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Effect of vitamin E supplementation on α-tocopherol and β-carotene concentrations in tissues from pasture- and grain-fed cattle

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Abstract

The effects of dietary vitamin E supplementation of grain-fed cattle on lipid oxidation and meat colour have been extensively investigated, but little attention has been given to pasture-fed cattle where meat is likely to contain naturally high amounts of α-tocopherol and carotenoids. In the work described, we evaluated the effects of pasture-feeding alone and with vitamin E supplementation on tissue levels of anti-oxidants and compared the findings with those obtained for grain-fed cattle with and without supplementation. Sorghum was the major component of the grained-based ration. α-Tocopherol concentrations in plasma, muscle and fat tissues of pasture-fed cattle were not affected by vitamin E supplementation (2500 IU/head/day for 132 days prior to slaughter) while those of grain-fed cattle increased significantly. The α-tocopherol concentrations in the supplemented grain-fed cattle were similar in muscle and liver to pasture-fed animals but were lower in their fat ($P<0.05$). The major carotenoid present in all tissues studied from pasture-fed was β-carotene and its contents in plasma, liver, fat and muscles were decreased ($P<0.05$) by supplementation with vitamin E. Carotenoids were essentially absent in grain-fed cattle except for small amounts in liver. The implication of this study for the meat industry is that cattle grazed on good pasture can achieve concentrations of α-tocopherol in muscles and other tissues at least as high as those obtained by supra-nutritional supplementation of grain-fed cattle with vitamin E. However, α-tocopherol supplementation of pasture-fed cattle reduced tissue concentrations of β-carotene, which would reduce carcase fat yellowness and make pasture-fed cattle more acceptable to some Asian markets.

Keywords: Vitamin E supplementation; Pasture- and grain-fed beef; α-Tocopherol; β-Carotene; Fat colour

1. Introduction

Meat colour and lipid stability are major factors limiting the quality and acceptability of meat and meat products (Arnold, Scheller, Arp, Williams, Buege, & Schaefer, 1992). Lipid oxidation results in the production of free radicals, which may lead to the oxidation of meat pigments and to the generation of rancid odours and flavours. The oxidative stability of muscle depends upon the balance between anti-oxidants, such as α-tocopherol and some carotenoids, and pro-oxidants including the concentrations of polyunsaturated fatty acids (PUFA) and free iron in the muscle (Kanner, 1992).

Vitamin E is a potent and widely studied anti-oxidant in biological systems. Supplementing grain-fed cattle with supra-nutritional levels of vitamin E (α-tocopheryl acetate) has improved meat colour and lipid stability (Arnold, Arp, Scheller, Williams, & Schaefer, 1993; Arnold, Scheller, Arp, Williams, & Schaefer, 1993; Fautsman, Cassens, Schaefer, Buege, Williams, & Scheller, 1989; Liu, Scheller, Arp, Schaefer, & Frigg, 1996; Lynch, Kerry, Buckley, Faustman, & Morrissey, 1999; Sherbeck, Wulf, Morgan, Tatum, Smith, & Williams, 1995). However, in many countries, such as Australia and New Zealand, cattle production systems are largely based on pasture grazing and the need for further supplementation of cattle to improve anti-oxidant status is unknown as green pasture contains high amounts of tocopherols (Jukola, Hakkarainen, Saloniemi, & Sankari, 1996; Tramontano, Ganci, Pennino, & Dierenfeld, 1993), carotenoids (Yang, Larsen, & Tume, 1992) and other anti-oxidants. There have been few investigations that have reported tissue concentrations of these components in pasture-fed cattle. Daly, Young,

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Graafhuis, and Moorhead (1999) reported that lean meat from steers fed rye/grass/clover pasture had higher tocopherol concentrations than meat from steers fed a maize-based diet. In their study, the meat from pasture-fed steers did have a higher fat content than that from the grain-fed steers, which may account for the increased tocopherol contents. Furthermore, it is not known how the tissue levels of α-tocopherol compare with the high values found for vitamin E supplemented grain-fed cattle or how pasture-fed cattle respond to supplementation. Therefore, this study was implemented to determine basal contents of α-tocopherol and β-carotene in tissues of grazing and grain-fed cattle and to assess the impact of supra-nutritional supplementation with vitamin E.

