets of barley relative to alfalfa hay were fed to sheep. Two explanations were proposed for the differences in lipogenesis resulting from dietary energy source. First, glucose or glucose precursors, insulin, and NADPH-linked dehydrogenases were increased by the grain diet relative to a roughage diet (Okine et al., 1997). Trenkle (1970) also reported a 50-60% increase in insulin level concomitant to the propionate increase that resulted from grain versus a hay diet. Secondly, the methylmalonyl-CoA produced from propionate may replace malonyl-CoA as a primer for lipogenesis (Okine et al., 1997). It appears that if the proper substrates are present, marbling deposition may occur early in the growing period with little subcutaneous fat deposition. Feeding early-weaned calves so that they never have a high-acetate fermentation, may allow us to increase marbling deposition while limiting back fat development.

Protein level in the diet may also influence marbling deposition. Unpublished data from the University of Illinois suggest that increasing the protein levels in diets of young calves to as high as 16% will increase marbling score at the same backfat endpoint. Richards et al. (2003) published data showing that casein infusion (0, 60, 120 or 180 g/day) into the abomasums of growing steers linearly increased alpha amylase concentrations in the pancreatic juice as well as secretion rates (units/hour). Baldwin et al. (2000) reported that growing steers fed a 13% crude protein, 60% concentrate-40% roughage diet had a longer small intestine with increased villus height in the duodenal and crypt depth in jejunal sections, compared to steers fed 10% crude protein. Lopez et al. (2001) fed growing heifers diets containing various levels of soybean meal resulting in 12, 14, 16 or 18% crude protein. Serum insulin concentrations were greatest ($P < 0.02$) for heifers fed 16% protein, while glucose concentrations were greatest ($P < 0.05$) in heifers consuming 18% protein diets. It is possible that increasing protein levels may improve starch digestion and absorption from the small intestine, especially on whole shelled corn based

diets, while simultaneously increasing blood insulin and glucose. The combined effect should lead to increased substrate availability for intramuscular adipocytes.

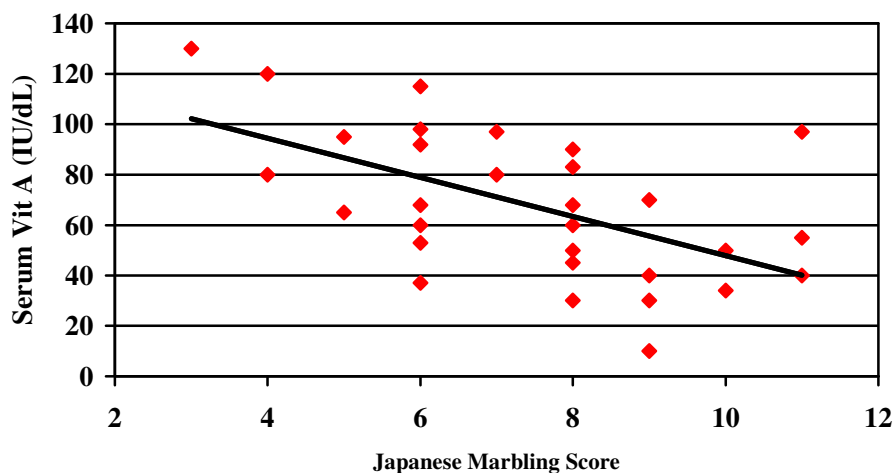
Effect of Season on Carcass Merit:

The effects of season of the year when cattle are slaughtered on percentage grading choice are well documented (Kreikemeier et al., 1998; Anderson, 2001). In general, the percentages of the carcasses that grade low Choice or better increases in the spring and peaks around April. It then gradually decreases to a low point in October. In November and December it starts to improve and the cycle is repeated. Based on supply and demand, the Choice-Select spread is usually lowest in the spring (\$3-\$4), and highest in the late fall (\$8-\$10). As more cattle are marketed on the basis of their individual carcass merit, quality grade can make a large difference in average price.

At first glance it may not seem like season of the year would have much affect on the nutrition of the cattle. Most feedlot diets have a relatively constant nutrient profile across season. However, when one considers that the nutrient profile consumed by the cattle six to eight months before slaughter may have a strong influence on quality grade, then the affects of the season of the year may make sense.

