Effect of low vitamin A diets with high-moisture or dry corn on marbling and adipose tissue fatty acid composition of beef steers

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ABSTRACT: Angus-cross steers (n = 165; 295 ± 16 kg of BW) were used evaluate the effect of low vitamin A diets with high-moisture corn (HMC) or dry corn (DC) on marbling and fatty acid composition. Steers were allotted to 24 pens (7 steers/pen), such that each pen had the same average initial BW. Treatments were randomly allotted to the pens. The experiment had a completely randomized design, with a 2 × 2 factorial arrangement of treatments: low vitamin A (Lo, no supplemental vitamin A) and HMC (LoHMC); LoDC; high vitamin A (Hi, supplemented with 2,200 IU of vitamin A/kg of DM) and HMC (HiHMC); and HiDC. Diets contained 76% corn, 10% corn silage, 11% protein supplement, and 3% soybean oil (DM basis). Samples of feed ingredients were collected for carotenoid analysis. Blood samples were collected for serum retinol determination. Steers were slaughtered after 145 d on feed. Carcass characteristics and LM composition were determined. Samples from the s.c. fat depot were analyzed for fatty acid composition. High-moisture corn had a greater vitamin A content, based on its carotenoid content, than DC (614 vs. 366 IU/kg of DM, $P < 0.01$). No vitamin A × corn type interactions were detected for feedlot performance, carcass characteristics, or serum, s.c. fat, or liver retinol concentration. Average daily gain, DMI, and G:F were not affected by vitamin A ($P > 0.05$). Marbling score and USDA quality grade were greater ($P < 0.05$) in Lo vs. Hi steers. Hot carcass weight, backfat, and yield grade were not affected by the treatments ($P > 0.05$). Vitamin A and corn type did not affect LM composition (DM, ash, CP, or ether-extractable fat, $P > 0.05$). Vitamin A supplementation increased ($P < 0.06$) serum retinol on d 112 and 145 and increased ($P < 0.01$) liver retinol at slaughter (Lo = 38.7 vs. Hi = 102.9 μg/g). The s.c. fat retinol concentrations were less ($P < 0.01$) for Lo (0.8 μg/g) than for Hi (1.4 μg/g) at slaughter. Cell diameter of adipocytes in the i.m. depot was not affected by dietary vitamin A ($P > 0.05$). A vitamin A × corn type interaction was observed ($P < 0.05$) for the s.c. fat cellularity. Feeding HMC increased the number of cells per square millimeter when Lo diets were fed (LoHMC = 128 vs. LoDC = 100 cells/mm^2, $P < 0.05$), but not when Hi diets were fed (HiHMC = 109 vs. HiDC = 111 cells/mm^2, $P > 0.05$). The CLA content of adipose tissue was not affected by the treatments. Regardless of the corn type used, feeding low vitamin A diets for 145 d to Angus-cross steers increased marbling and quality grade without affecting yield grade, animal health, or performance.

Key words: beef, corn, marbling, vitamin A

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INTRODUCTION

Beef production is evolving to meet consumer demand for a higher quality product in terms of both quality and nutrient composition. Quality is associated with increasing the amount of i.m. fat, or marbling. Nutrient composition can be enhanced by increasing the concentration of CLA in beef, because CLA appears to possess anticarcinogenic and antidiabetic properties (Houseknecht et al., 1998). Feeding low vitamin A diets may be a management strategy to achieve these goals. We recently reported that low vitamin A diets can increase i.m. fat without affecting s.c. fat deposition under typical US feedlot conditions (Gorocica-Buenfil et al., 2007a,b). In those experiments we fed high-moisture corn (**HMC**) rather than dry corn (**DC**) to reduce the intake of provitamin A carotenoids from the basal dietary ingredients. Dry corn is more commonly fed to cattle than HMC. No direct comparisons between HMC and DC have been reported in the literature to determine their effect in low vitamin A diets on marbling in beef. Furthermore, the assumption that carotenoids are lower in HMC than in DC (NRC, 1996) may not be

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correct. Accurate characterization of the carotenoid content of HMC and many other feedstuffs is limiting.

The vitamin A precursor, β-carotene, has been reported to reduce the activity of desaturase enzyme activity (Alam and Alam, 1985). Therefore, feeding low amounts of vitamin A may increase desaturase activity, thus increasing the CLA content of ruminant products.

The objectives of this experiment were 1) to determine the effect of corn source (HMC vs. DC) and vitamin A supplementation (0 vs. 2,200 IU/kg of DM) on the distribution, fatty acid composition, and cellularity of beef adipose tissue; and 2) to determine the provitamin A carotenoid composition of HMC and DC. It was hypothesized that 1) low vitamin A diets would increase i.m. fat and CLA deposition without affecting s.c. fat deposition or animal health; and 2) beneficial effects of low vitamin A intake would be magnified when HMC rather than DC was fed because of their differing carotenoid content.

MATERIALS AND METHODS

Animal care followed guidelines recommended by the Federation of Animal Science Societies (1998).

A cattle performance experiment was initiated in November 2005 at the Ohio State University feedlot in Wooster, OH. A total of 168 Angus-cross steers (initial BW 295 ± 15.8 kg) were randomly allotted to one of the following experimental treatments: low vitamin A (Lo, no supplemental vitamin A) and HMC (LoHMC); low vitamin A and DC (LoDC); high vitamin A (Hi, supplemented at 2,200 IU of vitamin A/kg of DM) and HMC (HiHMC); and high vitamin A and DC (HiDC). The composition of the experimental diets is shown in Table 1. Both HMC and DC were fed whole, although, based on visual appraisal, approximately 30% of HMC kernels were broken. Diets were offered for ad libitum intake throughout the trial. Soybean oil was included in the diet as a source of linoleic acid for the synthesis of CLA.

Steers were distributed into 24 pens, with 7 steers per pen. Pens (5.4 × 5.4 m) were constructed of metal gates and cable, had concrete-slatted floors, and were located in an open-sided barn.

Six weeks before arrival at the feedlot, steers were vaccinated for infectious bovine rhinotracheitis, parainfluenza-3, *Histophilus somni, Pasteurella,* and *Clostridia* (Quadraplex, Somnugen 2P, and Dybelon, respectively; Bioceutic, St. Joseph, MO), and treated against parasites with Ivomec pour-on (Merial, Duluth, GA). Steers were revaccinated 14 d later. Before initiation of the trial, all steers received the same 65% concentrate receiving diet for 40 d. Supplemental vitamin A concentration in the receiving diet was 2,200 IU/kg of DM. After adaptation was completed, steers were weighed on 2 consecutive days to determine initial BW, and the second initial weighing day was considered d 1 of the experiment. Steers were weighed every 14 d, and at the end of the experiment they were weighed on 2 consecutive days to determine final BW. Steers were weighed

