FATTY ACID COMPOSITION OF DIETS, METABOLISM, AND DEPOSITION IN SUBCUTANEOUS ADIPOSE TISSUE OF PASTURE AND FEEDLOT FINISHED CATTLE

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FATTY ACID COMPOSITION OF DIETS, METABOLISM, AND DEPOSITION IN SUBCUTANEOUS ADIPOSE TISSUE OF PASTURE AND FEEDLOT FINISHED CATTLE

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(ABSTRACT)

An experiment was conducted to evaluate the effects of pasture finishing versus high-concentrate finishing, over time, on fatty acid metabolism in Angus crossbred (n = 24) beef steers. Ruminal fluid, serum, and adipose tissue biposies were obtained on d 0, 28, 84, and 140. Pasture forages and diet ingredient samples were obtained at 14 d intervals to determine nutritive value and fatty acid composition. The high-concentrate diet consisted of corn silage, cracked corn, soybean meal, and a vitamin and mineral supplement. The pasture-finished steers grazed sequentially on triticale (*Triticale hexaploide*)/annual ryegrass (*Lolium multiflorum*), alfalfa (*Medicago sativa*)/orchardgrass (*Dactylis glomerata*), and a cool-season grass/legume mixture.

The high-concentrate diet consisted of 57 % linoleic acid and 7 % linolenic acid (of total fatty acids). The pasture forages contained an average 9 % linoleic acid and 66 % linolenic acid (of total fatty acids).

Adipose tissue concentrations of 18:2 *cis*-9, *trans*-11 CLA were higher ($P < 0.05$) in the pasture-finished steers than high-concentrate finished steers. Concentrations of 18:2 *cis*-9, *trans*-11 CLA declined in the high-concentrate finished steers ($P < 0.05$) from d 0 to 28 and d 28 to 84. In the pasture-finished steers concentrations peaked ($P < 0.10$) on d 28, and remained high throughout the duration of the study.

Concentrations of linolenic acid were higher ($P < 0.05$) in adipose tissue, ruminal fluid, and serum of the pasture-finished steers, compared to the high-concentrate finished steers. In the pasture-finished steers linolenic acid concentrations peaked ($P < 0.05$) on d 28, and remained high throughout the study. Concentrations of linolenic acid gradually decreased ($P < 0.05$) over time within the high-concentrate finished steers. Thus, it appears that only a short time is needed to alter the omega-3 and CLA composition of adipose tissue in cattle finished on pasture.

DEDICATION

To my husband, Aaron Guay.

To my parents, John and Elizabeth Fincham.

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Introduction

The current practice of beef cattle finishing in the United States is to feed a high-grain diet in feedlots. However, there is considerable concern among consumers over consumption of beef due to the high fat and saturated fatty acid (SFA) content of beef, as a consequence of grain-finishing. The U.S.D.A. recommends that consumption of SFA be limited to less than 10% of caloric intake (Anonymous, 2005). Consumption of lean meat and avoidance of "marbled steaks" are recommended. Although there are no current U.S.D.A. guidelines on consumption of polyunsaturated fatty acids (PUFA), the U.S.D.A recommends increased consumption of PUFA and omega-3 fatty acids. In the United Kingdom, current recommendations by the Department of Health is consumption of PUFA:SFA at a ratio of 0.45 (or greater), but beef contains a PUFA:SFA ratio of 0.11 (Enser et al., 1988; Wood et al., 2003). The United Kingdom Department of Health recommends omega-6:omega-3 (*n*-6:*n*-3) intake ratios of 4.0 or less (Enser et al., 1998).

Pasture-finishing may make beef a healthier product for consumers, as it is lower in SFA and higher in omega-3 PUFA (French et al., 2000; Steen et al., 2003; Realini et al., 2004). Benefits of increased omega-3 fatty acid intake include reducing the occurrence of chronic heart disease, the incidence of mortality as a result of a heart attack, reduced hypertension, reduced inflammation, and cholesterol reduction (De Deckere et al., 1998). Pasture-finished beef is also leaner, compared to grain-finished beef.

An additional benefit of pasture-finishing is an increase in the conjugated linoleic acid (CLA) content of beef (Shantha et al., 1997; French et al., 2000; Steen and Porter, 2003; Realini et al., 2004). Conjugated linoleic acid (CLA) is the common name given to

numerous isomers of octadecadienoic (linoleic) acid with conjugated double bonds, and as many as 20 isomers have been isolated in cheese. The most common isomer present in ruminant products is 18:2 *cis*-9*, trans*-11 octadecadienoic acid (18:2 $\Delta^{9,11}$).

Ruminant products, including lamb, beef, and dairy products, are natural sources of CLA. Conjugated linoleic acid is believed to have several health benefits. Numerous studies using animal models have demonstrated the anticarcinogenic property of CLA (Ha et al., 1990; Ip et al., 1999; Futakuchi et al., 2002; Yang et al., 2002a). Animal models have also shown that CLA has cholesterol lowering and antiatherosclerosis properties (Nicolosi et al., 1997; Kritchevsky et al., 2000).

An increase in CLA and omega-3 fatty acids in food products may be beneficial to consumer health. Pasture-finished beef consumption may be one method of increasing these fatty acids in the diet. However, the time needed to finish cattle on pasture to optimize CLA and omega-3 fatty acids is unknown.

The objectives of this research were to determine the differences in the fatty acid composition of adipose tissue from pasture-finished versus high-concentrate finished cattle, and to determine the time needed for changes in fatty acids to occur. The metabolism of fatty acids (including CLA and omega-3), and changes in metabolism over time, in cattle finished on pasture and on a high-concentrate diet were also investigated. The relationship of pasture forages and high-concentrate diets to fatty acid metabolism, and the concentrations of fatty acids in adipose tissue were also evaluated.

Review of Literature

The fatty acid content of forages

Generally, palmitic (16:0), stearic (18:0), oleic (18:1), linoleic (18:2), and linolenic (18:3) acids comprise over 90 % of the fatty acids in forages (Garton, 1960; Ohlrogge and Browse, 1995; Samala et al., 1998; Rhee et al., 2000). Linolenic acid is an omega-3 fatty acid and is the only omega-3 fatty acid found in forages (Rhee et al., 2000); however, the fatty acid profiles of forages are subject to change. Preserving forages in the form of hay or silage has the potential to alter the fatty acid content (Thafvelin and Oksanen, 1966; Czerkawski, 1967; Dewhurst and King, 1998; Boufaïed et al., 2003). Additionally, N fertilization can increase the fatty acid content and alter the composition of forages (Boufaïed et al., 2003).

Effect of species, management, and forage maturity. Dewhurst et al. (2001) evaluated the fatty acid content and composition of several species and cultivars of grasses, including perennial ryegrass (*Lolium perenne*), tall fescue (*Festuca arundinacea*), a ryegrass-fescue cross (*Festulolium*), orchardgrass (*Dactylis glomerata*), and timothy (*Phleum pratense*). Cutting date influenced the linoleic and linolenic acid content of the grasses. In general, linoleic, linolenic, and total fatty acid concentrations were higher in spring and fall, compared to summer. Thafvelin and Oksanen (1966) observed similar results with timothy.

Increasing the cutting interval from 20 to 38 d resulted in a decrease in the fatty acid content (Dewhurst et al., 2001). The average linolenic acid content of perennial ryegrass was 1.7 and 0.9 %, DM basis, for the 20 and 38 d cutting intervals, respectively. The authors suggested that leaf proportion is an important factor determining the fatty

acid content of forages. Gerson et al. (1986) observed a decline in the linolenic acid content of perennial ryegrass with increased maturity. The linolenic acid composition of immature, mature and, senescent perennial ryegrass was 0.3, 0.2, and .01 % of DM, respectively. Boufaïed et al. (2003) and Elgersma et al. (2003) also observed an inverse relationship between forage maturity and fatty acid content.

Dewhurst et al. (2001) reported that the linoleic acid content of forages was highly variable and was influenced by species and cultivar. They observed that the effect of species resulted in as much as 36 % variation in the linolenic acid content of the grasses. Boufaïed et al. (2003) also observed variation in the fatty acid content and composition of several species and cultivars of grasses and legumes, including annual ryegrass (*Lolium multiflorum*), meadow fescue (*Festuca pratensis*), orchardgrass, tall fescue (*Festuca arundinacea*), smooth bromegrass (*Bromus inermis*), timothy, Kentucky bluegrass (*Poa pratensis*), meadow bromegrass (*Bromus riparius*), white clover (*Trifolium repens*), birdsfoot trefoil (*Lotus corniculatus*), red clover (*Trifolium pratense*), and alfalfa (*Medicago sativa*). Grasses generally had a higher content of linolenic acid than legumes. Annual ryegrass and white clover had the highest linolenic acid content (2.1 and 1.7 % of DM, respectively), while timothy and alfalfa had the lowest (0.8 and 0.6 % of DM, respectively).

These studies suggest that there is a significant genetic component influencing fatty acid content of grasses which provides a potential for plant breeders to increase lipid levels in grasses. Increasing the linoleic and linolenic acid levels in grasses through breeding may provide a way to increase the CLA content of beef and milk.

Fatty acid content of hay. Minimal changes occurred in the fatty acid content of perennial ryegrass as a result of drying (Czerkawski, 1967). Fresh perennial ryegrass contained 11.8, 1.5, 2.2, 12.7, and 70.0 % palmitic, stearic, oleic, linoleic, and linolenic acid (of total fatty acids), respectively, while the dried forage contained 13.2, 1.3, 2.0, 13.5, and 66.9 %, respectively. Boufaïed et al. (2003) observed that hay contained a lower concentration of fatty acid than fresh grass.

The occurrence of high relative humidity or high temperature resulted in a greater change in the fatty acids composition (Czerkawski, 1967). When the relative humidity was over 80 %, the linolenic acid content decreased to less than 40 % of total fatty acids after 13 mo of storage. A concurrent increase in linoleic, oleic, stearic, and palmitic acids occurred. Drying perennial ryegrass at 50 and 100° C also decreased the linolenic acid content from 70 % of total fatty acids in the fresh forage to 62.7 and 62.8 % of total fatty acids in the forage dried at 50 and 100° C, respectively, with a subsequent increase in the palmitic acid content. The author also observed changes in the fatty acid composition of perennial ryegrass from long-term storage. Palmitic, stearic, and oleic acids increased, while linolenic acid decreased from 67.8 (1 mo) to 61.0 % (13 mo) in hay stored (of total fatty acids). Thafvelin and Oksanen (1966) observed similar results due to the method of drying and high moisture in hay.

Fatty acid content of silages. The fatty acid composition of silage is dependent upon the type of forage ensiled. The fatty acid composition of corn (*Zea mays*) silage is approximately 20, 2, 18, 50, and 5 % (of total fatty acids) palmitic, stearic, oleic, linoleic, and linolenic acid, respectively (Kalscheur et al., 1997; Dhiman et al, 1999b). Alfalfa (*Medicago sativa*) silage contains approximately 36, 16, 2, 3, and 25 % (of total fatty

acids) linolenic, linoleic, oleic, stearic, and palmitic acid, respectively (Kalscheur et al., 1997; Dhiman et al, 1999b). The fatty acid composition of grass silage is approximately 50, 15, 4, 2, and 18 % (of total fatty acids) linolenic, linoleic, oleic, stearic, and palmitic acid, respectively (French et al., 2000; Scollan et al., 2001b).

If properly ensiled, the fatty acid content of the forage will not be greatly altered. Dewhurst and King (1998) observed that the ensiling of perennial ryegrass altered the fatty acid content of the silage to a minimal extent. However, when compared to unwilted silage, an extended wilting prior to ensiling resulted in a marked decrease in the total fatty acid content (2.46 vs. 1.75 % of DM) and the linolenic acid content (55 vs. 48 % of total fatty acids) of the ryegrass silage (Dewhurst and King, 1998). Boufaïed et al. (2003) reported that wilting resulted in a reduction of the fatty acid content of timothy (1.9 versus 1.6 % of DM). Elgersma et al. (2003) ensiled wilted perennial ryegrass and observed a lower fatty acid content, compared to fresh forage (1.9 versus 2.9 % of DM, respectively).

Effect of cold acclimation. Another factor which influences the fatty acid composition of forages is cold acclimation (De La Roche et al., 1972; Willemot et al., 1977; Uemura and Steponkus, 1994; Samala et al., 1998). Winter wheat (*Triticum aestivum*) seedlings grown at 2° C had an increased amount of phospholipid compared to seedlings grown at 24° (De La Roche et al., 1972). The authors observed an increase in linolenic acid and a decrease in linoleic acid. Similar results were obtained by Samala et al. (1998) with bermudagrass (*Cynodon dactlyon*), and Uemura and Steponkus (1994) with oat (*Avena sativa*) and rye (*Secale cereale*). Samala et al. (1998) observed as much as a 43 % increase in linolenic acid and suggested that by increasing the polyunsaturated

fatty acid (PUFA) content of membranes, plants become cold acclimated, which is a mechanism to maintain membrane fluidity and avoid cold damage. De La Roche et al. (1972), Willemot et al. (1977), and Uemura and Steponkus (1994) also noted the changes in fatty acid content of forages related to cold tolerance. These findings further support and may partially explain observations made by Dewhurst et al. (2001), who observed higher unsaturated fatty acid levels in grass during the spring and fall.

Microbial production of conjugated linoleic acid

Microbes in the rumen produce CLA from dietary linoleic acid, which has been demonstrated with numerous *in vitro* studies by incubating linoleic acid with rumen microbes (Harfoot, 1988). However, these studies also demonstrated that CLA is not produced by microbes from linolenic acid. Kepler et al. (1966) observed that when linoleic acid was incubated with *Butyrivibrio fibrisolvens* strain A38 for 2 h, 18:2 *cis*-9, *trans*-11 CLA was the main fatty acid product (68 %), with vaccenic acid (*trans*-11 18:1) being the other main product (23 %). Yokoyama and Davis (1971) observed that CLA was produced by *Treponema* (Borrelia) and was the major product up to approximately 8 h of incubation. However, when incubation time lasted longer than 8 to 10 h, CLA levels dropped, as it was further hydrogenated into vaccenic acid. The authors observed that vaccenic acid was the major end product of incubation of linolenic acid after an extended incubation time (8 h up to 24 h). Kemp et al. (1975) demonstrated that *Ruminococcus albus*, two *Eubacterium* spp., and two *Fusocillus* spp. produced CLA from linoleic acid, but not linolenic acid. The authors stated that even during short incubation periods, the amount of CLA produced was less than 10 % of the end products. Kellens et al. (1986) also observed that CLA was produced in small amounts (less than 20 % of end products)

and was completely degraded by 10 h of incubation. Shorland et al. (1957) also demonstrated that CLA was produced from linoleic acid by ruminal fluid obtained from sheep. Kellens et al. (1986), in agreement with earlier research, also found that CLA is an intermediate in biohydrogenation of linoleic acid and not linolenic acid. Therefore, CLA is an intermediate in the biohydrogenation of linoleic acid to vaccenic acid, with vaccenic acid being the major end product.

Recently, Kim et al. (2002) identified a strain of bacteria, *Megasphaera elsdenii* YJ-4, which produces significant amounts of the *trans*-10, *cis*-12 isomer of CLA. This bacteria was isolated from the ruminal fluid collected from cows fed a diet consisting of 90 % cracked corn.

Fatty acid hydrogenation. Kellens et al. (1986) found that linoleic and linolenic acids were converted to vaccenic acid. The authors also noted that in *in vitro* cultures, using a mixed population of ruminal microorganisms, vaccenic acid was converted to stearic acid. The monocultures used in the studies by Kepler et al. (1966), Yokoyama and Davis (1971), and Kemp et al. (1975) did not produce stearic acid. Kemp and Lander (1984) characterized two different types of bacteria; the first termed group A (included *Ruminococcus albus* and *Butyrivibro* sp.) was able to convert linoleic acid and linolenic acid to vaccenic acid. The second type of bacteria, group B (included *Fusocillus* spp.) converted vaccenic acid to stearic acid. Therefore, a mixed culture of ruminal bacteria is needed to convert linoleic and linolenic acids to stearic acid (Kemp and Lander, 1984). Similar results were obtained by Hazlewood et al. (1976).