Further, we investigated an apparent interaction between α-tocopherol and β-carotene, both lipid-soluble components, as it has been reported that high concentrations of one appear to reduce the tissue concentrations of the other (Pellett, Andersen, Chen, & Tappel, 1994). For example, α-tocopherol, like other lipids and fat-soluble vitamins, is dependent upon micellar formation for transport across intestinal membranes (Hollander, 1981) where it is incorporated into lipoproteins and secreted into the intestinal lymph (Bjørneboe, Bjørneboe, & Drevon, 1990) for distribution to other tissues. High concentrations of other components compete for these sites in the micelle and in the absorption and transport process. Knight and colleagues (Knight and Death, 1999; Knight, Death, Muir, Ridland, & Wyeth, 1996) observed that oral vitamin A significantly reduced the concentration of plasma carotenoids in grazing cattle and Pellett et al. (1994) described an interaction between β-carotene and α-tocopherol in chickens. As high concentrations of β-carotene impart an undesirable yellow colour to beef fat this study also investigated the effect of high intakes of α-tocopherol on tissue contents of this carotenoid.

2. Materials and methods

2.1. Animals and diets

Thirty-two Hereford cross steers (mean 294±9.5 kg live wt.) were divided into four groups of eight animals each and randomly assigned to one of the four treatments during summer (December–April) for 132 days prior to slaughter. The treatments were pasture (predominantly Rhodes grass, *Chloris gayana* L.) supplemented with 0 or 2500 IU vitamin E per head per day, or grain-fed on a sorghum-based feedlot ration supplemented with 0 or 2500 IU vitamin E per head per day. The formulation (on a weight basis) consisted of approximately 78% red sorghum, 5% cottonseed meal, 10% Rhodes grass hay (*Chloris gayana* L.) and other additives (Yang, McLennan, Armstrong, Larsen, Shaw, & Tume, 1993). Vitamin E was obtained as a gift from Roche Products Pty Ltd, Vitamins and Fine Chemical Division, Goodna, Queensland as *dl*-α-tocopheryl acetate. For the pasture-fed group, the supplement, *dl*-α-tocopheryl acetate, was mixed with molasses (1 kg/head/day) and was fed once a day from a trough. The control pasture-fed cattle received the same amount of molasses without supplement. For the feedlot group, the supplement was uniformly mixed with the dry ration. The animals were weighed weekly during the experimental period and blood samples were taken fortnightly for the first 2 months and then monthly until slaughter. Feed samples were also collected periodically for the analysis of α-tocopherol and β-carotene (results not reported).

2.2. Sample collections

Samples of abomasum contents and liver were obtained on the day of slaughter. Muscles *m. longissimus dorsi* (LD), *m. semimembranosus* (SM) and *m. gluteus medius* (GM) and subcutaneous fat samples were removed from each carcase 20 h post-mortem. Samples from each muscle and from the fat were stored at −18°C until required for analysis.

2.3. Chemical analysis

Plasma α-tocopherol and β-carotene were extracted according to the method of Yang, Larsen, and Tume (1992) and β-carotene concentration was determined according to the same method. α-Tocopherol and β-carotene in muscles were extracted using the method of Liu, Scheller, and Schaefer (1996) using hexane as the extracting solvent. The concentrations of α-tocopherol in all extracts were determined using the same high-performance liquid chromatography system for β-carotene (Yang et al., 1992) with α-tocopherol being detected with a fluorescence detector.

2.4. Statistical analysis

All data were analysed for the analysis of variance between treatment differences using the mixed procedure of SAS (SAS, 1998).