In the past 10 years we have begun to understand the factors that regulates the conversion of preadipocytes to adipocytes that can fill and be detected as marbling (Kawada et al., 1990). These researchers showed that fat-soluble vitamins inhibited the conversion of preadipocytes to adipocytes, while vitamin B₆ and vitamin C stimulated differentiation. Although this work was done in vitro using the 3T3-L1 preadipocytes as a model, it appears to apply to cattle. Oka et al. (1992) was the first to show a relationship between serum vitamin A concentrations and marbling deposition (Figure 3). The regression line was $Y = 104.9 - 5.3x$, with an $R^2 = -0.37$ ($P < 0.05$). A similar (negative) relationship was detected between liver vitamin A levels and marbling index (data not shown). More recently, Adachi et al. (1999) reported that the serum vitamin A levels 4-6 months prior to harvest were significantly ($P < 0.05$) lower in high-marbling steers compared to low-marbling steers. The high-marbling steers (9.0 marbling index) averaged 30 and the low-marbling steers (4.8 marbling index) 49 IU of vitamin A/dl, respectively.

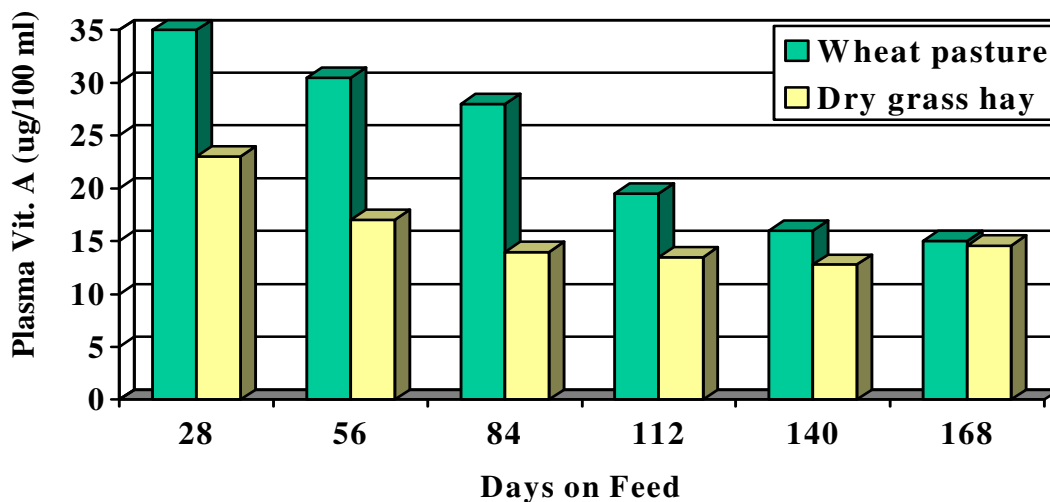
Figure 3. Relationship between marbling score and serum vitamin A (Oka et al., 1992).



Kawada et al. (1996) reviewed how vitamin A could influence preadipocyte differentiation. High levels of vitamins A and D can act in the nucleus of the cell to inhibit the conversion of preadipocytes to adipocytes, which eventually are detected as marbling.

The logical question to ask is if vitamin A and D levels in the diet don't change with season of the year, why should we suspect that they influence seasonal quality grade trends? The answer lies in the fact that the lowest point on the seasonal quality grade pattern is usually in the fall. If you count back 4-5 months, those cattle will often enter the feedlot in late spring or early summer. The majority of those cattle will have been on lush growing grasses or wheat pasture that can have 100,000-300,000 IU vitamin A activity per kilogram (NRC, 1989). Kohlmeier and Burroughs (1970) evaluated the depletion rate of plasma vitamin A of steers coming off wheat pasture or grass-legume hay diets (Figure 4). The feedlot diets were low in vitamin A activity (2.4 mg carotene/kg).