Stearic acid is the final end product of unsaturated C18 fatty acid biohydrogenation, comprising over 40 % of the fatty acids present in ruminal digesta

(Shorland et al., 1955; Hawke and Robertson, 1964; Katz and Keeney, 1966). Monounsaturated 18 carbon fatty acids comprised approximately 7 % of the fatty acids present in ruminal digesta, of which *trans* fatty acids comprised 75 % (Katz and Keeney, 1966). The authors also observed that 75 % of the *trans* 18:1 fatty acids was vaccenic acid. The remainder of the *trans* isomers with double bond positions from carbon seven through 15 comprised less than 7 % of the total *trans* isomers.

Linoleate isomerase. Kepler and Tove (1967), Kepler et al. (1970), and Yokoyama and Davis (1971) isolated and characterized the enzyme, linoleate isomerase, contained in ruminal bacteria, which is responsible for converting linoleic acid to CLA. The optimal pH for the isomerase is approximately 7.0 (Kepler and Tove, 1967; Yokoyama and Davis, 1971). It was shown that the isomerase has a substrate specificity for *cis*-9, *cis*-12 bonds and the requirement for a free carboxyl group (Kepler et al., 1970; Yokoyama and Davis, 1971). Additionally, some inhibitors of the isomerase have been identified, including fatty acids such as isomers of oleic acid and linoleic acid and chemicals such as EDTA and *p*-Chloromercuribenzoate (Kepler et al., 1970; Yokoyama and Davis, 1971).

Characteristics of bacteria. Biohydrogenation levels by ruminal bacteria *B. fibrisolvens* were higher under H_2 atmospheres, compared to other gases such as CO_2 or N_2 (Polan et al., 1964). The bacteria which were adherent to food particles had high biohydrogenation ability, while bacteria associated with the liquid phase had minimal ability to hydrogenate fatty acids (Harfoot et al., 1973b; Singh and Hawke, 1979; Bauchart et al., 1990).

Effects of diet on biohydrogenation. The particle size of the diet may influence the ability of bacteria to colonize particles, which in turn may potentially affect biohydrogenation. Outen et al. (1975) observed reduced biohydrogenation of lipids when red clover was fed to sheep in the form of either chopped, wafered or ground and pelleted, compared to fresh (frozen) forage. Oleic and linoleic acids flowing to the duodenum were higher in the sheep fed the chopped or ground diets, compared to the sheep fed fresh forage. Gerson et al. (1988), in an *in vitro* study, observed that microbial populations were six times higher on hay ground to 1 to 2 mm, compared to hay ground to 0.1 to 0.4 mm. The authors also observed increased rates of lipolysis and biohydrogenation, as a result of the increased particle size.

Biohydrogenation may also be influenced by fiber source. Alfalfa silage was replaced by whole cottonseed in the diets of cannulated Holstein cows in a study conducted by Harvatine et al. (2002). Biohydrogenation of total fatty acids was increased by the replacement of silage with cottonseed, as did total tract digestion of fatty acids. The production of CLA and its precursor, vaccenic acid, were not investigated in this study, but potentially may have been altered due the changes in intakes and metabolism of 18:2 and 18:3 when silage was replaced with whole cottonseed.

Inhibition of fatty acid degradation. Dietary starch can also inhibit lipolysis and biohydrogenation. Decreased biohydrogenation and lipolysis of linoleic acid, by as much as 50 %, was observed with *in vitro* cultures inoculated with ruminal fluid from sheep fed high-starch, low-fiber diets (Gerson et al., 1985). A comparison of the effects of dietary fiber and starch levels on the proportions of bacterial species in the rumen of cows was conducted by Latham et al. (1971). The cows were fed three diets: hay alone, 20 % hay

and 80 % corn or barley. The authors observed a decrease in the population of cellulose hydrolyzing bacteria (eg. *Butyrivibrio* spp.) and increased numbers of starch utilizing bacteria , such as *Lactobacillus* spp., and *Streptococcus* spp when grain was added. Latham et al. (1972) observed a decrease in *Butyrivibrio* spp. and an increase in lactic and propionic acid producers when cows were fed a milk fat depressing (high-concentrate) diet.

An additional effect of feeding a high-starch diet is a reduction of ruminal pH. Van Nevel and Demeyer (1996) observed some reduction in biohydrogenation of linoleic acid in *in vitro* cultures maintained at lower pH values; however, lipolysis was inhibited to a greater extent. The authors suggested that other factors besides a decline in pH were responsible for reduced lipid digestion in ruminants fed high-concentrate diets. Martin and Jenkins (2002) observed a decrease in the production of CLA and *trans*-C18:1 fatty acids in continuous culture fermenters when the pH was reduced.

The supplementation of oil in ruminant diets may decrease biohydrogenation. Galbraith et al. (1971) observed that *in vitro* cultures supplemented with long-chain fatty acids resulted in reduced numbers and growth rates of cellulose degrading ruminal bacteria. Maczulak et al. (1981) found that fatty acids had an inhibitory effect on cellulolytic bacterial species. However, the inclusion of cellulose along with the fatty acid in the *in vitro* cultures reduced the inhibitory effect of the fatty acid on the microorganisms. The authors concluded that absorption of the long-chain fatty acids by fiber particles is the mechanism responsible for the reduction of inhibition. The authors also noted that vaccenic acid had a lower inhibitory effect than oleic acid.

Supplementation of oil in ruminant diets may also be a way of altering the biohydrogenation pathway and proportions of end products. Harfoot et al. (1973a) observed that when linoleic acid was added to *in vitro* cultures at levels greater than 1.0 mg/ml of ruminal contents obtained from sheep, the main end product was vaccenic acid, compared to the main end product which was oleic acid in cultures when linoleic acid was added at less than 1.0 mg/ml. The authors also observed an increase in the amount of CLA produced as a result of increasing levels of linoleic acid substrate added to the cultures. Similar results were obtained with *in vitro* culture experiments conducted by Noble et al. (1974).

Effects of antimicrobials. Biohydrogenation may potentially be inhibited by antimicrobials. Chen and Wolin (1979) observed that *R. albus*, *R. flavefaciens*, and *B. fibrisolvens* were inhibited by monensin and lasalocid, while other bacterial species were favored. This alteration of bacterial populations may potentially influence the biohydrogenation of lipids by ruminal microorganisms. Kobayashi et al. (1992) observed that sheep fed salinomycin had higher amounts of PUFA flowing to the duodenum than control sheep. The salinomycin fed sheep had oleic and linoleic acids present at 23.6 and 6.2 % of digesta, respectively, while the control sheep had oleic and linoleic acids present at 9.1 and 4.7 % of digesta, respectively. Van Nevel and Demeyer (1995) observed reduced lipolyis and biohydrogenation by numerous antimicrobial compounds in an *in vitro* study. Some examples include monensin, lasalocid, carbadox, and terramycin. Similar results were obtained by Fellner et al. (1997) with monensin, nigericin, and tetronasin. Additionally, the authors observed an increase in CLA content of *in vitro* culture contents from 0.5 % of total fatty acids in the control culture to 1.2, 1.6, and 1.9

% of total fatty acids in the cultures containing monensin, nigericin, and tetronasin, respectively. The authors concluded that the increase in linoleic acid and CLA was due to inhibition of biohydrogenation to stearic acid. However, Dhiman et al. (1999a) observed no increase in the content of CLA in milk fat when cows were supplemented with monensin. Andrae et al. (2002) observed a decrease in duodenal flow of CLA and C18 PUFA in monensin fed steers.

Endogenous synthesis of conjugated linoleic acid

Animals have the ability to synthesize CLA endogenously such as in liver, mammary, and adipose tissues. Pollard et al. (1980) observed CLA production in rat liver tissue by the enzyme, Δ^9 desaturase (stearoyl coenzyme A desaturase) from vaccenic acid. Santora et al. (2000) found that when vaccenic acid was fed to mice, the CLA composition of the triacylglycerol fraction of the mice carcasses increased. The authors stated that conversion of dietary vaccenic acid to CLA by mice averaged 11.4 %. Adlof et al. (2000) observed the production of CLA from vaccenic acid by humans in a clinical trial. Consumption of vaccenic acid resulted in a 30 % increase in serum CLA levels. A study was conducted by Wahle (1974) to compare the Δ^9 desaturase activity in sheep, rats, and chickens. The authors observed that liver tissue from sheep had lower Δ^9 desaturase activity than that of rats and chickens. However, the adipose tissue from sheep had higher Δ^9 desaturase activity, compared to liver tissue from rats and chickens. The authors also found that mammary tissue of lactating ewes had similar Δ^9 desaturase activity as adipose tissue.

Desaturase activity in beef cattle. The activity of Δ^9 desaturase has also been evaluated in beef cattle. Martin et al. (1999) studied the gene expression of Δ^9 desaturase

in subcutaneous adipose tissue of Angus calves from 2.5 wk up to 18 mo of age, and observed peak expression at approximately 12 mo of age. The authors concluded that the Δ^9 desaturase mRNA levels may be an indication of lipid filling of adipose tissue. St. John et al. (1991) further quantified the Δ^9 desaturase activity of liver and subcutaneous adipose tissue in 16 mo old Angus steers, 12 to 14 mo old Angus heifers, and 10 to 12 mo old Braford heifers. The adipose tissue from the Angus steers had similar Δ^9 desaturase activity as that of the rat liver, 0.21 and 0.15 nmol·min^{-1}·mg protein^{-1}, respectively, while the Angus liver tissue had no detectable desaturase activity. The Δ^9 desaturase activity in the adipose tissues of the Angus and Braford heifers was similar, .95 and 1.06 nmol·7min·mg protein, respectively. No Δ^9 desaturase activity was detected in the liver samples of either breed of heifers (St. John et al., 1991). Cameron et al. (1994) observed comparable Δ^9 desaturase activity as that observed by St. John et al. (1991) and no differences in Δ^9 desaturase activity due to breed when comparing Angus and Wagyu steers.

Diet was also observed to be a factor that influenced Δ^9 desaturase activity (Chang et al., 1992). Simmental steer calves, approximately 8 to 15 mo of age, were fed either a conventional high-concentrate control diet or one supplemented with high oleate sunflower seed. The Δ^9 desaturase activities of the adipose tissue from the steers fed the supplemented and control diets were 1.15 and 0.57 nmol·7min^{-1}·mg protein^{-1}, respectively. Liver and longissimus dorsi muscle tissues also had elevated Δ^9 desaturase activity as a result of diet supplementation. Liver tissue Δ^9 desaturase activities were 0.48 and 0.95, nmol·7min·mg^{-1} protein^{-1} in the control and supplemented treatments,

respectively. Muscle tissue Δ^9 desaturase activities were 0.06, and 0.44 nmol·7min^{-1}·mg protein^{-1} in the control and supplemented treatments, respectively.

The ratios and proportions of monounsaturated fatty acids (MUFA) to saturated fatty acids (SFA) in tissues can be an indirect method to compare Δ^9 desaturase activities. St. John et al. (1991) noted that the proportion of MUFA was considerably higher in the adipose tissue as compared to liver tissue, indicating the higher Δ^9 desaturase activity in adipose tissue. Adipose tissue contained 54 % MUFA, while liver tissue contained only 35 %. Chang et al. (1992) noted higher levels of oleic acid and lower levels of stearic acid in steers fed a diet supplemented with high oleate sunflower seed, compared to a conventional diet. The authors concluded that these differences in fatty acids may have been a result of higher Δ^9 desaturase activity.

Mammary tissue desaturase activity. Research has been conducted on the Δ^9 desaturase activity in mammary tissue of lactating mammals. Kinsella (1972) observed that 1 to 2 wk prior to calving, dairy cows had no Δ^9 desaturase activity in mammary tissue. Two days prior to calving, Δ^9 desaturase activity increased slightly, while 3 mo after calving Δ^9 desaturase activity was high. Bickerstaffe and Annison (1970) compared the activity of Δ^9 desaturase in mammary tissues of goats, pigs, and rabbits. The authors observed higher Δ^9 desaturase activity in the goats than in pigs or rabbits. They also observed that 17 % of the stearic acid in the *in vitro* culture media was desaturated after 40 to 60 minutes of incubation.

The CLA content of milk formed by Δ^9 desaturase was estimated by Griinari et al. (2000). Abomasal infusion of dairy cows with a mixture of vaccenic acid and *trans*-12 18:1 resulted in a 31 % increase in the CLA of the milk fat. Similar results were obtained

by Corl et al. (1998). In a subsequent experiment by Griinari et al. (2000), an inhibitor of Δ^9 desaturase (sterculic oil) was infused abomasally. The sterculic oil treatment resulted in a 45 % drop in the CLA content of milk fat and an increase in the ratio of SFA to the MUFA counter part. They stated that 14:0 originates only from mammary gland synthesis (and not diet); therefore, 14:1 can be used as an indicator of Δ^9 desaturase activity. The authors concluded, by using the change in the ratio of 14:0 to 14:1, an estimated 64 % of the CLA in milk was of endogenous origin.

Similar results were obtained by Corl et al. (2001), who used partially hydrogenated vegetable oil (PHVO) (rich in *trans* isomers of 18:1) as the CLA precursor. Abomasal infusions of PHVO resulted in a 17 % increase in the CLA content of milk fat. Sterculic oil infusion resulted in a 60 to 65 % reduction in the CLA content of milk. Corl et al. (2001) also used 14:0 to 14:1 ratios to estimate sterculic oil inhibition of Δ^9 desaturase, and concluded that 78 % of the CLA in milk was from endogenous origin. Also, the authors observed a depression of total milk fat percentage in the milk as a result of PHVO infusion, but no change in milk fat due to sterculic oil. Kay et al. (2004) estimated that endogenous synthesis contributed over 91 % of the CLA production by sterculic oil infusion. The authors observed no reduction in the total milk fat as a result of sunflower oil or sterculic oil infusion in cows obtaining all of their DMI from pasture. In contrast, Bickerstaffe and Johnson (1972) observed a reduction of both the percentage total milk fat and Δ^9 desaturase activity when sterculic oil was infused into the jugular vein of lactating goats fed a high-concentrate diet. Perhaps the reduction in milk fat was a result of the high-concentrate diet rather than the sterculic oil infusion.

Inhibition of desaturase in beef cattle. Inhibition of Δ^9 desaturase activity has been observed when cattle were fed ruminally protected cottonseed oil which contains cyclopropene fatty acids (Yang et al., 1999). A 55 % drop in the Δ^9 desaturase activity in subcutaneous adipose tissue was observed when cattle were fed ruminally protected cottonseed oil. An average activity of 1.14 nmol·mg protein^{-1}·min^{-1} was observed in the control group as compared to 0.62 nmol·mg protein^{-1}·min^{-1} in the cottonseed oil supplemented group. However, Page et al. (1997) observed no differences in Δ^9 desaturase activity as a result of feeding whole cottonseeds to cattle.

Yang et al. (1999) also compared the Δ^9 desaturase activity of subcutaneous adipose tissue in pasture-fed and grain-fed cattle. The Δ^9 desaturase activity of adipose tissue from pasture-finished cattle (1.48 nmol·mg protein^{-1}·min^{-1}) was greater than grain-finished cattle (approximately 0.85 nmol·mg protein^{-1}·min^{-1}), which could partially explain the differences in the CLA content of pasture-finished and grain-finished beef. Generally, the pasture-fed cattle had lower ratios of SFA to MUFA, also indicating higher Δ^9 desaturase activity.

Inhibition of desaturase in dairy cows. Several studies have been conducted using dairy cows to determine the influence of CLA infused post-ruminally on fatty acid profiles of milk and total milk fat yield. Chouinard et al. (1999b) infused mixtures of CLA, containing 18:2 *cis*-9*, trans*-11 CLA, *cis*-8, *trans*-10 CLA; *cis*-10, *trans*-12 CLA, and *cis*-11, *trans*-13 CLA. Control cows receiving no CLA infusion produced milk with a CLA content of 0.43 g/100 g fat. Infusion of CLA resulted in increased milk CLA of up to 1.52 g/100g fat. However, CLA infusion resulted in a depression of total milk fat

and Δ^9 desaturase activity, as indicated by SFA to MUFA ratios. Similar results were observed by Chouinard et al. (1999a) and Loor and Herbein (1998).