Table 1. Diet composition

Item	Diet[1]			
	LoHMC	HiHMC	LoDC	HiDC
Ingredient	% of DM			
Corn, high moisture	76.00	76.00	—	—
Corn, whole shelled	—	—	76.00	76.00
Corn silage	10.00	10.00	10.00	10.00
Soybean oil	3.00	3.00	3.00	3.00
Soybean meal, 44%	7.40	7.39	7.40	7.39
Urea	1.05	1.05	1.05	1.05
Limestone	1.42	1.42	1.42	1.42
Trace mineral salt[2]	0.48	0.48	0.48	0.48
Vitamin A, 30,000 IU/g	—	0.0075	—	0.0075
Vitamin D, 3,000 IU/g	0.009	0.009	0.009	0.009
Vitamin E, 44 IU/g	0.028	0.028	0.028	0.028
Selenium premix, 201 mg/kg	0.048	0.048	0.048	0.048
Rumensin-80[3]	0.017	0.017	0.017	0.017
Tylan-10[3]	0.048	0.048	0.048	0.048
Potassium chloride	0.39	0.39	0.39	0.39
Animal-vegetable fat	0.11	0.11	0.11	0.11
Nutrient composition				
DM, %	65.5	65.5	79.5	79.5
OM, %	95.6	95.8	95.9	96.1
CP, %	13.1	13.0	13.4	13.2
NDF, %	12.4	12.4	12.4	12.4
Vitamin A,[4] kIU/kg	1.3	3.6	1.1	3.4
Calcium,[5] %	0.55	0.55	0.55	0.55
Phosphorus,[5] %	0.31	0.31	0.31	0.31
Potassium,[5] %	0.71	0.71	0.71	0.71
NE_m,[5] Mcal/kg	2.234	2.234	2.234	2.234
NE_g,[5] Mcal/kg	1.547	1.547	1.547	1.547

[1]LoHMC = low vitamin A (Lo, no supplemental vitamin A) and high-moisture corn (HMC); HiHMC = high vitamin A (Hi, supplemented at 2,200 IU of vitamin A/kg of DM) and HMC; LoDC = low vitamin A and dry corn (DC); and HiDC = high vitamin A and DC.

[2]Contained >93% NaCl, 0.35% Zn, 0.28% Mn, 0.175% Fe, 0.035% Cu, 0.007% I, and 0.007% Co.

[3]Elanco (Greenfield, IN).

[4]Calculated based on the values reported in Table 2.

[5]Calculated by using NRC (1996) values.

before feeding at 0800 and were not withheld from feed or water. Steers were monitored daily for signs of respiratory disease (nasal mucous discharge, coughing, and rapid breathing). Body weight was monitored at 14-d intervals to identify animals that might have lost weight. Any animal exhibiting the above signs and having a body temperature above 39.7°C was treated with antibiotics. Although not anticipated, animals were monitored daily for signs of blindness (watery, swollen eyes; disoriented). All health problems were recorded. Steers were implanted on d 1 and reimplanted on d 112 with Synovex-S (20 mg of estradiol benzoate, 200 mg of progesterone; Fort Dodge Animal Health, Overland Park, KS).

Steers were offered feed once daily beginning at 0800. Daily intake was recorded, and feedstuff samples were collected weekly to adjust dietary DM and determine DMI. Diet samples were collected every 2 wk and composited at the end of the trial for nutrient analysis. Composite feed samples were freeze-dried, ground to

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pass through a 1-mm screen, and analyzed for DM, OM, and N (AOAC, 1996).

Samples of corn silage, protein supplement, HMC, and DC were collected every 2 wk for analysis of provitamin A carotenoids (β-cryptoxanthin, and α- and β-carotene). Samples were taken from the feed mixer immediately before ingredients were mixed for the day's feeding. Samples were put in plastic bags, kept in the dark to avoid light damage to the carotenoids, and stored frozen at –20°C until carotenoid analyses were performed.

For the carotenoid analysis, all chemicals used were of analytical grade or superior. Unless otherwise stated, all chemicals were obtained from Sigma (St. Louis, MO). All analyses were carried out on ice and under dim light. Extraction of carotenoids from feed samples was based on a modified method described by Ferruzzi et al. (1998). Briefly, approximately 200 g of sample material was transferred into a blender (Blend Master, Hamilton Beach, Washington, NC) and ground for 4 min. An aliquot of 1.5 to 2.0 g was then weighed into a 16-mL centrifuge tube, and 300 mg of calcium carbonate and 10 mL of methanol were added. After 3 min of sonication and vortexing, samples were centrifuged for 5 min at 1,000 × *g* at room temperature (IEC HN-SII centrifuge, Damon IEC, Needham, MA). All supernatant was pipetted into a 50-mL centrifuge tube, and the extraction was repeated twice with 10 mL of hexane/acetone (1:1, vol/vol). To the combined extracts was added 20 mL of saturated aqueous sodium chloride solution, and the mixture was carefully shaken for 2 min and centrifuged to facilitate phase separation. The supernatant hexane phase was transferred into a graded 16-mL centrifuge tube, and the lower watery phase was reextracted with 10 mL of hexane and combined with the first extract. A 5-mL aliquot was pipetted from the combined extracts into a 10-mL glass vial, evaporated to dryness under a stream of N_2, overlayered with argon, and sealed. All samples were stored at –80°C until analysis. For HPLC analysis, samples were reconstituted in 1 mL of methanol:methyl *t*-butyl ether (**MTBE**), 70:30 (vol/vol), and filtered through 0.2-μm nylon filters. All samples were run in duplicate, and means are reported.

The β-carotene, α-carotene, and β-cryptoxanthin in the extracted feed samples and standards (Sigma) were analyzed following a modified method described by Sander et al. (1994). Detection and quantification was achieved by HPLC (Waters 2996, Waters, Milford, MA) in combination with a photodiode array detector (Waters 2996). For HPLC separation, a YMC carotenoid C-30 column (150 × 4.6 mm, 5-μm particle size, Waters) was used in combination with gradient elution of methanol:water:ammonium acetate buffer:MTBE (88:5:2:5, by vol, A) and MTBE:methanol:water:ammonium acetate buffer (79:16:3:2, by vol, B) changing from 100% A (0 to 5 min) to 65% B (during min 5 to 21), changing to 100% B until min 29, holding this constant for 1 min, changing back to 100% A until min 31, and keeping this for 4 min. The flow rate was 1.2 mL/min, the temperature was 27.5°C, and the injection volume was 75 μL. Quantification was based on external calibration curves by using their specific absorption coefficients (Weast, 1973).

Blood samples were collected from all steers on d 0, d 112, and at slaughter to determine serum retinol concentrations. Ten-milliliter blood samples were taken from the jugular vein. Tubes containing blood samples were immediately wrapped in aluminum foil to avoid retinol light damage and were kept on ice until reaching the laboratory for serum harvest. Serum was obtained by centrifuging blood samples at 2,200 × *g* at 4°C for 10 min. Samples were frozen at –20°C until vitamin A analyses were performed by HPLC. Hepatic and s.c. fat vitamin A stores were also determined. Liver and s.c. fat samples were collected at slaughter and were immediately placed on ice and protected from light damage. Samples were stored at –20°C. Hepatic, s.c. fat, and serum vitamin A concentrations were analyzed by HPLC, as previously described (Gorocica-Buenfil et al., 2007b). All-*trans* retinol obtained from Sigma Chemical Co. was used as the standard.