3. Results and Discussion

3.1. Animal growth, carcase data and intakes of α-tocopherol and β-carotene

Each group of cattle commenced the trial at the same weight but the pasture-fed cattle grew at about 0.9 kg/day less than the grain-fed groups (0.40 compared with

1.33 kg/day for pasture and grain-fed, respectively). Cattle were slaughtered at the same time from the beginning of the trial, resulting in a difference of about 80 kg between mean carcase weights of the groups (Table 1). Carcase fatness (subcutaneous fat depth measured at the 8th rib site) was also affected by the feeding system. Pasture-fed cattle produced carcases with a mean fat depth of about 3 mm compared with nearly 18 mm for carcases from grain-fed cattle. Supplementation with vitamin E did not affect carcase weight or fatness.

Based on our previous work we assumed that the concentration of α-tocopherol and β-carotene in abomasum contents would be a good indicator of the amount of these anti-oxidants available for absorption in the small intestine (Yang et al., 1992), given that there is evidence that α-tocopherol is not degraded in the rumen (Leedle, Leedle, & Butine, 1993). Supplementation of pasture-fed cattle with 2500 IU vitamin E/head/day resulted in a significant increase ($P<0.05$) in the mean concentration of α-tocopherol in abomasum contents (Table 2). A similar increase was observed when grain-fed cattle were supplemented with a similar amount of vitamin E. Only trace amounts of carotenoids were detected in abomasum contents of the grain-fed groups, clearly highlighting the differences that do exist in intakes of carotenoids by cattle from various dietary backgrounds. Furthermore, the concentrations of β-carotene in abomasum contents were not affected by dietary supplementation with vitamin E.

We calculated daily intakes of α-tocopherol and β-carotene based upon analyses of abomasum contents (Table 2). Attempts to estimate intakes from analyses of α-tocopherol and β-carotene (data not given) in cut pasture grass taken at various times during the experiment proved difficult because it was not possible to measure daily feed intakes for the pasture-fed cattle. However, using measured concentrations of the anti-oxidants in abomasum contents, and knowing the daily intake of supplemented vitamin E, the intakes for the treatment groups were estimated to be approximately 2200 and 300 mg α-tocopherol /head/day for the non-supplemented pasture- and grain-fed cattle and 4700 and 2800 mg α-tocopherol /head/day for the supplemented groups. For β-carotene, intakes were estimated to be 1500 and 4 mg/head/day for the pasture- and grain-fed groups, respectively.

3.2. α-Tocopherol and β-carotene concentrations in plasma

Fig. 1 shows the changes in α-tocopherol and β-carotene concentrations in plasma over the course of the experiment. All cattle were grown together on the same pasture prior to the start of the trial. This pasture was not as lush as that used for the trial and this probably

Table 1
Mean live weights and carcase data (with pooled S.E.) of pasture- and grain-fed cattle ($n=8$)

	Pasture		Grain		Pooled S.E.
	Control	Supplemented	Control	Supplemented	
Live weight (kg)					
Start	293.5	294.9	292.9	293.5	3.52
Finish	354.5 b[a]	348.8 b	502.6 a	474.5 a	12.29
Average weight gain (kg/day)	0.39 b	0.41 b	1.43 a	1.23 a	0.076
Carcase weight (kg)	184.6b	185.0b	279.1a	265.3a	5.82
Fat depth (mm)	3.6b	3.3b	17.9a	17.6a	1.41

[a] Means within the same row with the same letter are not statistically different ($P>0.05$).

Table 2
Mean concentrations (with pooled S.E.) of α-tocopherol and β-carotene in abomasum contents (μg/g dry wt.) and estimates of intakes (mg/day) of pasture- and grain-fed cattle with or without vitamin E supplement($n=8$)

	Pasture		Grain		Pooled S.E.
	Control	Supplemented	Control	Supplemented	
Abomasum contents (μg/g dry wt.)					
α-Tocopherol	311b[a]	651a	55c	258b	31.8
β-Carotene	181a	179a	0.6b	0.5b	7.20
Estimated intakes[b] (mg/head/day)					
α-Tocopherol	2200	4700	300	2800	
β-Carotene	1500	1500	4	4	

[a] Means within the same row with the same letter are not statistically different ($P>0.05$).
[b] Estimated from measurements on abomasum contents, given that a known amount of vitamin E supplement was ingested daily.