Figure 4. Plasma Vitamin A Levels of Cattle in the Feedlot after Grazing Wheat Pasture or Dried Grass (Kohlmeier and Burroughs, 1970)

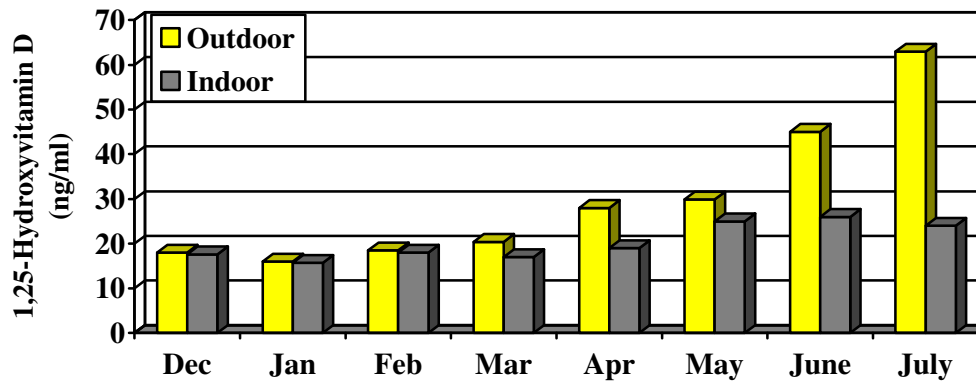


Cattle grazing wheat pasture had greater circulating plasma vitamin A at placement, requiring over 84 d to diminish levels to placement concentrations of hay-fed steers. Only at 140 days did plasma vitamin A levels approach those observed as increasing marbling in the Adachi (1999) trial. Galyean and Gleghorn (2001) summarized vitamin A data from 13 consulting nutritionist that indicated their receiving diets averaged 3,660 IU/lb (range 1,600 to 7,000) and typical finishing diets averaged 2,070 IU/lb (range 1,500 to 3,300). These concentrations of supplemental vitamin A may be slowing adipocyte differentiation, especially in cattle entering the feedlot in spring or summer coming off lush forages. The vitamin A requirement for growing and finishing beef cattle is 1000 IU vitamin A activity per lb. of diet DM (NRC, 1996).

Vitamin D may be just as important as vitamin A in preventing adipocyte differentiation. Unfortunately, most of the circulating vitamin D in feedlot cattle comes from endogenous synthesis and not the diet. Hidioglou et al. (1979) reported plasma vitamin D₃ levels changed

with the season of the year in heifers fed grass-legume silage (Figure 5). Half the heifers were housed indoors and half were outdoors exposed to UV light.

Figure 5. Effects of Day Length on Plasma Vitamin D₃ (Hidiroglou et al., 1979)



This trial was conducted in Canada where the variation in sunlight between the shortest (December) and the longest (June) photoperiod is greater than for much of the U.S. However, cattle that were outside showed a dramatic increase in plasma vitamin D as the exposure to light increased. Cattle housed indoors should reflect the baseline level of vitamin D provided by the diet. Cattle that grade poorly in the fall will have been exposed to maximum sunlight in the late spring and summer. This will increase circulating vitamin D, which can inhibit adipocyte differentiation at a time which could then contribute to the poor grading in the fall.

Conclusions:

Understanding the mechanisms that allow for the production of cattle that are lean, yet deposit a high degree of marbling may enhance beef consumption, efficiency of production and profitability. Calves that are fed high starch diets early in life will have more marbling at the same backfat than calves grown on forages. Glucose and or propionate are the main energy sources for marbling. Acetate, which is increased by fiber fermentation in the rumen, is the main energy source for backfat. The amount of time cattle are gaining above their maximum protein deposition on a high starch diets is more important than age in determining if they will reach their genetic potential to marble. Feeding calves high starch-low fiber diets as creep feeds or as their total diet will favor marbling deposition. High levels of circulating vitamins A or D may inhibit the conversion of preadipocytes to adipocytes that can fill and be detected as marbling. Seasonal variation in vitamin A intake and endogenous synthesis of vitamin D may help explain why cattle slaughtered in the late summer and fall tend to grade lower than those harvested in the winter and spring. Factors affecting marbling deposition, include primarily genetics, nutrition, management and environment, and must be examined in an integrated systems approach to make practical recommendations.