Steers were slaughtered after 145 d on feed when the backfat (**BF**) of all steers was visually estimated to average approximately 1.27 cm. Hot carcass weight, BF, LM area, and KPH were determined by qualified Ohio State University personnel. Carcass yield grade (**YG**) was calculated (USDA, 1997). Quality grade and marbling score were determined by a USDA official. Carcass characteristics were measured after a 48-h chill.

Longissimus muscle from the 11th to 12th thoracic ribs was collected, trimmed of external fat, and ground (Hobart model #4822, Hobart Co., Troy, OH), and samples were analyzed for moisture, ash, protein, and ether-extractable lipid (**EE**) content (AOAC, 1996). Additionally, fatty acids in s.c. adipose tissue were extracted and methylated by alkaline transesterification and analyzed as described by Kramer et al. (1997). Methyl esters of fatty acids were separated on a 0.25-mm × 100-m fused-silica column (Supelco, Inc., Bellefonte, PA) with a Hewlett-Packard 5890 gas chromatograph with automated injection and data reduction (HP 3365 ChemStation software, Hewlett-Packard Co., Santa Clarita, CA). Standards for the CLA isomers *cis*-9, *trans*-11; *trans*-10, *cis*-12; and *trans*-9, *trans*-11 were obtained from Matreya Inc. (Pleasant Gap, PA).

Subcutaneous and i.m. adipose tissue were collected from the sixth to eighth thoracic ribs after a 48-h chill. These samples were stored at –20°C until adipose cellularity analysis. To determine adipocyte size and number, frozen adipose tissue samples were fixed and sectioned at a thickness of 8 μm in a CM1900 Leica cryostat (Meyer Instruments Inc., Houston, TX). Samples were mounted on Superfrost Plus slides (Fisher, Pittsburgh, PA) and stained with a hematoxylin and eosin solution (Merck, Darmstadt, Germany). Cell number and mean cell diameter were determined by computerized image

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Table 2. Provitamin A carotenoid content of the diet ingredients

Ingredient	Samples, n	β-Cryptoxanthin[1]	α-Carotene[1]	β-Carotene[1,2]	Vitamin A[3,4]
		Mean ± SD			
High-moisture corn	12	78.9 ± 6.0	42.6 ± 6.2	92.8 ± 8.2	614 ± 37
Dry corn	9	56.1 ± 3.7	24.2 ± 4.4	51.4 ± 4.3	366 ± 29
Corn silage	1	78.3	ND[5]	2,098.3	8,550
Supplement	2	0.7 ± 1.0	1.4 ± 0.62	9.6 ± 5.8	43 ± 22

[1]Expressed as μg/100 g of DM.
[2]Includes 9 *cis* and all-*trans* β-carotene.
[3]Expressed as IU/kg of DM.
[4]Calculated as: 1 mg of β-carotene = 400 IU of vitamin A; 1 mg of β-cryptoxanthin = 200 IU of vitamin A; 1 mg of α-carotene = 200 IU of vitamin A (FAO/WHO Joint Expert Consultation, 1988; NRC, 1996).
[5]Not detected.

analysis (Image-Pro Plus v. 4.5, MediaCybernetics Inc., Silver Spring, MD).

Experimental data were analyzed by using the MIXED procedure (SAS Inst. Inc., Cary, NC). Serum retinol data were analyzed in a completely randomized design with repeated measures. The model included terms for vitamin A concentration, corn type, days on feed at the time of sample collection, and their respective interactions. The error structure used was autoregressive, because it resulted in the lowest Bayesian criteria. Time effects were partitioned into linear and quadratic contrasts. Regressions for marbling score and serum and liver retinol were calculated by using the REG procedure of SAS.

Feedlot performance, carcass characteristics, fatty acid composition, and adipose cellularity data were analyzed as a completely randomized design. The model included the main effects of vitamin A concentration and corn type and their interaction. For the cellularity analysis, the fat depot (i.m. or s.c.) term and its respective interactions also were included in the model. Treatment means were compared by using the PDIFF statement of SAS when protected by a significant ($P < 0.05$) F-value. Pen was used as the experimental unit for all statistical analyses.

RESULTS AND DISCUSSION

Ingredients of plant origin do not have considerable amounts of vitamin A, but may contain significant quantities of biological vitamin A precursors, such as β-carotene. Dry corn is the most common ingredient in feedlot cattle diets in the United States, especially in the Midwest region. Dry corn was reported to have 600 to 1,000 IU of vitamin A precursors/kg (Egesel et al., 2003).

Assessment of the vitamin A and carotenoid content of major feed ingredients now used in cattle diets has been neglected for years. The provitamin A carotenoid content of diet ingredients used in the present trial is presented in Table 2. To our knowledge, this is the first report of the content of provitamin A carotenoids of HMC published in the literature. The carotenoid content of DC was lower than previously reported (Egesel et al., 2003), perhaps reflecting carotenoid degradation during the forced-air drying process before corn storage in feed bins. Surprisingly, all provitamin A carotenoids (e.g., β-cryptoxanthin, α-carotene, and β-carotene) were numerically higher in HMC than in DC. In the NRC (1996) ingredient list, the DC vitamin A content is listed as 1,000 IU/kg of DM. High-moisture corn vitamin A is not presented. It is possible that forced-air drying degrades provitamin A carotenoids more extensively than fermentation during HMC storage. However, the factors affecting the content of carotenoids in HMC and DC remain to be determined. Many factors influence the carotenoid composition of feeds. Many preharvest conditions (seed variety, environmental and agronomical conditions, etc.) affect the carotenoid composition of corn (Aurand et al., 1947). Postharvest conditions (temperature, humidity, and duration of storage) can also affect carotenoid composition (Porteb et al., 1946), but the importance of these factors in relation to the final carotenoid content requires further research. In this experiment the provitamin A content of both HMC and DC was relatively low [provided less than 30% of the NRC (1996) recommendation for beef cattle]. Improving our understanding of carotenoid losses during storage is necessary to accurately formulate diets for vitamin A content. Furthermore, in view of the promising effects of low vitamin A diets to increase marbling (Gorocica-Buenfil et al., 2007a,b), an updated and more accurate estimate of the carotenoid composition of feedstuffs used by the beef industry is required. The fact that all analyzed ingredients differed considerably from the values listed by the NRC (1996) reflects the need to update these values by using modern techniques, such as the HPLC method reported in the current experiment.

No vitamin A × corn type interactions ($P > 0.19$) were observed for feedlot performance, carcass characteristics, LM composition, or fatty acid composition of s.c. fat. In addition, no vitamin A × corn type interactions ($P > 0.17$) were observed for serum, liver, and s.c. fat retinol. Therefore, the main effects are presented and discussed. Feedlot performance data are presented in

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Table 3. Main effects of dietary vitamin A concentration and corn type on feedlot performance of Angus-cross steers

	Vitamin A[1]		Corn type[2]			P-value[3]		
Item	Lo	Hi	DC	HMC	SEM	VA	CT	VA × CT
BW, kg								
Initial	300.0	299.8	300.0	299.7	0.72	0.86	0.76	0.09
Final	554.2	555.7	551.6	558.3	4.50	0.81	0.30	0.82
ADG, kg/d	1.70	1.72	1.69	1.73	0.016	0.62	0.08	0.37
DMI, kg/d	8.3	8.3	8.4	8.2	0.067	0.99	0.05	0.89
G:F, g/kg	205.9	207.5	201.6	211.8	2.3	0.63	<0.01	0.49

[1]Lo = no supplemental vitamin A, and Hi = vitamin A supplemented at 2,200 IU/kg of DM.
[2]DC = dry corn, and HMC = high-moisture corn.
[3]VA = vitamin A, and CT = corn type.