accounted for the significant ($P<0.05$) increases in α-tocopherol and β-carotene concentrations in plasma that were observed in the pasture treatments during the first 28 days. Mean plasma α-tocopherol concentration did not change significantly in the control grain-fed cattle but increased significantly in each of the other treatments during the first 4 weeks ($P<0.05$). Plasma from supplemented grain-fed cattle had the highest mean concentration of α-tocopherol throughout the experiment ($P<0.05$), followed by the two pasture-fed treatments. Arnold, Arp et al., (1993; Arnold, Scheller et al., 1993b) also reported an increase in mean plasma α-tocopherol concentrations in supplemented grain-fed cattle. For the first 56 days, supplementing pasture-fed cattle with α-tocopherol did not increase α-tocopherol concentrations beyond those observed in control pasture-fed animals; however, supplementation subsequently resulted in a small but significant ($P<0.05$) increase. The comparable plasma α-tocopherol concentrations in the two pasture-fed treatments clearly resulted from the high amount of this compound available in the green pasture. The fact that supplementation did not considerably increase plasma concentrations in the pasture groups suggested that either the intestinal absorption of tocopherols was limited, or that the plasma lipoproteins, which are carriers of α-tocopherol and β-carotene, were saturated. However, at each time,

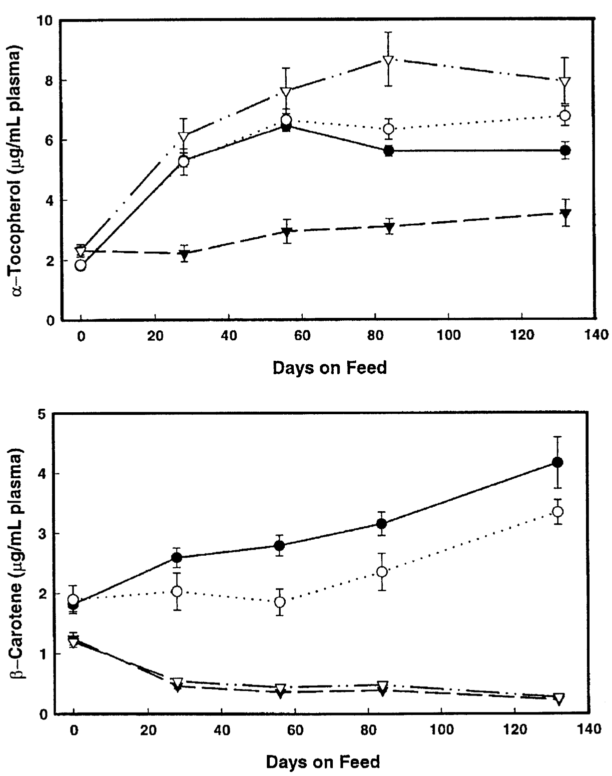

Fig. 1. α-Tocopherol and β-carotene concentrations (μg/ml) in plasma of pasture- (P) and grain-fed (G) cattle with or without vitamin E supplement during the feeding period ($n=8$), (● P0, ○ P2500, ▼G0, ▽ G2500).

the mean plasma α-tocopherol concentration of the supplemented grain-fed group was significantly ($P<0.05$) higher than that of the supplemented pasture cattle. The reason for this is not known but could result from lack of competition from β-carotene and other plant lipids during the absorption process (Pellett et al., 1994).

As expected from previous studies (Yang et al., 1993), the mean plasma β-carotene concentration decreased within 14 days of the steers commencing on a grain-based rations. The mean plasma β-carotene concentration increased in pasture-fed steers throughout the course of the experiment with the control pasture-fed steers exhibiting the fastest increase. The control pasture-fed steers also maintained a higher mean plasma β-carotene concentration than the pasture-fed steers supplemented with α-tocopherol ($P<0.05$). Furthermore, in the supplemented pasture group, plasma β-carotene did not increase during at least the first 56 days, again suggesting that high tocopherol concentrations were interfering with β-carotene absorption or transport.