Milk fat depression has been related to decreased Δ^9 desaturase activity. Loor and Herbein (1998) and Chouinard et al. (1999a, 1999b) observed increased ratios of SFA to MUFA in milk obtained from cows with depressed milk fat as a result of CLA supplementation, compared to control cows with normal milk fat production. However, Piperova et al. (2000) observed an opposite change in the ratios of SFA to MUFA when cows were fed a high-concentrate milk fat depressing diet.

Fatty acids linked to milk fat depression. Identification of the isomers of fatty acids responsible for milk fat depression has been attempted. Gaynor et al. (1994) observed that supplementation of *trans* 18:1 fatty acids, from vegetable shortening, in the diet of cows resulted in a depression in milk fat, while supplementation of *cis* 18:1 fatty acids from high oleate sunflower oil did not depress milk fat. Gaynor et al. (1995) also noticed in cows producing a depressed level of milk fat as a result of feeding a high-concentrate diet, there was a higher proportion of *trans* 18:1 fatty acids in their milk, as compared to cows producing a normal amount of milk fat.

Piperova et al. (2000) noted that milk fat samples obtained from cows experiencing depressed milk fat production had decreased proportions of vaccenic acid and 18:2 *cis*-9*, trans*-11 CLA, and increased proportions of *trans*-10 18:1, *trans*-7, *cis*-9 CLA and *trans*-10, *cis*-12 CLA. The authors concluded that one or more of these isomers might be responsible for milk fat depression. Griinari et al. (1998) observed an increase in *trans*-10 18:1 and a decrease in vaccenic acid in cows exhibiting milk fat depression. LeDoux et al. (2002) observed a substantial increase in the *trans*-10 18:1 content of milk

produced by dairy goats fed a low roughage diet. The authors also observed a decrease in vaccenic acid and a slight increase in *trans*-12 18:1 in dairy-goat milk.

Lin (2000) found that *trans*-10, *cis*-12 CLA caused a much greater reduction in milk fat in cows, as compared to 18:2 *cis*-9*, trans*-11 CLA. Similar results were obtained by Baumgard et al. (2000), Baumgard et al. (2001), and Loor (2001). Additionally, Baumgard et al. (2000), and Baumgard et al. (2001) observed that *trans*-10, *cis*-12 CLA reduced Δ^9 desaturase activity. Similar results were obtained by Park et al. (2000). However, Park et al. (2000) observed that *trans*-10 18:1 did not decrease Δ^9 desaturase activity, but *cis*-12 18:1 did. Jayan (1998) and Lee et al. (1998) concluded that vaccenic acid and 18:2 *cis*-9*, trans*-11 CLA were not the isomers responsible for inhibition of Δ^9 desaturase.

Loor and Herbein (2003b) infused Holstein cows abomasally with either 18:2 *cis*-9*, trans*-11 or *trans*-10, *cis*-12 CLA at a rate of 0.625g/h. The authors observed a 25 % reduction in milk fat when the *trans*-10, *cis*-12 CLA isomer was infused, while no depression was observed due to the 18:2 *cis*-9*, trans*-11 CLA isomer. Additionally, the authors observed altered ratios of unsaturated to saturated fatty acids, indicating reduced Δ^9 desaturase activity. Viswanadha et al. (2003) observed a linear depression in milk fat (from 4.17 to 3.53, 3.29, and 2.92) when *trans*-10, *cis*-12 CLA was infused intravenously at rates of 0, 2, 4, and 6 g/d, respectively.

Cellular and molecular studies investigating the effects of trans-10, cis-12 CLA. Choi et al.(2000) observed that the *trans*-10, *cis*-12 isomer of CLA resulted in a dose dependent reduction of Δ^9 desaturase gene expression and enzyme activity in mouse preadipocytes. However, human Δ^9 desaturase gene expression was not decreased as a

result of treatment with *trans*-10, *cis*-12 CLA (Choi et al., 2001). The authors suggested that the reduction in human Δ^9 desaturase activity was the result of a posttranslational mechanism.

The *trans*-10, *cis*-12 isomer of CLA affects other aspects of lipid metabolism. Mouse adipocytes treated with *trans*-10, *cis*-12 CLA demonstrated a reduced glucose and fatty acid uptake (Xu et al., 2003). Lipoprotein lipase activity was reduced (Lin et al., 2001; Xu et al., 2003). However, Xu et al. (2003) reported that *trans*-10, *cis*-12 CLA did not induce lipolysis. Similar results have been observed in human adipose tissue (Brown et al., 2001). Therefore, reduced adiposity may be a result of reduced lipogenesis rather than increased lipolysis. These findings have potential implications concerning human health.

Supplemental *trans*-10, *cis*-12 CLA may be detrimental to human health as a result of insulin resistance/increased blood glucose, increased blood fatty acids, and increased liver mass. Warren et al. (2003) fed mice diets supplemented with *trans*-10, *cis*-12 CLA or 18:2 cis-9, trans-11 CLA, or a control diet. The *trans*-10, *cis*-12 CLA supplemented mice had liver mass 100 % greater than those of the control group and had lipid content five times that of the control group. The 18:2 cis-9, trans-11 CLA supplemented mice did not differ from the mice fed the control diet.

Similar alterations in lipid metabolism in mammary tissues of dairy cows has been observed as a result of *trans*-10, *cis*-12 CLA administration, leading to potential mechanisms of action linking milk fat depression to *trans*-10, *cis*-12 CLA. In a study conducted by Baumgard et al. (2002b), mammary tissue biopsies were obtained from dairy cows abomasally infused with *trans*-10, *cis*-12 CLA. The authors observed an 82

% decrease in lipogenic capacity and reductions in the mRNA expression of acetyl CoA carboxylase, fatty acid synthetase, Δ^9 desaturase, lipoprotein lipase, fatty acid binding protein, glycerol phosphate acyltransferase, and acylglycerol phosphate acyltransferase. Similar results were observed by Peterson et al. (2003) when a high-concentrate diet was fed to dairy cows to induce milk fat depression.

However, dairy cows do not seem to experience the adipose tissue alterations in lipid metabolism as non-ruminants. Baumgard et al. (2002a) found that *trans*-10, *cis*-12 CLA had no effect on plasma glucose, insulin, leptin, and nonesterified fatty acids. There was a slight reduction in the ability to mobilize fatty acids stored in adipose tissue, as a reaction to an epinephrine challenge. The authors suggested that the cows were in a state of enhanced lipogenisis, perhaps due to an alteration in energy balance from reduced milk fat secretion. The infusion of *trans*-10, *cis*-12 CLA did lead to milk fat depression in this study. The authors concluded that the effects of *trans*-10, *cis*-12 CLA on lipid metabolism are specific for the mammary gland. This hypothesis is supported by the fact that when high-concentrate diets (analogous to a milk fat depressing diet) are fed to beef cattle, adipose tissue does not seem to be affected in the same manner and fat accumulates in the forms of subcutaneous and intramuscular fat. Similar results were observed by Perfield et al. (2002), who supplemented dairy cows with *trans*-10, *cis*-12 CLA for a period of 140 d. The authors observed that *trans*-10, *cis*-12 CLA did not alter body weight gain, body condition score, or net energy balance.

The effect of breed on fatty acid composition of ruminant products

Results from a study conducted by Pitchford et al. (2002) suggested that fatty acid composition, desaturase activity, and elongase activity are heritable. Itoh et al. (1999),

Laborde et al. (2001), and Mir et al. (2002) observed differences in some fatty acids as a result of cattle breed. However, no differences in CLA due to breed were observed (Laborde et al., 2001; Mir et al., 2002).

In contrast, Dhiman et al. (2002) observed differences in CLA content of milk due to dairy cow breed. In a pasture-based study, the authors observed that milk produced by Brown Swiss cows contained higher amounts of CLA than that from Holstein and Jersey cows. In a second experiment using conserved forages and grain, the authors observed that milk from Ayrshire and Holstein cows contained higher CLA than from Guernsey and Jersey cows.

Fatty acid content of products from forage-fed ruminants

Conjugated linoleic acid content of meat. Forage finishing of cattle may result in beef with higher CLA content, perhaps as a result of optimal ruminal biohydrogenation or Δ^9 desaturase activity. However, minimal research has been conducted evaluating the differences in CLA content of grain-finished versus forage finished beef. French et al. (2000) observed that with increasing amounts of pasture intake, the amount of CLA in the intramuscular fat of steers increased. The treatment diets were a high grass-silage diet, a high-concentrate diet, or pasture-based diets with grain supplementation. Grain was supplemented to the steers in decreasing amounts so that pasture intake would increase. The intramuscular fat contained 0.54, 0.66, and 1.08 g CLA/100 g fatty acids from the steers on pasture supplemented with grain at a rate of 5, 2.5, or 0 $kg \cdot head^{-1} \cdot d^{-1}$, respectively. The steers on a conventional grain-based diet had the lowest level of CLA (0.37 g/100 g fatty acids). The fat from steers fed a high-silage diet had an

intermediate level of CLA (0.47 g/100 g fatty acids) and was similar to the steers on pasture supplemented with the highest level of grain.

Steen and Porter (2003) compared the effects of a high-concentrate or a high-forage diet (perennial ryegrass pasture and silage) on the CLA composition of beef. The CLA content of the forage finished beef was 0.05, 0.02, 0.04, 0.06, and 1.98 g/100 g fresh tissue for the *gluteobiceps*, *semimembranosus*, *longissimus dorsi*, *deltoideous*, and subcutaneous fat, respectively. The CLA content of the grain-finished beef was 0.02, 0.01, 0.02, 0.02, and 0.58 g/100 g fresh tissue for the *gluteobiceps*, *semimembranosus*, *longissimus dorsi*, *deltoideous*, and subcutaneous fat, respectively. The data were also reported as total CLA content of total lipids. The CLA content of the *gluteobiceps*, *semimembranosus*, *longissimus dorsi*, *deltoideous*, and subcutaneous fat in the forage finished beef was 1.35, 0.96, 1.07, 1.24, and 2.26 g/100 g fatty acids, as compared to the CLA content in the grain-finished beef, which was 0.43, 0.33, 0.31, 0.47, and 0.70 g/100 g fatty acids, respectively.

Realini et al. (2004) compared the CLA content of forage versus grain-finished beef. The authors observed that the forage finished beef contained 0.41 g CLA/100 g fatty acids, and the grain-finished beef, 0.23 g CLA/100 g fatty acids. The pasture consisted of a mixture of perennial ryegrass, birdsfoot trefoil, white clover, and tall fescue.

Shantha et al. (1997) observed that muscle tissue from cattle which consumed pasture alone had higher levels of CLA, compared to cattle on pasture that were allowed a cracked corn supplement. The CLA content of the muscle tissues was 0.77 and 0.52 g/100 g fat for the pasture only or pasture plus grain supplement groups, respectively.

Also, the authors observed that zeranol implantation of supplemented cattle had no effect on the CLA content of the beef. Similarly, Santos-Silva et al (2002) and Auroussearu et al. (2004) found that pasture-raised lambs had higher CLA content of meat, as compared to lambs raised on a high-concentrate diet. Rule et al. (2002) observed higher CLA concentrations in the muscles of range fed, as compared to feedlot fed beef cattle, and bison.

Conjugated linoleic acid content of milk. Riel (1963) observed that there was a seasonal variation in milk components. The author found that milk contained higher amounts of conjugated dienes during the summer, as compared to winter (1.46 versus 0.78 % of milk fat, respectively). Similarly, Timmen and Patton (1988) observed that grazing cows produced milk with a higher CLA content than cows fed grass silage in a barn (1.34 versus 0.27 % of milk fat, respectively). Dhiman et al. (1999a) and Ward et al. (2003) observed that as DMI of pasture increased, the CLA content of the milk also increased. The authors estimated that cows receiving all of their DMI from pasture-produced milk with a 500 % higher concentration of CLA, compared to conventionally-fed cows (2.2 versus 0.38 g/100 g fatty acids, respectively). Jahreis et al. (1997) observed cows that had high intake of pasture and legume/grass silages generally produced milk with a higher CLA content than cows that were confined and fed a corn silage based diet (0.80 versus 0.34 % of fatty acids, respectively). Kelly et al. (1998b) compared the CLA content of milk produced from cows grazing pasture or receiving a total mixed diet (control). The cows in the grazing group produced a higher amount of CLA in the milk, as compared to the control group (1.09 versus 0.46 % of fatty acids, respectively).

Similar results were observed by Loor et al. (2003b), where the cows were allowed access to pasture (either in the morning or afternoon) in addition to a total mixed diet (access in the afternoon or morning, respectively). The cows that grazed pasture in the afternoon produced the highest level of CLA, perhaps due to a lower intake of the total mixed diet, and presumably higher pasture intake. However, Jiang et al. (1996) observed no differences in the CLA content of milk from cows fed forage at either 50 or 35 % of the diet (0.66 versus 0.50 g/100 g fat). The lack of response to forage level was perhaps due to the fact that the forages used were preserved (silage and hay) instead of fresh pasture. Additionally, the highest level of forage utilized was only 50 % of the diet. Dhiman et al. (1999a) found no differences in the CLA content of milk from cows fed 98, 66, or 50 % grass hay diet. Also, they noted that neither coarsely chopped or finely chopped hay influenced the CLA content of milk.

Incorporation of legumes in the diets of cattle may be beneficial to CLA production. Dewhurst et al. (2003) observed that cows consuming red clover or a red clover/ryegrass silage had higher CLA levels in their milk than cows consuming ryegrass silage (0.42, 0.45, and 0.36 % of fatty acids, respectively). However, cows consuming white clover silage produced milk with the lowest level of CLA (0.34 % of fatty acids).

Effect of oil supplementation on CLA content of ruminant products

Conjugated linoleic acid content of meat. McGuire et al. (1998) observed that feeding steers with high-oil corn did not result in increased CLA in muscle tissue, except when the amount of silage in the diet increased from 12 to 20 %. The high-oil corn with 12 % silage diet resulted in 0.38 g CLA/100 g lipid extracted from the muscle tissue,

while the high-oil corn with 20 % silage resulted in 0.49 g CLA/100 g lipid. A normal oil corn control diet with 12 % silage resulted in 0.39 g CLA/100 g lipid in the meat.

Madron et al. (2002) observed an increase in the CLA content of fat from steers fed a diet supplemented with full-fat soybeans, compared to a control diet containing corn and soybean meal. The fat samples contained 0.66, 0.67, and 0.77 g CLA/g fatty acids from steers fed a control diet, a diet containing 12.7 %, and a diet containing 25.6 % full-fat soybeans, respectively. Similar results were obtained by Ivan et al. (2001), Mir et al. (2000), Mir et al. (2002), Gibb et al. (2004), and Marks et al. (2004).

Beaulieu et al. (2002) found that supplementing a high corn diet with 2.5, 5.0, or 7.0 % soybean oil did not increase the 18:2 *cis*-9*, trans*-11 CLA content of heifer adipose tissue, which averaged 0.10 mg/100 g fatty acid. The authors observed an increase in 18:1 *trans* fatty acids and 18:2 *trans*-10, *cis*-12 CLA. Gillis et al. (2004) also observed a marginal increase in the 18:2 *cis*-9*, trans*-11 CLA and a substantial increase in the 18:2 *trans*-10, *cis*-12 CLA content of beef from heifers fed a high-concentrate diet supplemented with 4 % corn oil or 2 % rumen protected conjugated linoleic acid salt. The 18:2 *cis*-9*, trans*-11 CLA content of adipose tissues was 0.59, 0.66, and 0.67 g/100 g fatty acids, and the 18:2 *trans*-10, *cis*-12 CLA content was 0.005, 0.015, and 0.015 g/100 g fatty acids for the control, corn oil, and rumen-protected CLA treatments, respectively. Kott et al. (2003) observed a 2.25 fold increase in 18:2 *cis*-9*, trans*-11 CLA and a 6 fold increase in 18:2 *trans*-10, *cis*-12 CLA lamb adipose tissues supplemented with safflower seeds at 15 % of the diet. Similar results were obtained by Bolte et al. (2002). However, Griswold et al. (2003) observed a decrease in the 18:2 *cis*-9*, trans*-11 CLA content of

beef as a result of soybean oil supplementation of a high-concentrate diet (3.1 versus 2.5 mg/g fatty acids).