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Table 3. Vitamin A concentration did not affect ADG, DMI, or G:F ($P > 0.62$). No mortality, morbidity, or health problems were noted in this experiment. This is the third feeding experiment in which we have tested feeding diets with a vitamin A content below the NRC (1996) recommended concentration of 2,200 IU/kg of DM. In the present experiment, Lo diets averaged 1,200 IU of vitamin A and Hi diets averaged 3,500 IU of vitamin A/kg of DM (Table 1). We have not observed a reduction in animal performance or any adverse effect on animal health (not a single case of blindness, greater morbidity, etc.) in any of these experiments. The vitamin A requirements of growing cattle are poorly defined. The NRC (1996) recommendation is based on requirements established in 1976 (NRC, 1976). The NRC (1976) recommendation was based on sparse information published more than 35 yr ago (Perry et al., 1965, 1968; Eaton et al., 1972) when modern techniques to assess vitamin A status (such as HPLC and mass spectrometry) were not used. Considering our current findings, a more precise determination of vitamin A requirements for growing cattle is warranted.

Gain:feed was greater ($P < 0.01$) when HMC was fed. Steers fed HMC had lower DMI ($P = 0.05$) and tended ($P = 0.08$) to have greater ADG than those fed DC, reflecting the more extensive ruminal fermentation and whole-tract starch digestibility of HMC (Stock et al., 1987; Ladely et al., 1995). Because of its greater starch digestibility, HMC has a greater NE_g content. Thus, less feed based on HMC was required to achieve a weight gain similar to that achieved with feed based on DC.

Carcass characteristics are presented in Table 4. Hot carcass weight, BF, KPH, and YG were not affected ($P > 0.10$) by vitamin A or corn type. Marbling score was increased ($P = 0.02$) by approximately a third of a grade when Lo diets were fed. This resulted in increased quality grades in Lo steers ($P = 0.02$), almost doubling the percentage of carcasses grading average Choice or above (Lo = 27.8 vs. Hi = 15.7%, $P = 0.10$). This is the third consecutive experiment in which we have observed a significant improvement of either marbling score or quality grade when low vitamin A diets were fed. Furthermore, in this experiment and in our previous experiments, we have reported that feeding low vitamin A diets does not affect carcass BF and YG, or edible carcass composition (Gorocica-Buenfil, 2007a,b). Taken together, our results suggest that feeding low vitamin A diets may be an effective strategy to modulate the site of fat deposition in feedlot cattle, increasing i.m. fat deposition without affecting deposition in the s.c. depot.

To illustrate the relevance of these findings, the value of each carcass was calculated by using a grid price formula published by the USDA Market News Service for the week the animals were slaughtered (USDA Market News Service, 2006). On average, Lo carcasses were valued at $12.80 above Hi carcasses. Although this difference was not statistically significant ($P > 0.10$) and would vary depending on current market prices, the economic relevance of this finding should not be ignored and deserves further investigation.

Corn type did not affect any of the measured carcass characteristics ($P > 0.05$). However, feeding HMC numerically increased HCW and tended ($P = 0.08$) to increase the percentage of carcasses grading Choice$^-$ or above. Thus, when calculating carcass value as previously described, carcasses from steers fed HMC tended to have a greater value than those fed DC (HMC = $1,064.2 vs. DC = $1,035.4, $P = 0.11$).

Longissimus muscle compositions are presented in Table 5. Neither dietary vitamin A concentration nor corn type affected LM moisture content, ash, CP, or EE ($P > 0.05$). Determination of EE objectively measures the fat content of muscle. Thus, EE was expected to be greater in Lo vs. Hi steers based on the observed marbling scores. Although numerically greater, LM fat was not significantly greater in Lo vs. Hi steers. Furthermore, marbling score and muscle EE were not significantly correlated in this experiment (data not shown). The lack of agreement between marbling score and LM EE was reported in our previous experiments (Gorocica-Buenfil et al., 2007a,b). We hypothesized that low vitamin A diets would increase marbling by stimulating adipocyte differentiation in the i.m. depot. Increased adipocyte differentiation may increase the pres-

Table 4. Main effects of dietary vitamin A concentration and corn type on carcass characteristics of Angus-cross steers

	Vitamin A[1]		Corn type[2]			P value[3]		
Item	Lo	Hi	DC	HMC	SEM	VA	CT	VA × CT
HCW, kg	343.1	342.6	340.5	345.2	3.3	0.92	0.33	0.80
Backfat, cm	1.35	1.37	1.32	1.40	0.052	0.75	0.29	0.89
Dressing, %	61.9	61.6	61.7	61.8	0.18	0.33	0.68	0.87
Marbling score[4]	556	525	534	548	8.2	0.02	0.24	0.79
LM area, cm^2	80.5	80.6	79.4	81.7	0.97	0.94	0.10	0.19
KPH, %	2.34	2.40	2.29	2.45	0.16	0.81	0.50	0.60
Yield grade	3.18	3.19	3.17	3.20	0.089	0.90	0.79	0.70
Quality grade[5]	5.18	4.89	4.95	5.12	0.087	0.02	0.19	0.43
Select, %	27.0	31.2	33.9	24.2	3.8	0.45	0.08	0.40
Choice$^-$, %	45.2	53.2	47.8	50.6	5.4	0.31	0.72	0.57
Choice^o,%	16.7	12.1	10.9	17.9	4.7	0.50	0.31	0.75
Choice$^+$, %	5.0	3.6	5.0	3.6	2.1	0.64	0.64	0.74
Prime, %	6.2	0.0	2.4	3.8	1.6	0.01	0.55	0.55
≥Choice$^-$, %	73.0	68.9	66.1	75.8	3.8	0.44	0.08	0.40
≥Choice^o, %	27.8	15.7	18.3	25.2	5.0	0.10	0.34	0.98
Carcass value[6]								
$/carcass	1,056	1,043	1,035	1,064	12.4	0.47	0.11	0.51
$/45 kg	139.6	138.1	137.9	139.9	1.37	0.31	0.16	0.47

[1]Lo = no supplemental vitamin A, and Hi = vitamin A supplemented at 2,200 IU/kg of DM.
[2]DC = dry corn, and HMC = high-moisture corn.
[3]VA = vitamin A, and CT = corn type.
[4]Slight = 400 to 499, small = 500 to 599, modest = 600 to 699, and moderate = 700 to 799.
[5]4 = Select, 5 = Choice$^-$, 6 = Choice^o, 7 = Choice$^+$, and 8 = Prime$^-$.
[6]Based on HCW and the grid price formula published by the USDA Market News Service for the week of May 22, 2006: base price was $144.59/45 kg [Choice$^-$, yield grade (YG) 3.0]; premiums: Prime = $8.77/45 kg, Choice$^{o,+}$ = $4.37/45 kg; YG 1.0–1.9 = $2.75/45 kg; YG 2.0–2.5 = $1.32/45 kg; discounts: Select = –$19.67/45 kg; and YG 4.0–4.9 = –$13.27/45 kg.

ence of marbling flecks, which determines carcass quality grade as a first step, and then those small depots are enlarged as the adipocytes fill with triglycerides. If carcass quality is determined before the newly differentiated adipocytes undergo hypertrophy, it is possible that the EE may not change as notably as the marbling score. When determining the marbling score, the even distribution of small marbling flecks is more important than the presence of a single big marbling fleck in the LM. Conversely, for muscle EE composition, the presence of big marbling flecks may have a greater influence than the presence of more abundant, smaller flecks. Thus, it could be hypothesized that had days on feed been longer in this experiment, i.m. adipocytes of Lo steers would have had a greater degree of hypertrophy. Under this hypothesis, both marbling score and muscle EE would be greater in Lo compared with Hi steers with more days on feed. It can also be argued that in this experiment, the muscle EE had greater variability than marbling score based on the CV for these traits. A greater number of replications may be required to reach statistical significance in both marbling score and muscle EE.