3.3. α-Tocopherol and β-carotene contents in liver, fat and muscle tissues

Vitamin E supplementation significantly ($P<0.05$) increased the concentration of α-tocopherol in livers of grain-fed cattle to values similar to those observed for pasture-fed cattle (Table 3). Concentrations of β-carotene in liver were highest in the control pasture group, being significantly ($P<0.05$) higher than in livers of the supplemented pasture-fed group. Again, this is evidence that added α-tocopherol affected tissue concentrations of carotenoids, presumably through competition. The content of β-carotene in livers from grain-fed cattle was very low, as expected from their extremely low dietary intakes (Tables 2 and 3).

Whereas supplementation of pasture-fed cattle with vitamin E significantly increased the α-tocopherol concentration in the liver ($P<0.05$) there was no effect on α-tocopherol concentrations in fat tissues or in any of the muscles studied (Table 3). The amounts found (4–6 μg/g muscle) were similar to those reported for grain-fed cattle receiving supra-nutritional doses of vitamin E (Arnold, Arp et al., 1993). In contrast, supplementation produced a highly significant increase in the α-tocopherol contents in all the three muscles of grain-fed cattle ($P<0.05$), being similar to those observed for the pasture-fed animals. The concentration of α-tocopherol in subcutaneous fat of pasture-fed cattle was high (37–40 μg/g fat) compared with that from grain-fed cattle and was not affected by vitamin E supplementation.

Of the three muscles studied, GM tended to have higher mean concentrations of α-tocopherol and β-carotene than LD or SM but these differences were not significant. Arnold, Arp et al. (1993) showed that the GM had significantly higher α-tocopherol content than

Table 3
Mean concentrations (with pooled S.E.) of α-tocopherol and β-carotene in liver, fat and muscles (μg/g tissue) from pasture- and grain-fed cattle with or without vitamin E supplement ($n=8$)

		Pasture		Grain		Pooled S.E.
		Control	Supplemented	Control	Supplemented	
α-Tocopherol						
Liver		20.9b[a]	27.7a	5.9c	24.1ab	1.30
Fat		40.2a	37.0a	5.2c	17.7b	2.35
Muscle	LD	4.5a	4.6a	1.8b	4.3a	0.21
	SM	4.4a	4.3a	2.0b	5.3a	0.21
	GM	5.8a	6.1a	2.4b	6.0a	0.21
β-Carotene						
Liver		12.1a	8.1b	0.8c	1.0c	0.43
Fat		0.99a	0.67b	0.10c	0.09c	0.058
Muscle	LD	0.16a	0.10b	0.01c	0.03c	0.008
	SM	0.09a	0.05b	0.01b	0.03b	0.008
	GM	0.22a	0.16b	0.03c	0.05c	0.008

[a] Means within the same row with the same letter are not statistically different ($P>0.05$).

the LD. Lynch et al. (1999), however, reported that the GM of the control animals had more α-tocopherol than the LD but that this muscle difference was reversed for the supplemented group. For the three muscles from pasture-fed cattle in the present study, mean β-carotene content (μg/g tissue) was higher in the GM (0.20) and the SM (0.17) than in the LD (0.06, $P<0.001$).

These findings for muscle and fat indicate that, despite having the highest vitamin E intake of all the four treatments, the pasture-fed animals were unable to absorb and deposit more vitamin E in their tissues than the grain-fed supplemented cattle. This work supports previous findings that there appears to be a saturation level for absorption and deposition of α-tocopherol in muscle tissues. Arnold, Arp et al. (1993; Arnold, Scheller et al., 1993) observed tissue saturation at the levels of vitamin E supplementation used (1800–3600 IU vitamin E/animal/day) and that the LD took longer (120 days) to reach a saturation level, of about 7 μg/g, compared with other tissues. They estimated that the amount of vitamin E to be supplemented to feedlot cattle for them to reach saturation level in muscle was 1300 IU/animal/day.