Literature Cited:

Adachi, K., H. Kawano, K. Tsuno, Y. Nomura, N. Yamaoto, A. Arikawa, A. Ysuji, M. Adachi, T. Onimaru, and K. Ohwada. 1999. Relationship between serum biochemical values and marbling score in Japanese black steers. *J. Vet. Med. Sci.* 61:961-964.

- Anderson, Pete. 2001. Seasonality of performance and carcass data. Available at: <http://www.vetlife.com/vetlife/Partner/FramMacroLive>. Accessed on March 20, 2003.
- Baldwin, R.L., K.R. McLeod, T.H. Elsasser, S. Kahl, T.S. Rumsey, and M.N. Streeter. 2000. Influence of chlortetracycline and dietary protein on visceral organ mass of growing beef steers. *J. Anim. Sci.* 78:3169-3176.
- Cianzio, D.S., D.G. Topel, G.B. Whitehurst, D.C. Beitz, and H.L. Self. 1985. Adipose tissue and cellularity: changes in bovine adipocyte size and number. *J. Anim. Sci.* 60:970-976.
- Davis, S.R., T.N. Barry, and G.A. Hughson. 1981. Protein synthesis in tissues of growing lambs. *Brit. J. Nutr.* 46:409-419.
- Etherton, T.D. and C.M. Ewok. 1986. Stimulation of lipogenesis in bovine adipose tissue by insulin and insulin-like growth factor-I. *J. Anim. Sci.* 62:357-362.
- Faulkner, D.B., D.F. Hummel, D.D. Buskirk, L.L. Berger, D.F. Parrett, and G.F. Cmarik. 1994. Performance and nutrient metabolism by nursing calves supplemented with limited and unlimited corn or soyhulls. *J. Anim. Sci.* 72:470-477.
- Ferrell, C.L. and T.G. Jenkins. 1985. Cow type and the nutritional environment: nutritional aspects. *J. Anim. Sci.* 61:725-741.
- Ferrell, C.L., L.J. Koong, and J.A. Nienaber. 1986. Effect of previous nutrition on body composition and maintenance energy costs of growing lambs. *Brit. J. Nutr.* 56:595-605.
- Galyean, M.L. and J.F. Gleghorn. 2001. Summary of the 2000 Texas Tech University consulting nutritionist survey. Proc. High Plains Nutr. Council meeting. San Antonio, TX.
- Hood, R.L. and C.E. Allen. 1978. Lipogenesis in isolated intramuscular adipose tissue from four bovine muscles. *J. Anim. Sci.* 46:1626-1633.
- Hidiroglou, M., J.G. Proulx, and D. Roubos. 1979. 25-Hydroxyvitamin D in plasma of cattle. *J. Dairy Sci.* 62:1076-1080.
- Kawada, T., A. Naohito, K. Yasutomi, M. Katsuhiko, N. Sachiko, and S. Etsuro. 1990. Comparative investigation of vitamins and their analogues on terminal differentiation from preadipocytes to adipocytes of 3T3-L1 cells. *Comp. Biochem. Physiol.* 96A:323-326.
- Kawada, T., Y. Kamei, and E. Sugimoto. 1996. The possibility of active form of vitamins A and D as suppressors on adipocyte development via ligand-dependent transcriptional regulators. *Int. J. Obes. Relat. Metab. Disord.* 20(Suppl 3):S52-7.