Serum, liver, and s.c. retinol contents are presented in Table 6. Serum retinol concentrations on d 112 were 20% lower ($P < 0.02$) and tended ($P = 0.06$) to be lower at slaughter (d 145) in Lo steers compared with Hi steers. When Angus-based steers were fed a vitamin A-

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Table 5. Main effects of dietary vitamin A concentration and corn type on LM composition of Angus-cross steers

	Vitamin A[2]		Corn type[3]			P-value[4]		
Item[1]	Lo	Hi	DC	HMC	SEM	VA	CT	VA × CT
DM, %	30.2	30.0	30.0	30.1	0.17	0.35	0.72	0.89
Ash, %	4.9	4.8	4.9	4.8	0.45	0.98	0.76	0.26
CP, %	19.6	20.1	19.9	19.7	0.20	0.09	0.71	0.42
Ether extract, %	6.44	6.02	6.21	6.24	0.21	0.18	0.93	0.68

[1]As-is basis.
[2]Lo = no supplemental vitamin A, and Hi = vitamin A supplemented at 2,200 IU/kg of DM.
[3]DC = dry corn, and HMC = high-moisture corn.
[4]VA = vitamin A, and CT = corn type.

Table 6. Main effect of dietary vitamin A concentration and corn type on serum, liver, and s.c. fat retinol concentration in Angus-cross steers

	Vitamin A[1]		Corn type[2]			*P*-value[3]		
Item	Lo	Hi	DC	HMC	SEM	VA	CT	VA × CT
Serum retinol, μg/dL								
d 1	32.4	32.1	30.8	33.8	2.5	0.93	0.39	0.67
d 112	32.8	41.5	41.4	33.0	2.5	0.02	0.02	<0.01
d 145	31.9	39.0	36.9	33.6	2.5	0.06	0.34	0.22
Liver retinol, μg/g								
d 145	38.7	102.9	78.8	62.9	9.74	<0.01	0.26	0.83
s.c. fat retinol, μg/g								
d 145	0.79	1.41	1.05	1.15	0.14	<0.01	0.64	0.17

[1]Lo = no supplemental vitamin A, and Hi = vitamin A supplemented at 2,200 IU/kg of DM.
[2]DC = dry corn, and HMC = high-moisture corn.
[3]VA = vitamin A, and CT = corn type.

restricted diet for 168 d, serum retinol was significantly reduced at slaughter compared with nonrestricted steers (Gorocica-Buenfil et al., 2007a). In that experiment, vitamin A restriction reduced serum retinol after just 56 d on feed. Serum retinol is maintained relatively constant in the body because the liver stores and releases retinol to maintain normal bodily functions (Goodman and Blaner, 1984). Animals used in the current experiment were grazed on pasture before being transported and placed in the feedlot. Grazing animals are considered to have ample hepatic vitamin A stores, because green pastures are rich in the provitamin A carotenoid, β-carotene (Yang et al., 1992, 2002). To reduce serum retinol, hepatic vitamin A stores need to be depleted (Blaner and Olson, 1994). The lower ($P < 0.01$) liver retinol content of Lo vs. Hi steers suggests that hepatic vitamin A stores were becoming depleted but were still sufficient to partially attenuate serum retinol concentrations.

The vitamin A bioisomer, retinoic acid, has been shown both in vitro and in vivo to inhibit adipocyte differentiation (Sato et al., 1980; Bonet et al., 2003). The i.m. fat depot grows by both hypertrophy and hyperplasia during the finishing feeding period (Cianzio et al., 1985). We have hypothesized that feeding low vitamin A diets may increase adipocyte differentiation in the i.m. depot without greatly affecting the s.c. depot. The s.c. depot is considered to grow largely by hypertrophy during the finishing period (Hood and Allen, 1973; Cianzio et al., 1985); thus, any changes in hyperplasia during this period would not affect its development. We have speculated that to observe any changes in the site of fat deposition in growing cattle, liver stores and serum retinol concentrations would need to be depleted. The findings of this experiment support this assumption. Liver, and to a lesser degree serum retinol concentrations, at slaughter were lowered by dietary vitamin A restriction, whereas marbling score and quality grade were increased without changes in s.c. fat or YG. The duration and severity of vitamin A restriction required to observe changes in the site of fat deposition in growing cattle remain to be determined.

Japanese researchers have reported serum retinol to be negatively correlated with marbling score (Adachi et al., 1999; Oka et al., 1998). In the present experiment, the regressions between marbling score and serum or liver retinol were as follows: marbling score = 623 (±40) – 2.34 (±1.1) serum retinol, μg/dL ($P < 0.05$), and marbling score = 560 (±11) – 0.28 (±0.13) liver retinol, μg/g ($P < 0.05$). It is noteworthy that the negative relationships between marbling score and serum and liver retinol were significant. The nature of this negative relationship suggests that greater effects on marbling score could be expected if vitamin A stores were further reduced. Additional research in this field is advised to adjust current dietary recommendations to increase marbling and quality grade without incurring health or performance problems associated with vitamin A deficiencies.

Subcutaneous fat retinol was lower ($P < 0.01$) in Lo than in Hi steers in this experiment. Adipose tissue is the second largest retinol storage site in the body after the liver (Tsutsumi et al., 1992). Furthermore, because adipocyte differentiation takes place in this tissue, the retinol content of adipose tissue may modulate the extent of adipogenesis that occurs. In a previous experiment when Holstein steers were fed vitamin A-restricted diets for 243 d, serum and liver retinol, but not s.c. fat retinol, were reduced at slaughter (Gorocica-Buenfil et al., 2007b). Reasons for this discrepancy are not clear but could be due to improved extraction procedures in our laboratory for this experiment. In addition, differences between Angus-based and Holstein steers in s.c. fat retinol storage ability or responsiveness to dietary changes cannot be discounted.

Corn type did not affect ($P = 0.34$) serum retinol at slaughter. This lack of response in serum, liver, and s.c. fat to corn type can be explained by the relatively low content of vitamin A in both the HMC and DC diets. On d 112, a vitamin A × corn type interaction was observed ($P < 0.01$) for serum retinol. Steers fed the HiDC diet had significantly greater serum retinol concentrations than the other treatments (HiDC = 47.7; LoHMC = 30.6, LoDC = 35.0, HiHMC = 35.3 μg/dL).