Conjugated linoleic acid content of milk. Dhiman et al. (1999a) found that high-oil corn silage did not increase CLA in milk. However, Dhiman et al. (2000) observed that soybean oil supplementation increased CLA in milk, as compared to the control. Linseed oil supplementation also increased the CLA in milk. The CLA content of the milk in the control group, 3.6 % soybean oil, and 4.4 % linseed oil groups was 0.39, 2.10, and 1.63 % of fatty acids, respectively. Similarly, Chouinard et al. (2001) observed increases in CLA content of milk due to diet supplementation with canola oil, soybean oil, and linseed oil. The authors also observed that extrusion and roasting of soybeans resulted in an increased level of CLA in milk, compared to raw, ground soybeans. Fish oil supplementation also increased the amount of CLA in milk.

Similar to the results observed by McGuire et al. (1998), a small increase in the CLA content of milk as a result of feeding high-oil corn silage was observed by Chouinard et al. (2001). The CLA content of milk from cows fed normal corn was 2.8 mg/g fatty acid, while the CLA content of milk from cows fed high-oil corn was 4.6 mg/g fatty acid. Similar results with oil supplementation were observed by Lawless et al. (1998), Dhiman et al. (1999b), Donovan et al. (2000), Solomon et al. (2000), Abu-Ghazaleh et al. (2002), Loor et al. (2002b), Ward et al. (2002), Whitlock et al. (2002), Schroeder et al. (2003), Ward et al. (2003), and Whitlock et al. (2003). However, Kelly et al. (1998a) observed a 500 % increase in the CLA content of milk when the diet was supplemented with sunflower oil.

The effect of forage level and oil supplementation on 18:1 and CLA biohydrogenation

As forage level in the diet of ruminants was decreased, microbial production of *trans*-10, *cis*-12 CLA was increased and 18:2 *cis*-9*, trans*-11 CLA was decreased (Kucuk et al., 2001). Additionally, production of the CLA precursor (vaccenic acid) was decreased when high-concentrate diets were fed. The production of an alternate isomer (*trans*-10 18:1) was increased (Loor et al., 2003a, 2004).

Oil supplementation of high-concentrate diets appears to further contribute to the alterations in CLA and 18:1 fatty acid metabolism. Kucuk et al (2004) observed that when increasing levels of soybean oil were added to a high-concentrate diet, ruminal production of *trans*-10, *cis*-12 CLA was increased. Increased production of *trans*-10 18:1 was observed in dairy cows grazing pasture (predominantly perennial ryegrass) supplemented with soybean oil at 450 g/d (Kay et al., 2004). Duckett et al. (2002) conducted an experiment where high-oil corn replaced typical corn, or corn oil was added to a high-concentrate diet fed to steers. The high oil corn resulted in increased production of *trans*-10 18:1 and *trans*-10, *cis*-12 CLA. The corn oil supplementation resulted in the *trans*-10 18:1 and *trans*-10, *cis*-12 CLA being produced at a higher amount than vaccenic acid and 18:2 *cis*-9*, trans*-11 CLA. Similar results were observed by Sackmann et al. (2003) using different forage and sunflower oil supplementation levels. Shingfield et al. (2003) observed that soybean oil supplementation (which provided 18:2) stimulated *trans*-10 18:1 and *trans*-10, *cis*-12 CLA formation. Jenkins and Fellner (2002) observed that when soybean oil and monensin were used in combination in a continuous culture fermenter study, production of *trans*-10 18:1 was increased.

Kucuk et al. (2001) observed a decrease in duodenal flow of vaccenic acid when dietary forage was increased in ewes. Loor et al. (2004) observed an increase in 18:2 *cis*-9*, trans*-11 CLA and no change in *trans*-10, *cis*-12 CLA with linseed oil supplementation of either a low or high-concentrate diet. Similar results were observed by Loor et al. (2002a) with soybean oil supplementation. Kucuk et al. (2004) observed no change in 18:2 *cis*-9*, trans*-11 CLA when soybean oil was added to the diets in increasing amounts.

Loor et al. (2003a) observed increases in 18:2 *cis*-9*, trans*-11 and *trans*-10, *cis*-12 CLA, and *trans*-10 18:1 and vaccenic acid with increasing ground corn supplementation of a forage-based diet. Loor and Herbein (2003a) observed an increase in both *trans*-10 18:1 and vaccenic acid, and 18:2 *cis*-9*, trans*-11 CLA, but no change in *trans*-10, *cis*-12 CLA with soybean oil supplementation. Loor et al. (2002a) observed increases in *trans*-10 18:1 and vaccenic acid with oil supplementation. Loor et al. (2002a) and Mosley et al. (2002) observed that *trans*-10 18:1 is produced from oleic acid, and *trans*-10 18:1 concentrations increase when oleic acid is supplemented.

These conflicting results may explain why oil supplementation does not consistently increase the 18:2 *cis*-9*, trans*-11 CLA content of ruminant products. Perhaps individual animal variation, diet characteristics, supplemental oil type, fatty acid composition, and quantity may all influence the biohydrogenation of C18 fatty acids. In general, it would appear that oil supplementation of a high-concentrate diet further contributes to the increased production of *trans*-10, *cis*-12 CLA and *trans*-10 18:1, while decreasing the production of 18:2 *cis*-9*, trans*-11 CLA and vaccenic acid.

The omega-3 fatty acid content of ruminant products

Omega-3 fatty acid content of meat from forage-fed livestock. Omega-3 fatty acids are higher in forage-fed as compared to grain-fed beef (Shantha et al., 1997; French et al., 2000). Increased intake of pasture resulted in increased concentrations of 18:3 and 20:5 *n*-3 PUFA in beef (French et al., 2000). The authors observed that grain-fed beef contained 0.72 and 0.12 g/100 g fatty acid of 18:3 and 20:5, respectively, while the pasture-finished beef contained 1.13 and 0.23 g/100 g fatty acid of 18:3 and 20:5, respectively. Forage-finished, as compared to grain-supplemented beef also contained higher amounts of 18:3 and 22:6 *n*-3 PUFA (Shantha et al., 1997). The forage-finished beef contained 0.53 and 0.24 g/100 g fat of 18:3 and 22:6, respectively, while the grain-supplemented beef contained 0.28 and 0.09g/100 g fat of 18:3 and 22:6. Itoh et al. (1999), Rule et al. (2002), Yang et al. (2002b), Steen et al. (2003), Aurousseau et al. (2004), and Realini et al. (2004) also observed higher *n*-3 PUFA in forage-finished beef, compared to grain-finished. Similar differences in the concentrations of 18:3, 20:5, 22:5, and 22:6 *n*-3 PUFA between lambs finished on grass or grain were observed (Fisher et al., 2000; Santos-Silva et al., 2002).

Duckett et al. (1993) found that as time on a grain-based diet increased, the omega-3 fatty acid content of the beef decreased. The cattle were previously on an all-forage pasture-based diet. The highest omega-3 fatty acid concentrations were observed in beef obtained from steers that served as the forage-finished control, which were harvested at d 0, when the remaining steers were switched to the high-concentrate diet.

Omega-3 fatty acid content of meat from supplemented livestock. Linseed oil supplementation of steers, compared to the control group, resulted in increased levels of

18:3 *n*-3 (0.019 versus 0.010 mg/100 g muscle) and 20:5 *n*-3 (0.015 versus 0.010 mg/100 g muscle) (Scollan et al., 2001a). The authors also observed that fish oil supplementation doubled the amounts of 20:5 *n*-3 and 22:6 *n*-3 in muscle phospholipids. Andrae et al. (2001) also observed an increase in the 20:4 *n*-3 PUFA content of beef as a result of replacing typical corn with high-oil corn in a high-concentrate finishing diet. Similar results were observed in lambs (Lee et al., 2004) and steers (Ponnampalam et al., 2001a; Ponnampalam et al., 2001b; Mandell et al., 1997).

Objectives

The objectives of this research were to (i) determine the fatty acid composition of adipose tissue from cattle grazing pasture forages versus fed a high-concentrate diet, and changes with time (ii) evaluate vaccenic acid and 18:2 *cis*-9*, trans*-11 CLA production by rumen bacteria, (iii) compare the metabolism of dietary fatty acids and the production of 18:2 *cis*-9*, trans*-11 CLA in cattle finished on pasture and on a high-concentrate diet, over time, and (iv) relate the fatty acid composition of the dietary ingredients, ruminal fluid, and blood serum to adipose tissue fatty acids.

Materials and Methods

Finishing Study

Animals. All procedures were approved by the Virginia Tech Animal Care Committee. Twenty-four Angus crossbred steers (297.7 kg) were obtained from a stockering study conducted at Morgantown, WV, on April 21, 2003. The steers had been fed three diets formulated for three levels of ADG. The diets consisted of timothy (*Phleum pratense*) hay, soybean meal, soybean hulls, and a mineral supplement (Southern States SSC-377808 Livestock Mineral 6:1, Southern States Cooperative, Inc., Richmond, VA). Samples of diet ingredients were obtained for subsequent nutritive value and fatty acid analysis (Appendices A and B).

After the stockering phase the steers were blocked by body weight within stockering diet, and allotted at random to be finished in drylot on a corn silage-concentrate diet or on pasture. Steers were shipped from Morgantown to the finishing sites and were fed timothy hay in drylot until the following day, when the study began (Appendices A and C). Steers finished in drylot were kept at the Shenandoah Valley

Research and Extension Center, Steeles Tavern, VA, and those finished on pasture were kept at the West Virginia University Demonstration Farm, Willow Bend, WV. The drylot-kept steers were individually fed using Calan gates (American Calan, Northwood, NH). There were three pasture replicates at Willow Bend and three pens with 12 Calan gates in each at Steeles Tavern. At each location, 12 steers were allotted for the present study, and samples of ruminal fluid, blood, and adipose tissue were obtained at intervals (0, 28, 84, 140 d).

Treatments. The high concentrate diet consisted of corn silage, cracked corn, soybean meal, and a vitamin and mineral supplement (Table 1). Complete ingredient composition of the diet is shown in Appendix D. For the steers on the high concentrate diet, there was a transition period from hay to the high concentrate diet over a 7-d period. The diet was self-fed, and refusals were removed and new feed was fed once daily.

The pasture-finished steers were sequentially grazed on pastures comprised of triticale (*Triticale hexaploide*)/annual ryegrass (*Lolium multiflorum*), alfalfa (*Medicago sativa*)/orchardgrass (*Dactylis glomerata*), and a cool-season grass/legume mixture. The cool season grass/legume mixture consisted primarily of tall fescue (*Festuca arundinacea*), orchardgrass, Kentucky bluegrass (*Poa pratensis*), and white clover (*Trifolium repens*). Dates and forage types that steers grazed at Willow Bend, WV are presented in Appendix E. While on pasture, the steers had access to a mineral supplement (Vigortone FC No. 35S, Vigortone Ag Products, Cedar Rapids, IA). Complete chemical and fatty acid composition of the high-concentrate diets and pasture forages are shown in Appendices F, G, H, I, J, K, and L.

Table 1. Average ingredient composition of high-concentrate diets fed to steers at Steeles Tavern, VA

	Ingredient[ab]				
Time	Silage	Corn	Soybean meal	Limestone	TM salt[c]
	----------%----------				
d 0 to 28	88.77	1.75	8.90	0.22	0.37
d 28 to 84	37.45	55.60	6.53	0.16	0.27
d 84 to 140	17.47	76.60	5.57	0.14	0.23

[a]DM basis.
[b]Vitamin A added to the diet to provide 20,000 IU·head^{-1}·d^{-1}.
[c]Champions Choice, Cargill Inc., Minneapolis, MN.

Sample collection. Ruminal fluid, blood, and adipose tissue samples were obtained initially, and on d 28, 84, and 140, beginning at approximately 0800 at Steeles Tavern and 1300 at Willow Bend. Pasture forage samples were collected at Willow Bend immediately after samples were obtained from the animals. Pasture forage samples were also obtained at 14 d intervals throughout the study, beginning at approximately 0800.

Ruminal fluid was collected using a stomach tube with a strainer and a vacuum pump, then filtered through four layers of cheesecloth. A pH measurement of each sample was taken at that time using a portable pH meter (Acumet Mini pH Meter, Model AP61, Fisher Scientific Co., Pittsburgh, PA). Approximately 200 mL of filtered ruminal fluid was obtained for long-chain fatty acid analysis. Additionally, a 5 mL aliquot of ruminal fluid was preserved for VFA analysis. The 5 mL aliquot was placed in a 15 mL plastic storage tube containing 1 mL of metaphosphoric acid and 5 mL of an internal standard solution (20 μmol/mL 4-methyl valeric acid; Sigma Chemical Co., St. Louis, MO). Blood samples were obtained by jugular venipuncture, using two (15 mL) Vacutainer (no additive) tubes (Becton Dickinson Corp., Franklin Lakes, NJ).

Biopsies were conducted to obtain subcutaneous adipose tissue samples from the gluteal area immediately cranial to the tailhead, on the left side. The biopsy site was clipped and surgically prepared with three alternate scrubs of 100% isopropyl alcohol and a 7.5% povidone-iodine solution (Betadine Surgical Scrub, The Purdue Frederick Co., Stanford, CT). Lidocaine (total of 10 cc/animal) was injected subcutaneously cranial to the site. A linear incision (approximately 5 cm) was made with a sterile scalpel through the skin. Approximately 1 g of adipose tissue was obtained. The incision was stapled

closed. Penicillin (20 cc) was administered subcutaneously to minimize infection. Fly spray was administered, as needed.

The ruminal fluid (for long-chain fatty acid analysis) and adipose tissue samples were immediately placed on dry ice ($CO_{2\,(s)}$). The blood and ruminal fluid (for VFA analysis) samples were immediately placed on ice. Upon arrival at the laboratory, the blood was centrifuged at 816 x g for 15 min and serum was collected. The diet, ruminal fluid, serum, and adipose tissue samples were frozen at -65°C until later analysis.

Random grab samples of the forage from the pastures the steers were grazing at the time of sampling were collected. Also, samples from all pastures that the steers had grazed since the previous forage sampling date were collected. Two diagonal strips (in a criss-crossed pattern) were sampled per field, by stopping at regular intervals (every 10 to 30 steps, depending on pasture size) and clipping a handful of forage at approximately 5-cm cutting height. A portion (approximately 200 to 300 g, fresh weight) of each sample was double-bagged in plastic sample bags for macro DM (AOAC, 2000) and subsequent nutritive value determination. For subsequent fatty acid analysis, the remainder of each sample was placed into small cloth sample bags, immediately frozen in liquid N and placed in a cooler with dry ice. Upon return to the laboratory, the samples were stored in a freezer at -20°C. Corn silage, cracked corn, soybean meal and supplement samples were obtained daily, composited over the 14-d periods, and subsampled. The corn silage samples were frozen immediately after collection (-20°C).

Chemical analysis

Nutritive value. All feeds and pasture forages were ground to pass through a 1 mm screen using a Wiley mill (Thomas Wiley, Laboratory Mill Model 74, Arthur H.

Thomas Co. Philadelphia, PA). Prior to grinding, pasture forage samples were dried in a force draft oven at 60°C for 48 h. Micro DM was determined (AOAC, 2000). The forage and feed samples were sequentially analyzed for NDF, ADF, cellulose and lignin, (Goering and Van Soest, 1970), as modified by using the fiber bag technology of Ankom (Ankom Technology Corp., Fairport, NY). Freeze-dried silage and pasture forage samples were utilized in N analysis due to potential N volatilization as a result of oven drying. The forage and feed samples were analyzed for total N by the combustion method (AOAC, 2000) using a Perkin Elmer 2410 Nitrogen Analyzer (Perkin Elmer, Norwalk, CT). Total N was used to calculate CP (AOAC, 2000). Freeze-dried pasture forage samples were ground to 0.5mm using a Wiley mill and analyzed for total nonstructural carbohydrates (TNC) by the method of Smith (1981). However, due to potential diurnal variations in TNC, only the pasture forage samples collected on d 0, 28, 84 and 140 were analyzed. Water-soluble carbohydrate analysis was conducted on freeze-dried silage samples (ground to 0.5 mm) by utilizing the first step of the carbohydrate analysis method (for starch accumulators) of Smith (1981). Preserved silage extracts were analyzed for lactic acid using the colorimetric method of Barker and Summerson (1941), as modified by Pennington and Summerson (1956).