Intestinal absorption of α-tocopherol, β-carotene and other fat-soluble compounds is facilitated by high levels of dietary fat (Wolf, 1984). Whilst we did not analyse diets for fat contents it is likely that the grain-based formulation had a slightly higher fat content than the pasture (Harfoot, 1981). This may account for the significantly higher ($P<0.05$) plasma concentrations of α-tocopherol in plasma from grain-fed cattle. However, both pasture- and both grain-diets each had similar fat contents. This further supports the concept that there is a limit for the accumulation of α-tocopherol in muscle tissue.

In cattle, β-carotene is essentially the only carotenoid absorbed from the intestine (Yang et al., 1992; 1993). As expected, the pasture-fed cattle had significantly more β-carotene in all tissues than grain-fed animals ($P<0.001$, Table 3). The control pasture-fed cattle had approximately 50% more β-carotene in all the tissues studied than the supplemented pasture-fed cattle ($P<0.05$). These results suggested a possible interaction between dietary β-carotene and α-tocopherol on the deposition of these two compounds in tissues. High concentrations of vitamin E may interfere with the absorption of β-carotene and, as both β-carotene and α-tocopherol are bound to lipoproteins when transported in the blood, they may compete with each other for binding sites on the lipoprotein molecule. These results confirmed the observation that high intake of one fat-soluble vitamin can interfere with the uptake or utilisation of other fat-soluble vitamins (Pellett et al., 1994).

In summary, in this study it has been shown that cattle grazed on high quality pasture achieved high concentrations of α-tocopherol in their muscles and other tissues similar to those obtained when grain-fed cattle were supplemented with supra-nutritional doses of vitamin E. Meat of grazing cattle would, therefore, be expected to have properties similar to those observed for vitamin E supplemented grain-fed cattle, namely good colour stability and a reduced predisposition to oxidation or rancidity development (Arnold, Arp et al., 1993). Thomas (1981) reported that beef from pasture-fed steers showed the least colour change during retail display. In contrast, Reagan, Carpenter, Bauer, and Lowrey (1977) concluded that pasture-fed beef was less colour stable than that from grain-fed cattle. However, these studies did not consider the relationship between antioxidant content of the diet and colour stability of the muscle, which may have accounted for these disparities.

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References

Arnold, R. N., Arp, S. C., Scheller, K. K., Williams, S. N., & Schaefer, D. M. (1993). Tissue equilibration and subcellular distribution of vitamin E relative to myoglobin and lipid oxidation in displayed beef. *Journal of Animal Science*, *71*, 105–118.

Arnold, R. N., Scheller, K. K., Arp, S. C., Williams, S. N., Buege, D. R., & Schaefer, D. M. (1992). Effect of long- or short-term feeding of α-tocopheryl acetate to Holstein and crossbred beef steers on performance, carcass characteristics, and beef colour stability. *Journal of Animal Science*, *70*, 3055–3065.

Arnold, R. N., Scheller, K. K., Arp, S. C., Williams, S. N., & Schaefer, D.M (1993). Dietary α-tocopheryl acetate enhances beef quality in Holstein and beef breed steers. *Journal of Food Science*, *58*, 28–33.

Bjørneboe, A., Bjørneboe, G-E.A., & Drevon, C. A. (1990). Absorption, transport and distribution of vitamin E. *Journal of Nutrition*, *120*, 233–242.

Daly, C. C., Young, O. A., Graafhuis, A. E., & Moorhead, S. M. (1999). Some effects of diet on beef meat and fat attributes. *N.Z. J. Agricultural Research*, *42*, 279–287.

Fautsman, C, Cassens, R. G., Schaefer, D. M., Buege, Williams, S. N., & Scheller, K. K. (1989). Improvement of pigment and lipid stability in Holstein steer beef by dietary supplementation with vitamin E. *Journal of Food Science*, *54*, 858–862.

Harfoot, C. G. (1981). Lipid metabolism in the rumen. In W. W. Christie (Ed.), *Lipid metabolism in ruminant animals* (pp. 21–55). Oxford: Pergamon Press.

Hollander, D. (1981). Intestinal absorption of vitamins A, E, D, and K. J. *Lab. Clin. Med.*, *97*, 449–462.