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Table 7. Main effects of dietary vitamin A concentration and corn type on the i.m. adipose cellularity of Angus-cross steers

	Vitamin A[1]		Corn type[2]			*P*-value[3]		
Item[4]	Lo	Hi	DC	HMC	SEM	VA	CT	VA × CT
Cell number, per mm^2	163	171	179	154	9.4	0.71	0.02	0.45
Mean diameter, μm	85.8	84.9	82.0	88.8	2.5	0.70	<0.01	0.91
Cells ≤50 μm, % of total cells	20.7	21.8	23.3	19.2	2.8	0.70	0.15	0.47
Cells >50 and ≤100 μm, % of total cells	58.7	57.8	61.4	55.0	2.2	0.94	<0.01	0.57
Cells >100 μm, % of total cells	20.6	20.4	15.2	25.8	3.1	0.41	0.02	0.23

[1]Lo = no supplemental vitamin A, and Hi = vitamin A supplemented at 2,200 IU/kg of DM.
[2]DC = dry corn, and HMC = high-moisture corn.
[3]VA = vitamin A, and CT = corn type.
[4]Measured in hematoxylin- and eosin-stained adipose tissue slides (>1.5 mm^2/sample).

Reasons for this difference are unknown, but the fact that the interaction disappeared by d 145 ($P = 0.22$) suggests that the interaction on d 112 was spurious.

The effects of vitamin A restriction and corn type on i.m. fat cellularity are presented in Table 7. Vitamin A restriction did not affect mean adipocyte diameter or the number of adipocytes counted per square millimeter. The i.m. adipocyte distribution (according to adipocyte size) was not affected by vitamin A restriction (Figure 1). We previously reported evidence that vitamin A restriction increases i.m. adipocyte hyperplasia, which is the presumed mechanism of action by which low vitamin A diets increase marbling in growing cattle (Gorocica-Buenfil et al., 2007a). Results in this experiment do not support our previous observation. The increased marbling score in Lo steers suggests that the i.m. adipose depot was enlarged. Intramuscular fat is increased by a combination of both hypertrophy and hyperplasia. Our cellularity data do not provide evidence that hyperplasia occurred in the i.m. depot with 145 d of vitamin A restriction. However, hyperplasia in adipose tissue is difficult to estimate. Adipocyte differentiation is a dynamic process, and our ability to observe responses to dietary treatments may be hindered when histological methodologies, such as the one used in this experiment, are used. It is possible that vitamin A treatments affected i.m. adipose cellularity earlier in the feeding period, and those differences were no longer present at slaughter. Although we consider it unlikely based on information published in this area (Kumar et al., 1999; Felipe et al., 2003), low vitamin A diets may have stimulated hypertrophy in the i.m. depot.

The development of advanced techniques to evaluate the relative presence of hyperplasia in adipose tissue at different times during the feeding period is warranted. Feeding low vitamin A diets to increase marbling has potential as a technique that could be easily adopted by the beef industry. Improving our ability to understand the mechanisms of action prompting these responses is a necessary step to achieve that potential.

Corn type influenced i.m. adipose cellularity and the size-distribution pattern of adipocytes in the i.m. depot (Figure 2). Feeding DC reduced adipocyte diameter and

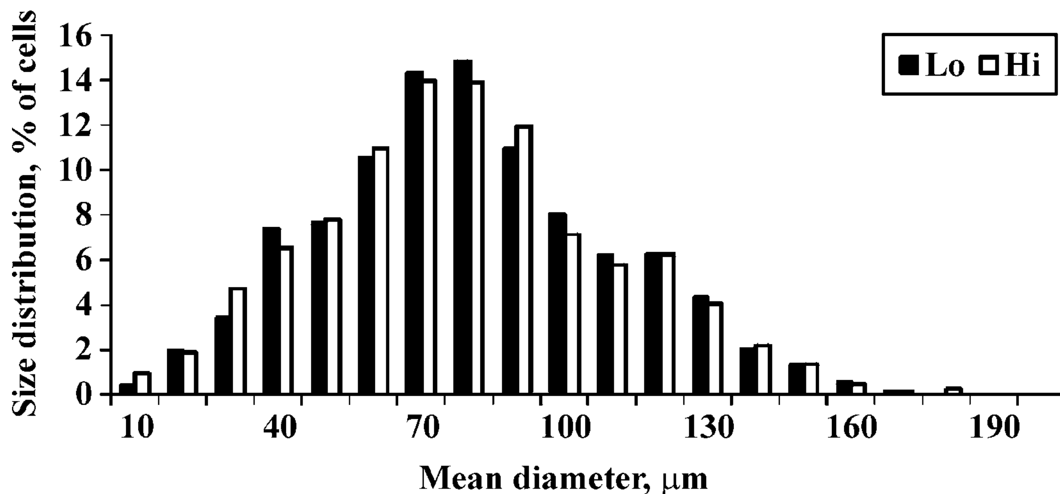

Figure 1. Main effect of dietary vitamin A concentration on i.m. adipocyte size distribution of Angus-crossbred steers. Treatment means do not differ, $P > 0.10$. Lo = no supplemental vitamin A, and Hi = supplemented with 2,200 IU of vitamin A/kg of DM.

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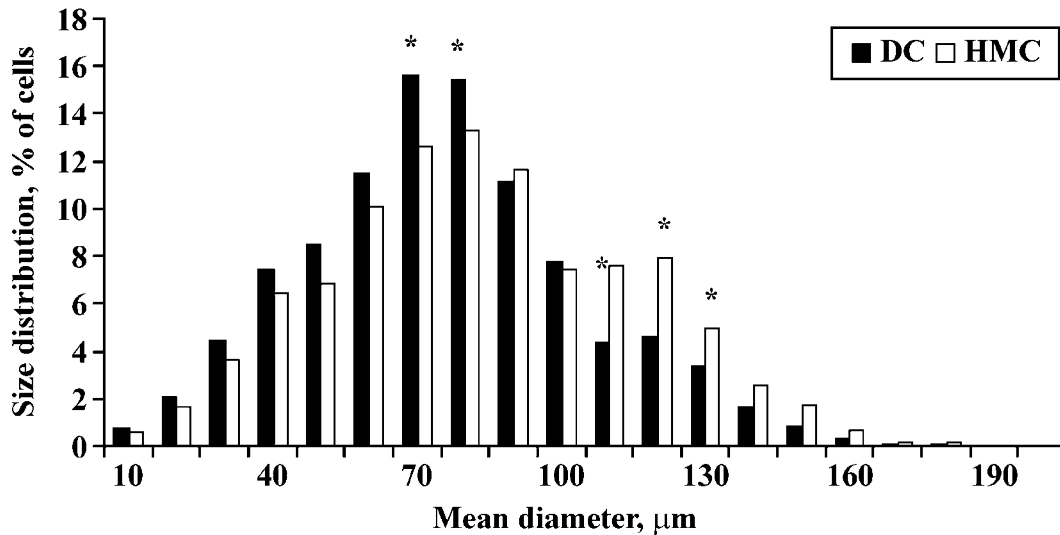

Figure 2. Main effect of corn type on i.m. adipocyte size distribution pattern of Angus-cross steers. DC = dry corn, and HMC = high-moisture corn. *$P \leq 0.05$.

increased the number of cells counted per square millimeter (both, $P < 0.05$). The presence of more abundant and smaller cells in the i.m. fat depot of DC steers suggests that hyperplasia occurred in this treatment. Furthermore, the presence of a relatively greater proportion of cells with a mean diameter of 70 and 80 μm in the DC-fed steers also suggests that a stimulus for adipocyte differentiation was present (Robelin, 1986; Schoonmaker et al., 2004). To our knowledge, there are no reports in the literature that suggest feeding DC increases hyperplasia in the i.m. adipose depot compared with feeding HMC. Caution is advised when interpreting these results, because there was no evidence that an enlargement of the i.m. depot occurred when DC was fed, based on carcass characteristics and LM composition data.