Mineral supplements were analyzed for Ca and P content. Samples were digested with 2:1 HNO_2:$HClO_4$ (Muchovej et al., 1986). Calcium was analyzed by flame atomic absorption spectroscopy (Perkin Elmer AAnalyst 800, Norwalk, CT). Phosphorus was determined colormetrically on a Titertek Multiscan MCC/340 (Titertek, Huntsville, AL) by the method of AOAC (2000).

Long chain fatty acid analysis. The fatty acid composition of forage, feed, ruminal fluid, serum, and adipose tissue was determined. Prior to analysis, pasture and silage samples were freeze-dried (FreeZone 12L Freeze Dry System, Labconco Corp., Kansas City, MO) (Appendices M and N) and ground to pass through a 0.5-mm screen using a Wiley mill (Thomas Wiley, Laboratory Mill Model 74, Arthur H. Thomas Co. Philadelphia, PA). Ground forage samples were composited within replication for the 14-d periods. Cracked corn and soybean meal samples were also ground to pass through a 0.5-mm screen. Ruminal fluid was freeze-dried and ground with a mortar and pestle (Appendices M and N). Adipose tissue samples were freeze-dried (Appendices M and N) and homogenized (Tissuemizer SDT-1810, Techmar Co., Cincinnati, OH).

Sample extraction and methylation of fatty acids was conducted by modification of the methods of Folch et al. (1957) and Park and Goins (1994) (Appendix O). Briefly, 500 mg of forage, 300 mg of corn, 1.0 g of soybean meal, 200 mg of soybean hulls, 500 mg of ruminal fluid, 15 to 20 mg of adipose tissue, or 2 mL of serum were extracted. Ground or liquid samples were vortexed and adipose tissue was homogenized in 2:1 chloroform:methanol. After a 1 h extraction, samples were filtered (Whatman filter paper, 541), and 0.88 % KCl was added to the sample. The sample was then shaken, centrifuged, and the aqueous layer discarded. The solvent was evaporated under N_2 using N-EVAP 112 Nitrogen Evaporation System (Organomation Associates Inc., Berlin, MA) and the samples were stored at -65°C until methlyation. For methylation, methylene chloride, hexane containing an internal standard, and 0.5N NaOH were added to the samples. The samples were heated at 90-95°C for 10 min in a hot water bath. A 14 % solution of BF_3 in methanol was added to each sample and heated as previously

described. Deionized H_2O and hexane were added to each sample, the samples were then shaken and centrifuged. Anhydrous Na_2SO_4 was added to the samples and an aliquot of the top (hexane) layer was collected for fatty acid analysis. Samples were stored at -65°C until analysis.

Analysis of fatty acid methyl esters (FAME) was performed on a HP 6890N gas chromatograph equipped with an autoinjector, autosampler, and flame ionization detector (Agilent Technologies, Inc., Wilmington, DE). Separation of FAME was performed using a 100 m x 0.25 mm internal diameter x 0.2 μm film thickness SP-2560 capillary column (Supelco, Bellefonte, PA). Ultra-pure H_2 was the carrier gas and ultra-pure N_2 was the make-up gas. The carrier gas was filtered prior to introduction into the instrument using an Agilent High Capacity Gas Purification System containing a hydrocarbon/moisture, high capacity oxygen, and indicating oxygen cartridges (Agilent Technologies, Inc., Wilmington, DE). Ultra-pure (net zero grade) air and ultra-pure H_2 were used by the flame ionization detector.

The gas chromatograph conditions for analysis of adipose tissue, forage, feed, and ruminal fluid samples were as follows: The injection amount was 0.5 μL and the split ratio was 70:1. A split inlet liner was used. The inlet temperature and pressure were held constant at 250ºC and 158.58 kPa, respectively. The oven was initially held for 1 min at 70ºC, then increased by 5ºC/min to 100º (held for 3 min), next increased by 10ºC/min to 175ºC (held for 45 min), and finally increased by 5ºC/min to 220ºC (held for 25 min). The detector was maintained at 300ºC. The H_2 flow at the detector was 30.0 mL/min and the air flow was 400.0 mL/min. The N_2 flow was 30.0 mL/min (constant make-up flow).

The gas chromatograph conditions for analysis of serum samples were as follows: The splitless injection amount was 1.0 µl. A split/splitless inlet liner was used. The purge valve was closed for 0.55 min after injection. The inlet temperature and pressure were held constant at 225ºC and 144.79 kPa, respectively. The oven was initially held for 1 min at 40ºC, then increased by 40ºC/min to 100ºC (held for 10 min), next increased by 25ºC/min to 175ºC (held for 45 min), and finally increased by 10ºC/min to 220ºC (held for 23 min). The detector was maintained at 300ºC. The H_2 flow at the detector was 30.0 mL/min and the air flow was 400.0 mL/min. The N_2 flow was 30.0 mL/min (constant make-up flow).

Fatty acid identification and quantification were performed using ChemStation Software 10.01 (Agilent Technologies, Inc., Wilmington, DE) by comparison to known standards (Matreya, L.L.C., Pleasant Gap, PA; Nu-Chek Prep, Inc., Elysian, MN) (Appendix P). Fifty µg of the nonesterified fatty acid form of 10-undecenoic acid (11:1) was included in all samples as the internal standard. Total fatty acids were calculated by summation of the fatty acids quantified (12:0, 14:0, 14:1, 15:0, 16:0, 16:1, 17:0, 17:1, 18:0, 18:1 *cis*-9, 18:1 *trans*-10, 18:1 *trans*-11, 18:2 *n*-6, 18:3 *n*-3, 20:2 *n*-6, 20:3 *n*-3, 20:4 *n*-6, 22:2 *n*-6, 22:3 *n*-3, 22:4 n-6, 22:5 *n*-3, 22:6 *n*-3).

Volatile fatty acid analysis. Ruminal fluid and silage samples were analyzed for VFA. Prior to analysis, silage samples were extracted by placing 25 g of wet silage and 225 mL of water in a blender (Osterizer 10-speed blender, Oster Corp., Milwaukee, WI). Samples were blended for 2 min and filtered through 4 layers of cheesecloth. An aliquot of silage extract was preserved. A 5 mL aliquot was placed in a 15 mL plastic storage tube containing 1 mL of metaphosphoric acid and 5 mL of an internal standard solution

(20 µmol/mL 4-methyl valeric acid; Sigma Chemical Co., St. Louis, MO). Preserved ruminal fluid and silage samples were filtered using 0.45 µm filters (MP Biomedicals, Inc., Aurora, OH). Analysis was conducted on a HP 6890N gas chromatograph equipped with an autoinjector, autosampler, and flame ionization detector (Agilent Technologies, Inc., Wilmington, DE). Acetic, propionic, butyric, valeric, isovaleric, and isobutyric were separated on a 30 m x 0.53 mm internal diameter x 1.0 µm film thickness DB-WAXetr megabore column (Agilent Technologies, Inc., Wilmington, DE). A 10 m guard column was used. The gas chromatograph conditions for analysis of VFA were as follows: inlet and detector temperature were both 250 ºC. The oven was initially held for 5 min at 125ºC, then increased by 15ºC/min to 180ºC (held for 6 min). Ultra-pure He was the carrier gas. The carrier gas flow was 4.2 mL/min. Ultra-pure (net zero grade) air and ultra-pure H_2 were used by the flame ionization detector, with flow rates of 450 and 40 mL/min, respectively. The injection amount was 0.5 µL, with a split ratio of 47:1. Individual VFA were identified by comparison to known standards (acetic acid, 50 µmol/mL; propionic acid, 30 µmol/mL; butyric acid, 11 µmol/mL; valeric acid, 5 µmol/mL; isovaleric acid, 5 µmol/mL; isobutyric acid, 5 µmol/mL; Sigma Chemical Co., St. Louis, MO).

Statistical Analyses

Long chain fatty acid, VFA, and ruminal fluid pH data were analyzed using the PROC GLM procedure of SAS (SAS Inst., Inc., Cary, NC) with animal as the experimental unit. The model statement included the effects treatment, date, and treatment x date interaction. Least squares means for treatment, date, and their interaction were generated and compared using Student's t-test. Specific contrasts were

performed, including a comparison of treatment effects within in date, and date effect comparisons within treatment (d 0 versus 28, d 0 versus 84, d 0 versus 140, d 28 versus 84, and d 84 versus 140).

Pasture forage fatty acid and nutritive value data were analyzed using the PROC GLM procedure of SAS. The model included date and replication. Least squares means were generated for dates.

Results and Discussion

Chemical composition of pasture forages and diets

Complete chemical and fatty acid composition of the high-concentrate diets and pasture forages are shown in Appendices F, G, H, I, J, K, and L. Average fiber components NDF (34.80 to 47.73 % of DM), ADF (17.86 to 27.73% of DM), cellulose (17.20 to 28.83 % of DM) and lignin (2.29 to 3.39 % of DM) increased in the silage in the high-concentrate finishing diets over time (Table 2). Average CP (7.84 to 9.73 % of DM) increased over time, and average water soluble carbohydrate decreased (50.02 to 32.43 % of DM) over time in the silage. Average fiber components in corn remained relatively constant throughout the study, as any changes in values were small. Average CP values in corn decreased from period 1 (d 0 to 28) to period 2 (d 28 to 84), then increased from period 2 to 3 (d 84 to 140). Average fiber components NDF, ADF, cellulose, and lignin decreased from period 1 to period 2, then increased from period 2 to 3 in soybean meal. The opposite effect was observed for soybean meal average CP, which increased from period 1 to 2, then decreased during the remainder of the study.

Average silage lactic acid, acetate, and butyrate concentrations decreased throughout the study (Table 3). Other volatile fatty acids were not detected in the silage samples. Average Ca content of the mineral supplements fed to steers in high-concentrate finishing treatment decreased slightly throughout the study, while average P remained relatively constant (Table 4).

The primary fatty acids in the high-concentrate diets consisted of palmitic acid (16:0), 4.15 to 7.54 mg/g DM, 11.93 to 15.80 % of total fatty acids, oleic acid (18:0),

Table 2. Average chemical composition of the high-concentrate diet ingredients fed to steers at Steeles Tavern, VA

			Component[a]						
Time	Ingredient	n	DM	NDF	ADF	Cellulose	Lignin	CP	WSC[b]
			----------%----------						
d 0 to 28	Corn silage	2	42.02	34.80	17.86	17.20	2.29	7.84	50.02
	Corn grain	1	87.04	10.56	2.17	3.08	0.68	7.94	-
	Soybean meal	2	90.11	11.62	5.10	5.94	0.90	49.88	-
d 28 to 84	Corn silage	4	41.64	42.10	23.05	21.96	2.83	9.11	43.24
	Corn grain	4	87.82	10.35	2.23	3.15	0.81	7.57	-
	Soybean meal	4	89.22	8.26	4.06	5.02	0.70	51.40	-
d 84 to 140	Corn silage	4	47.98	47.73	27.73	25.83	3.39	9.73	32.43
	Corn grain	4	85.97	10.03	2.02	2.96	1.00	8.05	-
	Soybean meal	4	87.40	9.08	4.32	5.29	0.85	50.72	-
SE	Corn silage		1.1669	1.8855	1.4373	1.2551	0.1720	0.2724	2.6900
	Corn grain		0.4544	0.2642	0.0859	0.0679	0.0500	0.1893	-
	Soybean meal		0.4501	0.5696	0.1740	0.1451	0.0632	0.4869	-

[a]DM basis.
[b]Water soluble carbohydrates.

Table 3. Average lactic acid and volatile fatty acid composition of corn silage fed to steers at Steeles Tavern, VA

	Component[ab]		
Time	Lactate	Acetate	Butyrate
	----------%----------		
d 0 to 28	2.25	2.20	0.23
d 28 to 84	1.65	2.07	0.17
d 84 to 140	1.07	0.78	-
SE	0.2034	0.2645	0.0285

[a]DM basis.
[b]Number of samples = 10.

Table 4. Average calcium and phosphorus composition of the mineral supplements fed to steers at Steeles Tavern, VA

	Component[ab]	
Time	Ca	P
	----------%----------	
d 0 to 28	5.94	0.41
d 28 to 84	5.69	0.43
d 84 to 140	5.61	0.44
SE	0.2263	0.0089

[a]DM basis.
[b]Number of samples = 10.

8.60 to 9.62 mg/g DM, 19.93 to 27.63 % of total fatty acids, and linoleic acid (18:2 *n*-6), 19.75 to 27.88 mg/g DM, 56.74 to 58.39 % of total fatty acids (Table 5). Each of the remaining fatty acids consisted of less than 1.5 mg/g DM or 3.1 % of total fatty acids. These values are similar to the fatty acid composition of high-concentrate diets observed by other researchers. Kalscheur et al. (1997) observed concentrations of 6.3, 20.8, and 2.5 mg/g DM of palmitic acid, linoleic acid, and linolenic acid (18:3 *n*-3), respectively, in a total mixed diet fed to dairy cows. French et al. (2000) found that palmitic acid, linoleic acid, and linolenic acid comprised 32.7, 16.53, and 1.86 % of total fatty acids in a high-concentrate diet fed to steers. In a high-grain diet fed to goats, palmitic acid, linoleic acid, and linolenic acid concentrations were 15.7, 48.3, and 2.3 % of total fatty acids (Rhee et al., 2000).

In the current study, concentrations (mg/g DM and % of total fatty acids) of palmitic acid decreased over time. Concentrations (mg/g DM) of oleic acid (18:1 *cis*-9) changed minimally during the study. When expressed as percentage of total fatty acids, oleic acid increased throughout the study. Concentrations (mg/g DM and % of total fatty acids) of linoleic acid decreased over time. These changes in fatty acids over time may be due to changes in the ingredient composition of the diets during the study (Table 1). The palmitic acid content of silage (4.90 to 8.0 g/g DM) and soybean meal (4.02 to 7.95 mg/g DM) tended to be higher than corn (1.89 to 4.59 mg/g DM), as shown in Appendix J. During the earlier sampling dates silage was higher in linoleic acid than corn, but during the later sampling dates the opposite was seen. Soybean meal linoleic acid content was similar to corn. Overall, linoleic acid values ranged from 13.15 to 33.28 mg/g DM. Concentrations of linolenic acid ranged from 0.18 to 3.5 mg/g DM.

Table 5. Average fatty acid composition of diets fed to steers at Steeles Tavern, VA

Fatty acid	Time			SE
	d 0 to 28	d 28 to 84	d 84 to 140	
	----------mg/g DM----------			
Myristic (14:0)	0.04	0.02	0.01	0.0021
Pentadecylic acid (15:0)	0.22	0.12	0.06	0.0126
Palmitic (16:0)	7.54	4.71	4.15	0.3123
Palmitoleic (16:1 *cis*-9)	0.06	0.04	0.02	0.0057
Stearic (18:0)	0.87	0.56	0.70	0.0321
Oleic (18:1 *cis*-9)	9.52	8.60	9.62	0.3049
Linoleic (18:2 *n*-6)	27.88	19.84	19.75	1.6734
Linolenic (18:3 *n*-3)	1.46	0.76	0.46	0.0987
20:2 *n*-6	0.15	0.07	0.04	0.0067
Total fatty acids[a]	47.75	34.71	34.80	
	----------% of total fatty acids----------			
Myristic (14:0)	0.09	0.05	0.03	0.0100
Pentadecylic acid (15:0)	0.46	0.32	0.16	0.0479
Palmitic (16:0)	15.80	13.42	11.93	0.5458
Palmitoleic (16:1 *cis*-9)	0.12	0.10	0.05	0.0126
Stearic (18:0)	1.82	1.60	2.03	0.0843
Oleic (18:1 *cis*-9)	19.93	25.07	27.63	1.0714
Linoleic (18:2 *n*-6)	58.39	57.05	56.74	0.3385
Linolenic (18:3 *n*-3)	3.06	2.19	1.33	0.2471
20:2 *n*-6	0.32	0.19	0.11	0.0302

[a]Includes the fatty acids measured.