- Kohlmeier, R.H. and W. Burroughs. 1970. Estimation of critical plasma and liver vitamin A levels in feedlot cattle with observation upon influences of body stores and daily dietary requirements. *J. Anim. Sci.* 30:1012-1018.
- Kreikemeier, K.K., J.A. Unruh, and T.P. Eck. 1998. Factors affecting the occurrence of dark-cutting beef and selected carcass traits in finished beef cattle. *J. Anim. Sci.* 76:388-395.
- Lopez, R., C.R. Krehbiel, M.G. Thomas, D.M. Hallford, D.H. Keisler, B.S. Obeidat, J.A. Hernandez, W.D. Bryant, M. Garcia and R. Flores. 2001. Effect of increasing level of dietary protein on serum concentrations of metabolic hormones and mammary development in Holstein heifers consuming a moderate-energy diet. *J. Dairy Sci.* 84(Suppl. 1):161.
- Myers, S.E., D.B. Faulkner, T.G. Nash, L.L. Berger, D.F. Parrett, and F.K. McKeith. 1999. Performance and carcass traits of early-weaned steers receiving either a pasture growing period or a finishing diet at weaning. *J. Anim. Sci.* 77:311-322.
- Myers, S.E., D.B. Faulkner, F.A. Ireland, and D.F. Parrett. 1999b. Comparison of three weaning ages on cow-calf performance and steer carcass traits. *J. Anim. Sci.* 77:323-329.
- NRC. 1989. *Nutrient Requirements of Dairy Cattle*. 6th Ed. National Academy Press. Washington, D.C.
- NRC. 1996. *Nutrient Requirements of Beef Cattle*. 7th Ed. National Academy Press. Washington, D.C.
- Oka A., T. Miki, Y. Maruo, M. Yamasaki, R. Ariyoshi, and H. Fujii. 1992. Effects of vitamin A on the quality of Japanese bovine marbling. *J. Clin. Veter. Med.* 10:34-40.
- Okine, E.K. and P.F. Arthur. Does the amount and rate of fatty acid deposition in ruminants depend on the type of diet or energy level of the diet? Available: <http://www.agric.gov.ab.ca/reseach/reseachupdate/97beef28.html>. Accessed: March 20, 2003.
- Prior, R.L. 1983. Lipogenesis and adipose tissue cellularity in steers switched from alfalfa hay to high concentrate diets. *J. Anim. Sci.* 56:483-492.
- Pyatt, N.A., L.L. Berger, D.B. Faulkner, and P.M. Walker. 2004. Factors contributing to carcass value and profitability in early-weaned Simmental steers. *J. Anim. Sci.* 82(Suppl. 2):accepted.
- Richards, C.J., K.C. Swanson, S.J. Paton, D.L. Harmon, and G.B. Huntington. 2003. Pancreatic exocrine secretion in steers infused postruminally with casein and cornstarch. *J. Anim. Sci.* 81:1051-1056.

- Schoonmaker, J.P., S.C. Loerch, F.L. Fluharty, T.B. Turner, S.J. Moeller, J.E. Rossi, W.R. Dayton, M.R. Hathaway, and D.M. Wulf. 2002. Effect of an accelerated finishing program on performance, carcass characteristics, and circulating insulin-like growth factor I concentration of early-weaned bulls and steers. *J. Anim. Sci.* 80:900-910.
- Shike, D.W., D.B. Faulkner, D.F. Parrett, F.A. Ireland, and M.J. Cecava. 2003. Influence of weaning age, creep feeding and type of creep on steer performance and carcass traits. *J. Anim. Sci.* 81(Suppl. 2):46-47.
- Smith, S.B. and J.D. Crouse. 1984. Relative contributions of acetate, lactate, and glucose to lipogenesis in bovine intramuscular and subcutaneous adipose tissue. *J. Nutr.* 114:792-800.
- Trenkle, A. 1970. Effects of short-chain fatty acids, feeding, fasting, and type of diet on plasma insulin levels. *J. Nutr.* 100:1323-1330.
- Wertz, A.E., L.L. Berger, P.M. Walker, D.B. Faulkner, F.K. McKeith, and S.L. Rodriguez-Zas. 2001. Early weaning and post weaning nutritional management affect feedlot performance of Angus X Simmental heifers and the relationship of 12th rib fat and marbling score to feed efficiency. *J. Anim. Sci.* 79:1660-1669.
- Wertz, A.E., L.L. Berger, P.M. Walker, D.B. Faulkner, F.K. McKeith, and S.L. Rodriguez-Zas. 2002. Early-weaning and postweaning nutritional management affect feedlot performance, carcass merit, and the relationship of 12th-rib fat, marbling score, and feed efficiency among Angus and Wagyu heifers. *J. Anim. Sci.* 80:28-37.
- Yano, H., S. Tanaka, S. Torli, M. Ohyama, N. Hino, and T. Matsui. 2000. Some factors to regulate adipocyte differentiation in beef cattle in relation to intramuscular fat accumulation. *Asian-Aus. J. Anim. Sci.* 13:219-226.