The adipose depot × vitamin A × corn type interaction was not significant; therefore, the depot term was dropped from the model. However, the corn type × adipose depot interaction for adipocyte size and number was significant ($P < 0.05$). Intriguingly, DC had an opposite effect in the s.c. depot compared with the i.m. depot. In the i.m. depot, DC appeared to increase hyperplasia, whereas in the s.c. depot it appeared to have diminished it (DC = 105.6 vs. HMC = 118.3 cells/mm^2, $P < 0.03$). The presumed different effects of corn type on i.m. and s.c. adipose depots should be further investigated, because the presence of the vitamin A × corn type interaction in the latter depot prevents a clear evaluation.

The number of s.c. adipose cells counted per square millimeter was reduced ($P < 0.05$) by DC when Lo, but not Hi, diets were fed (Table 8). As mentioned previously, it is interesting that the direction of this response was opposite what was observed in the i.m. depot. Hyperplasia, suggested by the increased number of cells per square millimeter, and the relative greater abundance of cells with a mean diameter of 60 and 70 μm (Figure 3) appeared to be stimulated only in the LoHMC treatment. We cannot explain this observation. It could be speculated that in this experiment, s.c. fat was responsive to the hyperplasia-stimulatory effects of vitamin A, and that the greater energy content in

Table 8. Effect of dietary vitamin A concentration and corn type on adipose tissue cellularity in the s.c. depot

	Diet[2]					P-value[3]		
Item[1]	LoHMC	HiHMC	LoDC	HiDC	SEM	VA	CT	VA × CT
Cell number, per mm^2	127.8^a	108.9^b	100.0^b	111.3^{ab}	6.3	0.83	0.03	0.05
Mean diameter, μm	100.9	105.5	111.6	106.0	2.4	0.77	0.74	0.21
Cells ≤50 μm, % of total cells	10.2	9.5	6.2	6.0	1.6	0.79	0.03	0.88
Cells >50 and ≤100 μm, % of total cells	48.5	45.3	43.3	48.4	3.2	0.89	0.16	0.20
Cells >100 μm, % of total cells	41.3^d	45.2^{cd}	50.5^c	45.7^{cd}	3.3	0.55	0.06	0.03

[a,b]Within a row, means without a common superscript letter differ ($P < 0.05$).
[c,d]Within a row, means without a common superscript letter differ ($P < 0.10$).
[1]Measured in hematoxylin- and eosin-stained adipose tissue slides (>1.5 mm^2 per sample).
[2]LoHMC = low vitamin A (Lo, no supplemental vitamin A) and high-moisture corn (HMC), HiHMC = high vitamin A (Hi, supplemented at 2,200 IU of vitamin A/kg of DM) and HMC, and LoDC = low vitamin A and dry corn (DC); HiDC = high vitamin A and DC.
[3]VA = vitamin A, and CT = corn type.

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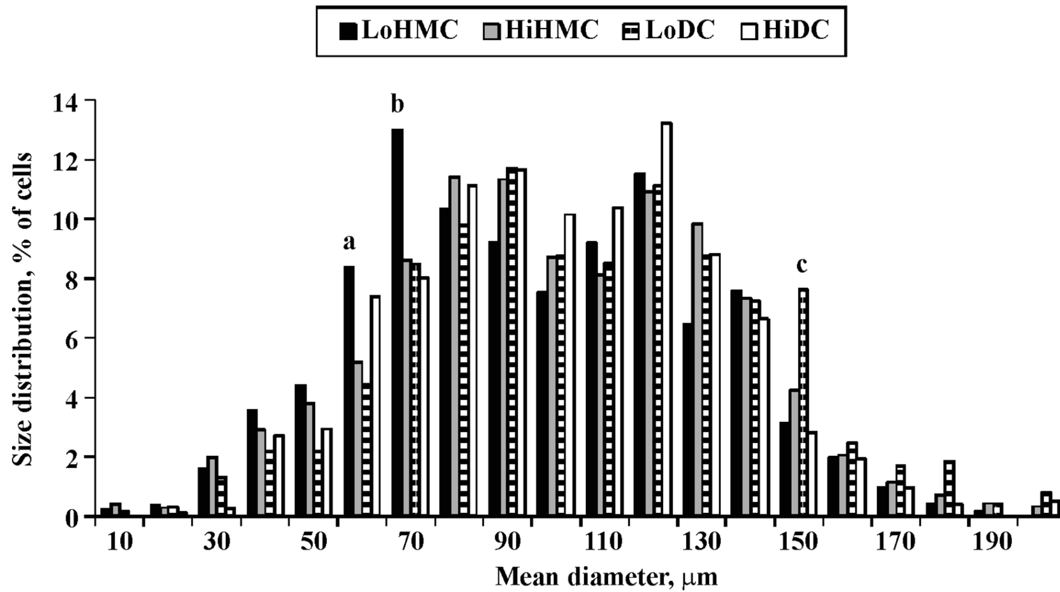

Figure 3. Effect of dietary vitamin A concentration and corn type on s.c. adipocyte size distribution pattern of Angus-crossbred steers. LoHMC = low vitamin A (Lo, no supplemental vitamin A) and high-moisture corn (HMC); HiHMC = high vitamin A (Hi, supplemented at 2,200 IU of vitamin A/kg of DM) and HMC; LoDC = low vitamin A and dry corn (DC); HiDC = high vitamin A and DC. [a]LoHMC vs. LoDC, $P < 0.05$. [b]LoHMC vs. LoDC, HiDC, and HiHMC, $P < 0.05$. [c]LoDC vs. LoHMC, HiDC, and HiHMC, $P < 0.05$.

HMC diets allowed new s.c. adipocytes to differentiate. However, the lack of differences in measured BF in the carcass and the consideration that s.c. fat grows largely by hypertrophy (Hood and Allen, 1973; Cianzio et al., 1985) makes this explanation doubtful.