Therefore, the proportions of individual diet ingredients and their fatty acid composition may have contributed to the variations in fatty acids observed.

Fiber components, NDF and lignin, increased over time in the pasture forages (Table 6). Pasture forage ADF, cellulose, and total nonstructural carbohydrate (TNC) values increased from period 1 to 2, then decreased from period 2 to 3. The opposite effect was observed for CP concentrations, which decreased from period 1 to 2, then increased from period 2 to 3.

The primary fatty acid in pasture forages was linolenic acid (18:3 *n*-3), 14.76 to 39.82 mg/g DM, 61.55 to 72.90 % of total fatty acids (Table 7.) Other fatty acids in relatively higher proportions were pentadecylic acid (15:0), palmitic acid (16:0), and linoleic acid (18:2 *n*-6). French et al. (2000) reported that palmitic acid, linoleic acid, and linolenic acid comprised 20.8, 14.0, and 49.2 % of total fatty acids in grass pastures grazed by steers. Dhiman et al. (1999b) observed concentrations 35.8, 15.3, and 21.5 % of total fatty acids for palmitic acid, linoleic acid, and linolenic acid, respectively in alfalfa hay. Scollan et al. (2001) evaluated the fatty acid composition of perennial ryegrass silage, and observed concentrations of 16.6, 15.1, and 51.7 % of total fatty acids for palmitic acid, linoleic acid, and linolenic acid, respectively.

In the current study, concentrations (% of total fatty acids) of linolenic acid in pasture forages decreased over time, while concentrations of pentadecylic acid, palmitic acid, and linoleic acid increased over time. The changes observed in the fatty acid composition of the forages may be related to maturity, season, or weather.

Table 6. Average chemical composition of pasture forage samples at Willow Bend, WV

		Component[a]					
Time	n	NDF	ADF	Cellulose	Lignin	CP	TNC[b]
		----------%----------					
d 0 to 28	9	56.35	27.59	26.40	2.61	20.35	10.10
d 28 to 84	12	61.69	33.97	30.36	4.26	12.74	12.39
d 84 to 140	12	62.00	33.08	28.32	5.60	16.03	6.50
SE		0.2994	0.1339	0.1327	0.0947	0.1793	0.3648

[a]DM basis.
[b]Total nonstructural carbohydrates.

Table 7. Average fatty acid composition of pasture forage samples at Willow Bend, WV

Fatty acid	Time			SE
	d 0 to 28	d 28 to 84	d 84 to 140	
No. of samples	9	12	12	
	----------mg/g DM----------			
Myristic (14:0)	0.05	0.05	0.05	0.0015
Pentadecylic acid (15:0)	3.09	1.86	1.89	0.0532
Palmitic (16:0)	5.07	3.28	3.01	0.1341
Palmitoleic (16:1 *cis*-9)	0.36	0.14	0.14	0.0099
Stearic (18:0)	0.26	0.25	0.23	0.0141
Oleic (18:1 *cis*-9)	0.53	0.57	0.35	0.0318
Linoleic (18:2 *n*-6)	3.65	2.56	2.41	0.0929
Linolenic (18:3 *n*-3)	39.82	18.02	14.76	0.6534
20:2 *n*-6	0.27	0.24	0.21	0.0062
22:2 *n*-6	0.30	0.31	0.18	0.0084
DPA (22:5 *n*-3)	0.27	0.20	0.19	0.0077
DHA (22:6 *n*-3)	0.59	0.32	0.35	0.0139
Total fatty acids[a]	54.25	27.78	23.78	
	----------% of total fatty acids----------			
Myristic (14:0)	0.09	0.20	0.21	0.0049
Pentadecylic acid (15:0)	5.75	6.89	8.24	0.1982
Palmitic (16:0)	9.48	11.92	12.66	0.1968
Palmitoleic (16:1 *cis*-9)	0.64	0.52	0.59	0.0233
Stearic (18:0)	0.48	0.91	0.97	0.0452
Oleic (18:1 *cis*-9)	1.03	2.14	1.54	0.1026
Linoleic (18:2 *n*-6)	6.92	9.41	10.13	0.1761
Linolenic (18:3 *n*-3)	72.90	63.90	61.55	0.4620
20:2 *n*-6	0.50	0.90	0.92	0.0253
22:2 *n*-6	0.58	1.22	0.79	0.0299
DPA (22:5 *n*-3)	0.51	0.75	0.84	0.0357
DHA (22:6 *n*-3)	1.11	1.25	1.56	0.0543

[a]Includes the fatty acids measured.

Gerson et al. (1986) observed a decline in the linolenic acid content of perennial ryegrass with increased maturity. The linolenic acid composition of immature, mature, and senescent perennial ryegrass was 0.3, 0.2, and .01 % of DM, respectively. The authors also observed subsequent increases in palmitic acid, stearic acid (18:0), oleic acid (18:1 *cis*-9), and linoleic acid (18:2 *n*-6). Dewhurst et al. (2001) evaluated the fatty acid content and composition of eight different grasses throughout the growing season. In general, linoleic, linolenic, and total fatty acid concentrations were higher in spring and fall, compared to summer. Winter wheat (*Triticum aestivum*) seedlings grown at 2° C had an increased amount of phospholipid compared to seedlings grown at 24° C (De La Roche et al., 1972). They observed an increase in linolenic acid and a decrease in linoleic acid. Samala et al. (1998) observed as much as a 43 % increase in linolenic acid and suggested that by increasing the polyunsaturated fatty acid (PUFA) content of membranes, plants become cold acclimated, which is a mechanism to maintain membrane fluidity and avoid cold damage.

Ruminal fluid pH

Ruminal fluid pH was lower ($P < 0.05$) (7.48 versus 7.89) for steers on the high-concentrate finishing treatment than pasture finishing treatment only on d 84 (Table 8). Within the high-concentrate and pasture finishing treatments, ruminal fluid pH was lower ($P < 0.05$) on d 0 than on d 84 and 140. Ruminal fluid pH values within the high-concentrate finishing and pasture finishing treatments were lower ($P < 0.05$) on d 28 than 84. Within the pasture finishing treatment, ruminal fluid pH was higher ($P < 0.05$) on d 84 than 140. Perhaps the ruminal fluid pH in the high-concentrate finished steers was not low because ruminal fluid samples were not obtained soon after feeding. Possibly, the

Table 8. The effect of high-concentrate or pasture finishing treatments on pH and volatile fatty acid composition of ruminal fluid

	High-concentrate finishing				Pasture finishing				
	Time								
Item	d 0	d 28	d 84	d 140	d 0	d 28	d 84	d 140	SE
No. of samples	11	12	12	12	12	12	12	12	
pH	7.01[ef]	6.94[c]	7.48[a]	7.49	6.90[ef]	6.97[c]	7.89[d]	7.55	0.0419
VFA	----------mol/100 mol----------								
Acetate	74.72[ef]	68.73[c]	59.37[ad]	66.46	73.55	71.07	72.50	71.47	0.8260
Propionate	15.26[bef]	20.20[c]	31.01[ad]	20.96[a]	16.24	16.32	15.54	15.46	0.5694
Isobutyrate	0.86[f]	0.92	0.76[d]	1.70[a]	1.03	0.99	0.76[d]	1.16	0.0461
Butyrate	7.33[e]	7.50[ac]	5.21[a]	6.02[a]	6.89[bef]	9.17	9.28	9.26	0.1960
Isovalerate	1.39[f]	2.10	1.63[d]	3.51[a]	1.68	1.71	1.38	1.90	0.0954
Valerate	0.44[ef]	0.56[c]	2.01[ad]	1.36[a]	0.62	0.74	0.54	0.75	0.0617

[a]Within date, high-concentrate and pasture finishing treatments differ ($P < 0.05$).
[b]Contrast: within treatment, d 0 and d 28 differ ($P < 0.05$).
[c]Contrast: within treatment, d 28 and d 84 differ ($P < 0.05$).
[d]Contrast: within treatment, d 84 and d 140 differ ($P < 0.05$).
[e]Contrast: within treatment, d 0 and d 84 differ ($P < 0.05$).
[f]Contrast: within treatment, d 0 and d 140 differ ($P < 0.05$).

steers had not consumed silage for several hours prior to sampling. Also, possible saliva contamination may have increased the pH of the samples. Tjardes et al. (2002) observed lower ruminal fluid pH (6.43 versus 6.72) in steers fed low-fiber as compared to high-fiber (corn silage-based) diets. Koenig et al. (2003) observed a slight decrease in ruminal fluid pH (5.95 to 5.72) when barley silage in the diets of cattle was reduced from 20 to 5 % of DM. In calves creep fed supplement (62 % field pea, 31 % wheat middlings, and 5 % molasses), Gelvin et al. (2004) observed a decrease (6.78 to 6.57) in ruminal fluid pH, compared to unsupplemented calves.

Fatty acids in ruminal fluid, blood serum, and adipose tissue

Ruminal fluid fatty acids. Molar proportions of acetate were lower ($P < 0.05$) (59.37 versus 72.50 mol/100 mol) in the high-concentrate fed steers than in the pasture finishing steers on d 84 (Table 8). Molar proportions of propionate were higher ($P < 0.05$) in the ruminal fluid from the high-concentrate finished steers (31.01 and 20.96 mol/100 mol) than pasture-finished steers on d 84 and 140 (15.54 and 15.46 mol/ 100 mol). On d 140, proportions of isobutyrate were higher ($P < 0.05$) in the ruminal fluid obtained from the high-concentrate finished steers than pasture-finished steers. Butyrate proportions were lower ($P < 0.05$) in the high-concentrate finishing treatment than pasture finishing treatment on d 28, 84, and 140. Isovalerate proportions were higher ($P < 0.05$) in the ruminal fluid obtained from the high-concentrate finished steers than pasture-finished steers on d 140. Molar proportions of valerate were higher ($P < 0.05$) in the high-concentrate finishing steers than in those finishing on pasture on d 84 and 140.

Within the high-concentrate finishing treatment, proportions of acetate decreased ($P < 0.05$) in ruminal fluid from d 0 to 84 and 140, and from d 28 to 84, and increased (P

< 0.05) from d 84 to 140. Molar proportions of propionate increased (P < 0.05) in ruminal fluid from high-concentrate finished steers, from d 0 to 28, 84, and 140, and from d 28 to 84, and decreased (P < 0.05) from d 84 to 140. Proportions of isobutyrate were lower (P < 0.05) on d 0 and 84 than on 140, and higher (P < 0.05) on d 28 than 84. Molar proportions of butyrate on d 0 and 28 were higher (P < 0.05) than on d 84, within the high-concentrate finishing treatment. On d 0 and 84, proportions of isovalerate were lower (P < 0.05) than on d 140. Proportions of valerate within the high-concentrate finishing treatment were lower (P < 0.05) on d 0 and 84 than on 140, and on d 28 than 84, but higher (P < 0.05) on d 84 than 140. Within the pasture finishing treatment, sampling date effects were observed for isobutyrate and butyrate. Molar proportions of isobutyrate were lower (P < 0.05) on d 84 than 140. Butyrate proportions were lower (P < 0.05) on d 0 than all other sampling dates.

The differences in VFA observed between the two treatments only on certain sampling dates, in the current study, may be attributed to variations in the high-concentrate diet composition. The variations in molar proportions of VFA seen within the high-concentrate finishing treatment may be a result of shifts in the ingredient composition of the diets during the study (Table 1). The proportion of silage decreased throughout the study, while corn increased. These shifts in ingredients influenced the fiber composition of the diets and subsequent VFA profiles of the ruminal fluid. Results from other studies have been inconsistent when evaluating dietary effects on VFA. Tjardes et al. (2002) observed a decrease in acetate and increases in propionate, butyrate, valerate, isobutyrate, and isovalerate in ruminal fluid from steers fed a low-fiber diet, compared to a high-fiber (corn silage based) diet. In contrast, Koenig et al. (2003)

observed decreases in acetate and butyrate, and an increase in propionate in ruminal fluid from cattle fed a 5 % barley silage diet, compared to cattle fed a 20 % barley silage diet. Lardy et al. (2004) evaluated the effects of increased barley supplementation (0.8, 1.6, and 2.4 kg/d) of steers fed grass hay. Acetate and butyrate increased in the supplemented steers, compared to the control, while there was no effect on propionate, isobutyrate, isovalerate, and valerate.

A listing of the symbolic and common names of long chain fatty acids is included in Table 9. The saturated fatty acids (SFA) myristic acid (14:0), pentadecylic acid (15:0), and margaric acid (17:0) concentrations (mg/g DM) were higher ($P < 0.05$) in the ruminal fluid obtained from the high-concentrate finished steers than the pasture-finished steers on d 84 and 140 (Table 10). Palmitic acid (16:0) and stearic acid (18:0) were higher ($P < 0.05$) in the ruminal fluid obtained from the high-concentrate finished steers than the pasture-finished steers on d 28, 84 and 140.

Some differences were observed when the ruminal fluid fatty acid values were expressed as a percentage of total fatty acids. On d 0, myristic acid, pentadecylic acid, and margaric acid concentrations in the ruminal fluid obtained from the high-concentrate were lower ($P < 0.05$) than that from pasture-finished steers. These differences were perhaps a result of expressing the values on a percentage basis, as there were no differences between treatments observed on d 0 when the data were reported as mg/g DM. Other possible influences could be randomization or sampling errors. On d 28, pentadecylic acid and margaric acid were lower ($P < 0.05$), while stearic acid was higher ($P< 0.05$) in the ruminal fluid obtained from the high-concentrate finished steers than the

Table 9. Symbolic and common names of long chain fatty acids

Symbolic name	Common name
12:0	Lauric
14:0	Myristic
14:1 *cis*-9	Myristoleic
15:0	Pentadecylic
16:0	Palmitic
16:1 *cis*-9	Palmitoleic
17:0	Margaric
17:1 *cis*-9	-
18:0	Stearic
18:1 *cis*-9	Oleic
18:1 *trans*-10	-
18:1 *trans*-11	Vaccenic or *trans*-vaccenic
18:2 *n-6*	Linoleic
18:2 *cis*-9, *trans*-11	Conjugated linoleic acid
18:2 *trans*-10, *cis*-12	Conjugated linoleic acid
18:2 *cis*-9, *cis*-11	Conjugated linoleic acid
18:2 *trans*-9, *trans*-11	Conjugated linoleic acid
18:3 *n-3*	Linolenic
20:2 *n-6*	-
20:3 *n-3*	-
20:3 *n-6*	Homogamma Linolenic
20:4 *n-6*	Arachidonic
22:2 *n-6*	-
22:3 *n-3*	-
22:4 *n-6*	-
22:5 *n-3*	DPA
22:6 *n-3*	DHA

Table 10. The effect of high-concentrate or pasture finishing treatments on fatty acid composition of ruminal fluid