Jukola, E., Hakkarainen, J., Saloniemi, H., & Sankari, S. (1996). Effect of fertilization on selenium in feedstuffs and selenium, vitamin E, and β-carotene concentrations in blood of cattle. *Journal of Dairy Science*, *79*, 831–837.

Kanner, J. (1992). Mechanism of nonenzymic lipid peroxidation in muscle foods. In A. J. St. Angelo (Ed.), *Lipid oxidation in food*. ACS Symposium Series 500, Washington, DC. pp 55–73.

Knight, T. W., & Death, A. F. (1999). Effects of oral and injected vitamin A (retinol) supplements on liver vitamin A and plasma carotenoid and cholesterol concentrations in cattle. *Animal Science*, *69*, 607–612.

Knight, T. W., Death, A. F., Muir, P. D., Ridland, M., & Wyeth, T. K. (1996). Effect of dietary vitamin A on plasma and liver carotenoid concentrations and fat colour in Angus and angus crossbred cattle. *N.Z. J. Agric. Res.*, *39*, 281–292.

Leedle, R. A., Leedle, J. A. Z., & Butine, M. D. (1993). Vitamin E is not degraded by ruminal microorganisms: Assessment with ruminal contents from a steer fed a high-concentrate diet. *Journal of Animal Science*, *71*, 3442–3450.

Liu, Q., Scheller, K. K., Arp, S. C., Schaefer, D. M., & Frigg, M. (1996). Colour coordinates for assessment of dietary vitamin E effects on beef colour stability. *Journal of Animal Science*, *74*, 106–113.

Liu, Q., Scheller, K. K., & Schaefer, D. M. (1996). Technical note: a simplified procedure for vitamin E determination in beef muscle. *Journal of Animal Science*, *74*, 2406–2410.

Lynch, M. P., Kerry, J. P., Buckley, D. J., Faustman, C., & Morrissey, P. A. (1999). Effect of dietary vitamin E supplementation on the colour and lipid stability of fresh, frozen and vacuum-packaged beef. *Meat Science*, *52*, 95–99.

Pellett, L. J., Andersen, H. J., Chen, H., & Tappel, A. L. (1994). β-Carotene alters vitamin E protection against heme protein oxidation and lipid peroxidation in chicken liver slices. *Journal of Nutritional Biochemistry*, *5*, 479–484.

Reagan, J. O., Carpenter, J. A., Bauer, F. T., & Lowrey, R. S. (1977). Packaging and palatability characteristics of grass and grass-grain fed beef. *Journal of Animal Science*, *45*, 716–721.

SAS. (1998). *SAS user's guide statistics*. Cary, NC, USA: SAS Institute.

Sherbeck, J. A., Wulf, D. M., Morgan, J. B., Tatum, J. D., Smith, G. C., & Williams, S. N. (1995). Dietary supplementation of vitamin E to feedlot cattle affects beef retail display properties. *Journal of Food Science*, *60*, 250–252.

Thomas, J. D. (1981). Quantitative and qualitative characteristics of forage and grain-fed beef and ultrastructure of beef muscle as affected by sample preparation and cookery method. *Diss. Abst. Int.*, *B42*(3).

Tramontano, W. A., Ganci, D., Pennino, M., & Dierenfeld, E. S. (1993). Distribution of α-tocopherol in early foliage samples in several forage crops. *Phytochemistry*, *34*, 389–390.

Wolf, G. (1984). Multiple functions of vitamin A. *Physiological Review*, *64*, 873–937.

Yang, A., Larsen, T. W., & Tume, R. K. (1992). Carotenoid and retinol concentrations in serum, adipose tissue and liver and carotenoid transport in sheep, goats and cattle. *Australian Journal of Agricultural Research*, *43*, 1807–1809.

Yang, A., McLennan, S. R., Armstrong, J., Larsen, T. W., Shaw, F. D., & Tume, R. K. (1993). Effect of short-term grain feeding on bovine body-fat colour: a cautionary note. *Australian Journal of Agricultural Research*, *44*, 215–220.