Beef adipose fatty acid composition is presented in Table 9. Fatty acid composition in beef can be altered by changes in Δ^9-stearoyl-CoA desaturase enzyme (**SCD**) activity (Corl et al. 2001). In particular, SCD is involved in the endogenous synthesis of CLA, which has special interest for beef producers (Parodi, 1999). Interest in increasing CLA in ruminant products arises from its beneficial effects on human health (Belury and Vanden Heuvel, 1999; McGuire et al., 1999). Most CLA in ruminants is synthesized endogenously by the desaturation of vaccenic to rumenic acid, an enzymatic reaction catalyzed by SCD (Bauman et al., 1999; Palmquist et al., 2004). Conflicting data are present in the literature about the effects of carotenoids and retinol on SCD activity and expression (Siebert and Zurk, 2004; Lucchi et al., 2005). We hypothesized that feeding low vitamin A diets may increase SCD activity and therefore the CLA content in beef. However, we did not observe any changes in rumenic or any other CLA in beef in response to our dietary treatments. Our previous results in this area were inconclusive; feeding low vitamin A diets to beef steers for 168 d tended to increase s.c. fat total CLA, whereas feeding low vitamin A diets to Holstein steers for 243 d did not affect s.c. fat total CLA (Gorocica-Buenfil et al., 2007a,b). Taken together, our data suggest that either dietary vitamin A restriction needs to be imposed for a longer period of time or that feeding low vitamin A diets is not an effective strategy to increase the CLA content in beef. Beaulieu et al. (2000) reported that increasing the CLA content of fat in feedlot cattle poses special challenges because of the rumen fermentation patterns present with low-forage diets (e.g., low rumen pH that affects bacterial populations). The speculated changes in SCD activity in response to dietary changes in the concentration of vitamin A may not have a significant effect in the overall synthesis of CLA in beef cattle. The lack of response in desaturase index and the 16:0/16:1 fatty acid ratio provides further evidence that SCD activity was not affected by vitamin A concentration, corn type, or the interaction of these factors. The 16:0/16:1 fatty acid ratio is considered a better indicator of SCD activity than the desaturase activity index, because it removes diet-originated MUFA from the calculations (S. B. Smith, personal communication). The proportions of MUFA, PUFA, and SFA were not different among treatments, suggesting that manipulating vitamin A concentration and corn type in the diets is not an effective strategy to modify the fatty acid profile of Angus-based steers fed high-concentrate diets for 145 d. Evaluation of the effectiveness of dietary vitamin A restriction imposed for a longer period of time on SCD activity and beef fatty acid composition is warranted.

In conclusion, feeding low vitamin A diets for 145 d to Angus-based steers increased marbling and quality grade without affecting YG, animal health, and performance, regardless of the corn type used. Further research is advised to establish the mechanism of action supporting this response.

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Table 9. Main effects of dietary vitamin A concentration and corn type on s.c. fat fatty acid composition of Angus-cross steers

	Vitamin A[1]		Corn type[2]			P-value[3]		
Item	Lo	Hi	DC	HMC	SEM	VA	CT	VA × CT
Fatty acid	g/100 g of total fatty acids							
14:0	5.05	4.99	4.88	5.15	0.47	0.89	0.58	0.67
14:1	0.87	0.76	0.86	0.77	0.081	0.20	0.29	0.11
15:0	0.78	0.81	0.78	0.81	0.071	0.70	0.73	0.25
16:0	30.3	31.7	30.9	31.1	2.0	0.52	0.92	0.62
16:1	2.38	2.43	2.67	2.13	0.38	0.89	0.18	0.72
17:0	1.84	2.05	1.91	1.98	0.14	0.14	0.59	0.07
17:1	0.86	0.80	0.85	0.80	0.063	0.37	0.49	0.59
18:0	13.26	14.15	13.20	14.21	0.74	0.25	0.20	0.16
18:1, total *trans*[4]	9.42	8.61	8.77	9.27	0.89	0.39	0.59	0.89
18:1 *cis*-9	29.0	28.1	29.1	28.0	2.3	0.69	0.64	0.43
18:1 *cis*-11	1.42	1.15	1.30	1.26	0.14	0.08	0.80	0.59
18:2	2.13	2.05	2.25	1.93	0.22	0.71	0.18	0.12
18:2 CLA, *cis*-9, *trans*-11	0.40	0.35	0.39	0.36	0.050	0.30	0.65	0.51
18:2 CLA, *trans*-10, *cis*-12	0.08	0.07	0.07	0.07	0.013	0.54	0.70	0.34
18:2, other CLA	0.06	0.06	0.07	0.06	0.012	0.89	0.79	0.89
18:3n-6	0.0077	0.0071	0.0081	0.0066	0.0044	0.88	0.88	0.88
18:3n-3	0.10	0.10	0.10	0.11	0.035	0.86	0.81	0.22
20:0	0.079	0.089	0.081	0.088	0.0067	0.18	0.36	0.49
20:1	0.29	0.24	0.28	0.25	0.034	0.24	0.47	0.91
20:2	0.12	0.19	0.13	0.17	0.052	0.21	0.51	0.26
20:3n-6	0.013	0.012	0.010	0.015	0.00711	0.86	0.54	0.86
20:3n-3	0.06	0.10	0.08	0.08	0.046	0.38	0.92	0.48
20:5	0.01	0.02	0.01	0.01	0.013	0.29	0.75	0.29
22:0	0.02	0.03	0.03	0.02	0.007	0.41	0.10	0.77
22:1	0.01	0.02	0.02	0.01	0.012	0.67	0.34	0.91
22:2	0.04	0.07	0.05	0.06	0.035	0.40	0.80	0.27
22:6	0.46	0.26	0.35	0.37	0.10	0.06	0.84	0.63
24:1	0.26	0.22	0.23	0.26	0.056	0.50	0.63	0.43
Total CLA	0.54	0.48	0.52	0.50	0.071	0.40	0.75	0.51
16:1/16:0	7.3	7.1	8.1	6.4	1.1	0.86	0.18	0.64
Desaturase index[5]	41.0	39.1	41.0	39.1	3.0	0.55	0.54	0.40
MUFA[6]	35.5	34.0	35.7	33.8	2.5	0.58	0.49	0.39
PUFA[7]	3.11	2.96	3.15	2.93	0.20	0.46	0.27	0.13
SFA[8]	51.5	53.9	51.9	53.5	3.1	0.45	0.63	0.40

[1]Lo = no supplemental vitamin A, and Hi = vitamin A supplemented at 2,200 IU/kg of DM.
[2]DC = dry corn, and HMC = high-moisture corn.
[3]VA = vitamin A, and CT = corn type.
[4]Includes 18:1 *trans*-6–8, *trans*-9, *trans*-10, *trans*-11, and *trans*-12; 18:1 *trans*-10 is considerably greater than the other 18:1 *trans* isomers.
[5](16:1 + 18:1 *cis*-9 + 18:1 cis-11)/(14:0 + 16:0 + 18:0 + 16:1 + 18:1 *cis*-9 + 18:1 *cis*-11).
[6]14:1 + 16:1 + 18:1 *trans*-10 + 18:1 *trans*-11 + 18:1 *trans*-other + 18:1 *cis*-9 + 18:1 *cis*-11 + 20:1 + 22:1 + 24:1.
[7]18:2 + 18:3n-6 + 18:3n-3 + 20:2 + 20:3n-6 + 20:3n-3 + 20:4 + 20:5 + 22:2 + 22:6.
[8]14:0 + 15:0 + 16:0 + 17:0 + 18:0 + 20:0 + 22:0 + 24:0.

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