	High-concentrate finishing				Pasture finishing				
	Time of sampling								
Fatty acid	d 0	d 28	d 84	d 140	d 0	d 28	d 84	d 140	SE
No. of samples	10	12	12	12	12	12	12	12	
	mg/g DM								
Myristic (14:0)	0.13[ef]	0.31[c]	0.78[ad]	1.05[a]	0.14	0.08	0.08	0.10	0.0340
Myristoleic (14:1)	0.31[ef]	0.57[a]	0.79[a]	0.74[a]	0.35	0.21	0.17	0.24	0.0341
Pentadecylic acid (15:0)	0.34[f]	0.43	0.53[a]	0.73[a]	0.39	0.23	0.21	0.25	0.0269
Palmitic (16:0)	3.30[bef]	9.54[a]	13.49[a]	14.88[a]	3.09	2.33	2.82	3.14	0.5299
Palmitoleic(16:1)	0.24	0.23[a]	0.23[a]	0.22[a]	0.19[bef]	0.07	0.09	0.08	0.0107
Margaric (17:0)	0.19[ef]	0.27[c]	0.59[a]	0.52[a]	0.19	0.11	0.12	0.12	0.0214
17:1	0.04[bef]	0.16[a]	0.22[a]	0.20[a]	0.03	0.02	0.03	0.03	0.0091
Stearic (18:0)	4.70[bef]	45.91[a]	64.19[ad]	98.38[a]	4.03	8.58	9.52	9.53	3.5725
Total fatty acids[g]	11.11	64.82	113.90	128.84	9.88	14.68	17.10	16.82	
	% of total fatty acids								
Myristic (14:0)	1.25[abef]	0.56	0.71	0.94[a]	1.50[bef]	0.52	0.66	0.58	0.0298
Myristoleic (14:1)	2.87[abef]	0.85[a]	0.57	0.55[a]	3.73[bef]	1.51[c]	0.89[d]	1.49	0.0650
Pentadecylic acid (15:0)	3.19[abef]	0.67[a]	0.41[a]	0.56[a]	4.01[bef]	1.60[c]	1.19[d]	1.55	0.0352
Palmitic (16:0)	30.38[bef]	15.15[c]	12.35[a]	12.65[a]	30.90[bef]	15.79	17.79	18.77	0.3426
Palmitoleic(16:1)	2.06[bef]	0.42	0.25[a]	0.22	1.89[bef]	0.46	0.70	0.49	0.0349
Margaric (17:0)	1.72[abef]	0.44[a]	0.53[d]	0.41[a]	1.91[bef]	0.76[c]	0.64	0.73	0.0154
17:1	0.38[aef]	0.28[a]	0.20	0.15	0.24[e]	0.16	0.14	0.20	0.0125
Stearic (18:0)	41.46[bef]	69.65[ac]	52.10[d]	68.62[a]	40.79[bf]	58.17[c]	48.97	56.51	1.1147

[a]Within date, high-concentrate and pasture finishing treatments differ ($P < 0.05$).
[b]Contrast: within treatment, d 0 and d 28 differ ($P < 0.05$).
[c]Contrast: within treatment, d 28 and d 84 differ ($P < 0.05$).
[d]Contrast: within treatment, d 84 and d 140 differ ($P < 0.05$).
[e]Contrast: within treatment, d 0 and d 84 differ ($P < 0.05$).
[f]Contrast: within treatment, d 0 and d 140 differ ($P < 0.05$).
[g]Includes the fatty acids measured.

pasture-finished steers. On d 84, pentadecylic acid and palmitic acid were lower ($P < 0.05$) in the ruminal fluid obtained from the high-concentrate finished steers than the pasture-finished steers. However, on d 140, myristic acid and stearic acid were higher ($P < 0.05$), while pentadecylic acid and palmitic acid were lower ($P < 0.05$) in the ruminal fluid obtained from the high-concentrate finished steers than the pasture-finished steers. Overall, palmitic acid and stearic acid comprised the greatest proportion of SFA observed in ruminal fluid (ranging from 12.35 to 30.90, and 40.79 to 69.95 % of total fatty acids, respectively). There were, however, differences in these two fatty acids due to dietary treatment, which may be attributed to differences in the fatty acid profiles of the diets (Tables 5 and 7), or differences in ruminal biohydrogenation of these fatty acids. Concentrations of palmitic acid were similar in the pasture forages and high-concentrate finishing diets. Therefore, differences in ruminal fluid palmitic acid between the two treatments were small and inconsistent when expressed as mg/g DM or percentage of total fatty acids. Concentrations of stearic and linoleic acids were higher in the high-concentrate diet than pasture forages, which contributed to the higher amounts of stearic acid observed in the ruminal fluid from high-concentrate finished versus pasture-finished steers.

Minimal research has been conducted comparing ruminal biohydrogenation of long chain fatty acids from pasture versus high-concentrate fed cattle. Sackmann et al. (2003) conducted a study with six cannulated (in the proximal duodenum) steers, which were fed diets consisting of three levels of forage (grass hay at 12, 24, and 36 % of DM), with two levels of sunflower oil supplementation (2 or 4 %). The authors observed increases in stearic acid resulting from an increased forage level in the diet. Flows of

stearic acid were 103.82, 152.15, and 155.64 g/d, in the 12, 24, and 36 % forage treatments, respectively. However, there were no consistent responses of myristic acid and palmitic acid. The authors observed 3.50, 3.56, and 2.67 g/d flow to the duodenum of myristic acid with dietary forage levels of 12, 24, and 36 %, respectively. Flows of palmitic acid were 52.40, 55.78, and 44.40 g/d for the 12, 24, and 36 % forage dietary treatments, respectively. Sunflower oil supplementation resulted in increased flows of myristic (0.64 to 0.90 g/d), palmitic (39.86 to 55.88 g/d), and stearic (6.91 to 9.88 g/d) acids. Kucuk et al. (2001) also observed increased flows (38.3 to 47.0 g/d) of stearic acid to the duodenum in ewes when increasing levels of forage (18.4 to 72.9 % of DM) were fed, and no consistent response of palmitic acid and margaric acid to the forage concentration in the diet. Although duodenal flows were not measured in the current study, duodenal flows may be indicative of ruminal biohydrogenation of fatty acids.

Loor et al. (2003a) observed increases in outputs of myristic acid, palmitic acid, and stearic acid from continuous culture fermenters fed forage based (spring and fall harvested orchardgrass and red clover) diets with increasing corn supplementation (0, 8, or 16 g/d). Average outflows of myristic acid were 11.1, 12.2, and 14.5 g/d for the 0, 8, or 16 g/d corn supplemented treatments. On average, outflows of palmitic acid were 125.7, 133.8, and 156.0 g/d from the 0, 8, or 16 g/d corn supplemented fermenters. Outflows of stearic acid average 235.4, 295.1, and 365.4 g/d for the, 8, or 16 g/d corn supplemented treatments.

Within the high-concentrate finishing treatment, some sampling date effects were observed in all SFA in ruminal fluid. The SFA palmitic acid and stearic acid concentrations (mg/g DM) increased ($P < 0.05$) from d 0 to d 28. Myristic acid and

margaric acid increased ($P < 0.05$) from d 28 to d 84, but the differences were small. Additionally, myristic acid and stearic acid increased ($P < 0.05$) from d 84 to 140. Myristic acid, palmitic acid, margaric acid, and stearic acid increased ($P < 0.05$) from d 0 to d 84, and d 0 to d 140. Pentadecylic acid increased ($P < 0.05$) only from d 0 to 140. No difference due to sampling date were observed in SFA in ruminal fluid obtained from steers in the pasture finishing treatment.

Sampling date effects were observed in all SFA in ruminal fluid obtained from steers in both treatments, when data were expressed as a percentage of total fatty acids. All SFA, with the exception of stearic acid, were higher ($P < 0.05$) on d 0 versus d 28, 84, and 140. In general, these SFA declined after d 0, and then no further differences due to sampling date were observed. This is perhaps due to the general decline in SFA in both the pasture forages and high-concentrate diets (Tables 5 and 7). Concentrations of myristic acid in the high-concentrate diets averaged 0.04, 0.02, and 0.01 mg/g DM, for periods 1 (d0 to 28), 2 (d 28 to 84), and 3 (84 to 140), respectively. Average pentadecylic acid concentrations in the high-concentrate diet were 0.22, 0.12, and 0.06 mg/g DM, for periods 1, 2, and 3, respectively. Concentrations of palmitic acid were 7.54, 4.71, and 4.15 mg/g DM, for periods 1, 2, and 3, respectively. In the pasture forages, pentadecylic acid concentrations average 3.09, 1.86, and 1.89 mg/g DM, in periods 1, 2, and 3, respectively. Concentrations of palmitic acid in the pasture forages were 5.07, 3.28, and 3.01 mg/g DM. In contrast, stearic acid did not decline in the diets of steers in either treatment. However, in ruminal fluid of feedlot finished steers there were some fluctuations in SFA concentrations in palmitic acid, margaric acid, and stearic acid, as indicated by differences ($P < 0.05$) between d 28 and 84, and d 84 and d 140.

The monounsaturated fatty acids (MUFA) myristoleic acid (14:1), palmitoleic acid (16:1), 17:1 and oleic acid (18:1 *cis*-9) concentrations (mg/g DM) were higher ($P < 0.05$) in ruminal fluid obtained from high-concentrate finished steers than pasture-finished steers on d 28, 84, and 140 (Tables 10 and 11). When data were expressed as a percentage of total fatty acids, average myristoleic acid and palmitoleic acid concentrations were lower ($P < 0.05$) in the ruminal fluid obtained from steers on the high-concentrate than the pasture finishing treatment. This effect was significant only on certain sampling dates for these two fatty acids. Concentrations of myristoleic acid were lower ($P < 0.05$) in the high-concentrate finished than pasture-finished steers on d 0, 28, and 140. On d 84, concentrations of palmitoleic acid were lower ($P < 0.05$) (0.25 versus 0.70 % of total fatty acids) in the high-concentrate finished than pasture-finished steers. The MUFA myristoleic acid was not observed in the pasture forages or the high-concentrate diets. Treatment differences in ruminal fluid palmitoleic acid may be attributed to differences in the concentration of this fatty acid in the pasture forages and high-concentrate diets (Tables 5 and 7). Concentrations of palmitoleic acid were higher in the pasture forages than the high-concentrate diets.

Sackmann et al. (2003) observed no differences in flows of palmitoleic acid to the duodenum in cannulated steers fed diets consisting of 12, 24, and 36% grass hay, despite differences in intakes. Flows of palmitoleic acid were 0.52, 0.52, and 0.49 g/d, for the 12, 24, and 36 % forage treatments, respectively. Intakes of palmitoleic acid were 1.12, 1.10, and 0.87 g/d for the 12, 24, and 36 % forage diets, respectively. Differences in biohydrogenation may have contributed to their results. The authors observed no differences in flow of oleic acid due to dietary treatment. Kucuk et al. (2001) also

Table 11. The effect of high-concentrate or pasture finishing treatments on conjugated linoleic acid and 18:1 fatty acid isomers in ruminal fluid

	High-concentrate finishing				Pasture finishing				
	Time of sampling								
Fatty acid	d 0	d 28	d 84	d 140	d 0	d 28	d 84	d 140	SE
Number of samples	10	12	12	12	12	12	12	12	
	mg/g DM								
Oleic (18:1 *cis*-9)	0.51[bef]	1.73[ac]	5.98[ad]	3.11[a]	0.35	0.29	0.83	0.50	0.1147
18:1 *trans*-10	0.03[e]	0.71[c]	18.36[ad]	4.23	0.01	0.06	0.05	0.06	0.9278
Vaccenic (18:1 *trans*-11)	0.31[be]	3.11[a]	2.75[d]	1.13	0.24[bef]	1.95	1.73	1.68	0.1439
Conjugated linoleic,									
18:2 *cis*-9, *trans*-11	0.18[bf]	0.45[ac]	0.27	0.35[a]	0.12	0.06	0.14	0.19	0.0202
18:2 *trans*-10, *cis*-12	-[ef]	-[c]	0.10[ad]	0.05[a]	-	-	-	-	0.0040
18:12 *cis*-9, *cis*-11	-	-[a]	-[a]	0.01[a]	-[bef]	0.04[c]	0.07[d]	0.04	0.0031
18:12 *trans*-9, *trans*-11	-[ef]	-[c]	0.03	0.02[a]	-	-	0.02	-	0.0026
Total fatty acids[g]	11.11	64.82	113.90	128.84	9.88	14.68	17.10	16.82	
	% of total fatty acids								
Oleic (18:1 *cis*-9)	4.53	3.18[c]	8.32	5.33	3.50[e]	1.94[c]	8.95[d]	2.83	0.5200
18:1 *trans*-10	0.20[e]	1.10[c]	13.55[ad]	3.17	0.05	0.41	0.25	0.35	0.5074
Vaccenic (18:1 *trans*-11)	2.72[bf]	4.54[ac]	2.07[a]	0.86[a]	2.49[bef]	13.57[c]	8.97	10.07	0.2173
Conjugated linoleic,									
18:2 *cis*-9, *trans*-11	1.58[abef]	0.79[c]	0.22[a]	0.25[a]	1.09[b]	0.41	0.80	1.06	0.0490
18:2 *trans*-10, *cis*-12	-[ef]	-[c]	0.08[ad]	0.04[a]	-	-	-	-	0.0037
18:12 *cis*-9, *cis*-11	-	-[a]	-[a]	-[a]	-[bef]	0.32	0.32	0.28	0.0153
18:12 *trans*-9, *trans*-11	-	-	0.03[a]	0.01	-[e]	-[c]	0.08[d]	-	0.0048

[a]Within date, high-concentrate and pasture finishing treatments differ ($P < 0.05$).
[b]Contrast: within treatment, d 0 and d 28 differ ($P < 0.05$).
[c]Contrast: within treatment, d 28 and d 84 differ ($P < 0.05$).
[d]Contrast: within treatment, d 84 and d 140 differ ($P < 0.05$).
[e]Contrast: within treatment, d 0 and d 84 differ ($P < 0.05$).
[f]Contrast: within treatment, d 0 and d 140 differ ($P < 0.05$).
[g]Includes the fatty acids measured.

observed no consistent response of palmitoleic acid or oleic acid flows to the duodendum to varying forage levels (18.4 to 72.9 % of DM). In contrast, Loor et al. (2003a) observed increased outflow of oleic acid from continuous culture fermenters with increasing corn supplementation (0, 8, and 16 g/d). Average outflows of oleic acid were 11.9, 23.8, and 29.7 g/d for the 0, 8, and 16 g/d corn supplemented treatments. Inconsistencies in results from previous studies may be due to the fact that forage-based and grain-based diets contain primarily linolenic acid and linoleic acid, respectively (Kalscheur et al., 1997; Dhiman et al., 1999b; French et al., 2000; Rhee et al., 2000). Both of these fatty acids may potentially be converted to oleic acid by ruminal bacteria (Kemp et al., 1975).

Within the high-concentrate finishing treatment, differences ($P < 0.05$) in myristoleic acid, 17:1, and oleic acid concentrations (mg/g DM) were seen due to sampling date. Concentrations of 17:1 decreased ($P < 0.05$) from d 0 to d 28, and myristoleic acid increased ($P < 0.05$) from d 0 to 84 and 140,and oleic acid increased ($P < 0.05$) from d 0 to 28, 84, and 140. Within the pasture finishing treatment, palmitoleic acid decreased ($P < 0.05$) from d 0 to 28, 84, and 140, and remained low.

Overall, when the data were expressed as a percentage of total fatty acids, in the feedlot- and pasture-finished steers, myristoleic acid, palmitoleic acid and 17:1 decreased after d 0 and remained low. For these fatty acids, concentrations on d 0 were higher ($P < 0.05$) than on d 28, 84, and 140. However, these effects were not observed in oleic acid. The concentrations of oleic acid varied over time within both treatments. Within the high-concentrate finishing treatment, concentrations of oleic acid generally decreased (concentrations were higher ($P < 0.05$) on d 0 than on 84 and 140). On d 28,

concentrations of oleic acid were higher ($P < 0.05$) than on d 84. Within the pasture finishing treatment, concentrations of oleic acid were higher ($P < 0.05$) on d 84 than 140. These fluctuation observed in oleic acid concentrations may have been a result of differences in ingredient composition and subsequent fatty acid composition of the diets fed to steers in the high-concentrate finishing treatment (Tables 1 and 5), or perhaps differences in ruminal biohydrogenation. Although oleic acid concentrations (% of total fatty acids) in the high-concentrate diets increased from periods 1 (d 0 to 28) to 2 (d 28 to 84) and 3 (d 84 to 140), ruminal fluid concentrations of this fatty acid decreased. Therefore, the decrease in oleic acid may have been attributed to the decrease in the precursors linoleic acid and linolenic acid (Kemp et al., 1975). Concentrations of linoleic acid and linolenic acid in the high-concentrate diet decreased throughout the present study.

Vaccenic acid (18:1 *trans*-11) concentration (mg/g DM) was higher ($P < 0.05$) in the ruminal fluid of the high-concentrate finished steers on d 28 than the pasture-finished steers (3.11 versus 1.95 mg/g DM) (Table 11). However, when expressed as a percentage of total fatty acids, vaccenic acid was higher ($P < 0.05$) in ruminal fluid obtained from pasture-finished steers (13.57, 8.97, and 10.07 % of total fatty acids) than high-concentrate finished steers (4.54, 2.07, and 0.86 % of total fatty acids) on d 28, 84, and 140, respectively. These discrepancies may have been a result of variation in the water content of the ruminal fluid samples. Although not measured in this study, water content would have an effect on the extent of dilution of fatty acids within the samples. These results may indicate that expressing fatty acids on a percentage basis, rather than absolute amounts, may be more indicative of ruminal function and subsequent CLA synthesis in

tissues, since water content of the sample would not have an impact on the proportions of fatty acids.

Fluctuations in vaccenic acid concentrations (mg/g DM and % of total fatty acids) were observed over time. Within the high-concentrate finishing treatment, vaccenic acid concentrations (% of total fatty acids) were higher ($P < 0.05$) on d 0 than 140, lower ($P < 0.05$) on d 0 than 28, and higher ($P < 0.05$) on d 28 than 84. These differences in vaccenic acid may be due to differences in diet ingredients and ruminal biohydrogenation. High-grain diets are thought to reduce ruminal production of vaccenic acid. Piperova et al. (2000) noted that milk fat samples contained reduced amounts of vaccenic acid (28.5 versus 10.9 % of total *trans*-18:1 isomers) when cows were fed high-concentrate (milk fat-depressing) diets as compared to the control diet. The authors hypothesized milk fatty acids reflected ruminal biohydrogention of 18:1 fatty acids. Kucuk et al. (2001) observed that when a 72.9 % (of DM) forage diet was fed to ewes, duodenal flow of vaccenic acid was 7.46 g/d, and when a 45.8 % (of DM) forage diet was fed, flow of vaccenic acid was reduced to 5.58 g/d. Sackmann et al. (2003) observed reduced duodenal flows of vaccenic acid (11.75 to 3.48 g/d) when forage levels in the diets of steers were decreased from 36 to 12 % of DM.

Within the pasture finishing treatment, vaccenic acid concentrations (mg/g DM and % of total fatty acids) were lower ($P < 0.05$) on d 0 than d 28, 84, and 140, and higher ($P < 0.05$) on d 28 than 84. Again, these fluctuations may be a result of varying ruminal function or fatty acid concentrations in the diets. A main precursor of vaccenic acid is linolenic acid (Kellens et al., 1986). French et al. (2000), Rhee et al. (2000), and Dewhurst et al. (2001) observed that linolenic acid is a major component of the fatty

acids found in pasture forages. Boufaïd et al. (2003) observed linolenic acid concentrations as high as 2.1 % of DM in annual ryegrass. In the current study, the linolenic acid concentrations in the pasture forages that the steers grazed declined sharply after d 28 and remained low, as compared to the first 28 d (Table 7). This may explain the similar pattern observed in ruminal fluid vaccenic acid content in the pasture-finished steers.

Concentrations (mg/g DM and % of total fatty acids) of 18:1 *trans*-10 were higher ($P < 0.05$) in ruminal fluid obtained from steers in the high-concentrate finishing treatment than pasture finishing treatment on d 84 (Table 11). There were no differences between sampling dates within the pasture finishing treatment, as values remained relatively low (0.05 to 0.41 % of total fatty acids).

Within the high-concentrate finishing treatment, 18:1 *trans*-10 values (mg/g DM and % of total fatty acids) on d 84 were higher ($P < 0.05$) than any other sampling date. Concentrations (mg/g DM and % of total fatty acids) of 18:1 *trans*-10 were lower ($P < 0.05$) on d 0 than on d 28. These fluctuations in 18:1 *trans*-10 may be attributed to shifts in ingredient composition of the diet, as low-forage/high-concentrate diets may lead to 18:1 *trans*-10 production in the rumen, and also may be an indicator of altered ruminal biohydrogenation.

During the current study, silage made up the 89 % (DM basis) of the high-concentrate diet during the period from d 0 to d 28 (Table 1). However, from d 28 to 84, the diet contained 37 % silage, while corn comprised 56%. During the last period of the study, d 84 to 140, the diet consisted of 77 % corn and only 17 % silage. The biohydrogenation of *trans* 18:1 isomers may have shifted away from the production of

vaccenic acid (18:1 *trans*-11) and toward the production of 18:1 *trans*-10 in the high-concentrate finished steers, which may have resulted in reduced vaccenic acid precursor for CLA production.

Piperova et al. (2000) observed an increase in 18:1 *trans*-10 (13.9 to 59.2 % of total *trans* -18:1 isomers) in milk from cows fed a high-concentrate (milk fat-depressing diet), compared to a control diet. LeDoux et al. (2002) observed increased 18:1 *trans*-10 (12.51 versus 15.57 % of total 18:1 *trans* fatty acid isomers) in milk from goats fed 60 or 30 % (of DM) alfalfa hay. Griinari et al. (1998) conducted a study with cows fed diets consisting of two forage levels (50 or 20 % of DM) and SFA or unsaturated fatty acid (UFA) oil supplementation. The authors observed increased concentrations of 18:1 *trans*-10 in milk in response to both decreased forage level and inclusion of UFA. Milk concentrations of 18:1 *trans*-10 were 0.33, 0.70, 0.42, and 2.90 % of total fatty acids for the high forage plus SFA, high forage plus UFA, low forage plus SFA, and high forage plus UFA treatments, respectively. Loor et al. (2004) observed increased flow of 18:1 *trans*-10 to the duodenum of cows as a result of feeding high-concentrate diets and linseed oil supplementation. They observed duodenal flows of 1.46, 6.61, 20.2, and 50.6 g/d in the low-concentrate, low-concentrate plus oil supplementation, high-concentrate, and high-concentrate plus oil supplementation treatments, respectively. Similar results were observed by Sackmann et al. (2003). Therefore, it appears that oil supplementation of a high-concentrate diet further exacerbates the altered rumen fermentation and increases 18:1 *trans*-10 production.

The direct impact of 18:1 *trans*-10 on CLA production in tissues is unclear; 18:1 *trans*-10 has not been shown to directly inhibit 18:2 *cis*-9, *trans*-11 CLA synthesis by the

Δ^9 desaturase enzyme. However, a closely related CLA isomer (18:2 *trans*-10, *cis*-12 CLA) has been shown to directly inhibit Δ^9 desaturase activity and 18:2 *cis*-9, *trans*-11 CLA synthesis (Choi et al, 2000, 2001; Baumgard et al, 2000, 2001; Loor 2001; Loor and Herbein, 2003b).

The 18:2 *trans*-10, *cis*-12 isomer of CLA was observed in low concentrations (0.08 and 0.04 % of total fatty acids) only in ruminal fluid from high-concentrate finished steers on d 84 and 140 (treatment and sampling date effects, $P < 0.05$; Table 11). Kim et al. (2002) identified a strain of bacteria, *Megasphaera elsdenii* YJ-4, which produces significant amounts of the 18:2 *trans*-10, *cis*-12 isomer of CLA. This bacterium was isolated from the ruminal fluid collected from cows fed a diet consisting of 90 % cracked corn. Sackmann et al. (2003) observed increased duodenal flows of 18:2 *trans*-10, *cis*-12 CLA (0.219, 0.257, and 0.397 g/d) in steers with decreasing forage levels (36, 24, and 12 % of DM). Kucuk et al. (2001) observed that duodenal flows of 18:2 *trans*-10, *cis*-12 CLA increased, from 0 to 0.09 g/d, in ewes fed diets containing decreasing amounts of forage, 72.9 to 18.4 % DM. Loor et al. (2003a) observed increased 18:2 *trans*-10, *cis*-12 CLA outflow from continuous culture fermenters fed orchardgrass or red clover with three levels of corn supplementation (0, 8, and 16 g/d). The authors observed flows of 0.55, 0.63, and 1.17 g/d for the 0, 8, and 16 g/d corn supplemented treatments. Therefore, decreasing forage and increasing grain in diets of ruminants may result in increased ruminal production of 18:2 *trans*-10, *cis*-12 CLA, as was observed in the current study, on d 84 and 140.

The 18:2 *cis*-9, *trans*-11 isomer was the primary isomer of CLA produced in the rumen by steers in both treatments (Table 11). The concentrations of 18:2 *cis*-9, *trans*-11

CLA were higher ($P < 0.05$) in ruminal fluid from the pasture-finished steers than the high-concentrate finished steers on d 84 and 140, when the data were presented as a percentage of total fatty acids. Ruminal concentrations of 18:2 *cis*-9, *trans*-11 CLA were lower ($P < 0.05$) than its precursor vaccenic acid, in the current study, indicating the importance of endogenous synthesis. In the current study, 18:2 *cis*-9, *trans*-11 CLA concentrations in ruminal fluid from the pasture-finished steers ranged from 0.41 to 1.09 % of total fatty acids, while the vaccenic acid concentrations ranged from 2.49 to 13.57 % of total fatty acids. Kucuk et al. (2001) observed vaccenic acid and 18:2 *cis*-9, *trans*-11 CLA duodenal flows of 7.46 and 0.19 g/d, respectively in ewes in the 72.9 % (of DM) forage dietary treatment. Loor et al. (2003a) observed vaccenic acid outflows from continuous culture fermenters ranging from 70.9 to 210.1 g/d, and 18:2 *cis*-9, *trans*-11 CLA outflow ranging from 0.51 to 4.4 g/d.

These findings, and the results of the current study, are in agreement with the hypothesis that ruminal production of 18:2 *cis*-9, *trans*-11 CLA is not the main pathway in which CLA concentrations increase in ruminant products, and that endogenous (adipose/mammary tissue) synthesis is the primary mechanism by which 18:2 *cis*-9, *trans*-11 CLA is produced (Griinari et al., 2000, Corl et al., 2001, Kay et al., 2004). By using the ratios of myristic acid (14:0) to myristoleic acid (14:1), Griinari et al. (2000) estimated that 64% of 18:2 *cis*-9, *trans*-11 CLA in milk was from endogenous synthesis. Corl et al. (2001) also used the ratios of myristic acid to myristoleic acid to estimate endogenous synthesis of 18:2 *cis*-9, *trans*-11 CLA, and concluded that 78% of 18:2 *cis*-9, *trans*-11 CLA in milk was of endogenous origin. Kay et al. (2004) estimated that

endogenous synthesis contributed to over 91 % of the CLA production by sterculic oil infusion (a Δ^9 desaturase inhibitor).

The 18:12 *cis*-9, *cis*-11 isomer of CLA was observed only in ruminal fluid obtained from pasture-finished steers on d 28, 84, and 140 (treatment and sampling date effects, $P< 0.05$), but concentrations were very low. The 18:12 *trans*-9, *trans*-11 was observed at low concentrations in both treatments on d 84, but only in the high-concentrate finishing treatment on d 140. The concentrations of 18:12 *cis*-9, *cis*-11 and 18:12 *trans*-9, *trans*-11 CLA in ruminal fluid were relatively small (less than 0.35 % of total fatty acids), and their potential importance to consumers' health is unclear, as no known research has been conducted on these specific and individual isomers of CLA.

Concentrations (mg/g DM) of linoleic acid (18:2 *n*-6) were higher ($P < 0.05$) in the high-concentrate finishing treatment than the pasture-finishing treatment on d 28, 84 and 140 (Table 12). When expressed as a percentage of total fatty acids, there were no treatment differences, although the values in the high-concentrate finishing treatment were numerically higher. Also, linoleic acid concentrations (mg/g DM) in the ruminal fluid from the high-concentrate finished steers increased ($P < 0.05$) from d 0 and 28 up to d 84, and decreased ($P < 0.05$) from d 84 to 140. No differences among sampling dates were observed in the pasture finishing treatment. The primary fatty acid in high-concentrate finishing diets was linoleic acid (Table 5). The linoleic acid content of the high-concentrate finishing diet averaged 58.39, 57.05, and 56.74 % of total fatty acids in periods 1 (d 0 to 28), 2 (d 28 to 84), and 3 (d 84 to 140), respectively. The linoleic acid concentration of the pasture forages averaged 6.92, 9.41, and 10.13 % of total fatty acids for periods 1, 2, and 3, respectively (Table 7). Kalscheur et al. (1997) and French et al.

Table 12. The effect of high-concentrate or pasture finishing treatments on *n*-3 and *n*-6 fatty acids in ruminal fluid

	High-concentrate finishing				Pasture finishing				
	Time of sampling								
Fatty acid	d 0	d 28	d 84	d 140	d 0	d 28	d 84	d 140	SE
No. of samples	10	12	12	12	12	12	12	12	
	mg/g DM								
Linoleic (18:2 *n*-6)	0.31[ef]	0.97[ac]	4.84[ad]	2.68[a]	0.21	0.14	0.61	0.40	0.0953
Linolenic (18:3 *n*-3)	0.13[e]	0.07[ac]	0.22[d]	0.13[a]	0.13[ef]	0.18[c]	0.26	0.21	0.0093
20:2 *n*-6	0.09[bef]	0.19[a]	0.21[a]	0.19[a]	0.10	0.07	0.12	0.08	0.0074
22:2 *n*-6	0.02[bef]	-[a]	-[a]	-[a]	0.02[bef]	0.04	0.04	0.03	0.0013
DPA (22:5 *n*-3)	0.23[bf]	0.09[c]	0.21[d]	0.11	0.23[f]	0.17	0.15	0.09	0.0143
DHA (22:6 *n*-3)	0.06[e]	0.06[c]	0.13[a]	0.10[a]	0.08	0.05	0.04	0.05	0.0064
Total fatty acids[g]	11.11	64.82	113.90	128.84	9.88	14.68	17.10	16.82	
	% of total fatty acids								
Linoleic (18:2 *n*-6)	2.70[e]	1.67[c]	7.61	5.40	2.13[e]	0.95[c]	5.74	2.34	0.4533
Linolenic (18:3 *n*-3)	1.26[bef]	0.13[a]	0.41[a]	0.33[a]	1.26	1.21[c]	1.59	1.30	0.0459
20:2 *n*-6	0.85[abef]	0.32	0.27[a]	0.20[a]	1.09[bef]	0.44[c]	0.71[d]	0.49	0.0255
22:2 *n*-6	0.18[bef]	-[a]	-[a]	-[a]	0.16[b]	0.31[c]	0.21	0.19	0.0108
DPA (22:5 *n*-3)	2.14[bef]	0.16[a]	0.20[a]	0.20	2.42[bef]	1.13	1.18[d]	0.50	0.0561
DHA (22:6 *n*-3)	0.54[abef]	0.11[a]	0.12	0.12[a]	0.83[bef]	0.35	0.24	0.28	0.0174

[a]Within date, high-concentrate and pasture finishing treatments differ ($P < 0.05$).
[b]Contrast: within treatment, d 0 and d 28 differ ($P < 0.05$).
[c]Contrast: within treatment, d 28 and d 84 differ ($P < 0.05$).
[d]Contrast: within treatment, d 84 and d 140 differ ($P < 0.05$).
[e]Contrast: within treatment, d 0 and d 84 differ ($P < 0.05$).
[f]Contrast: within treatment, d 0 and d 140 differ ($P < 0.05$).
[g]Includes the fatty acids measured.

(2000), and Rhee et al. (2000) observed that linoleic acid was the primary fatty acid in grain-based diets.

When expressed as mg/g DM, concentrations of linolenic acid (18:3 *n*-3) were lower ($P < 0.05$) for steers fed high-concentrate diets than pasture-finished steers on d 28 and 140, in the current study (Table 12). When expressed as a percentage of total fatty acids, concentrations of linolenic acid were higher ($P < 0.05$) in the ruminal fluid of pasture-finished (1.21, 1.59, and 1.30 % of total fatty acids) than the high-concentrate finished steers (0.13, 0.41, and 0.33 % of total fatty acids) on d 28, 84, and 140, respectively. The linolenic acid concentrations (% of total fatty acids) in the ruminal fluid from the high-concentrate finished steers decreased ($P < 0.05$) from d 0 to 28, 84, and 140. Concentrations (mg/g DM) of linolenic acid in the pasture-finished steers generally increased over time, as concentrations on d 84 were higher ($P < 0.05$) than on d 28 and 0. When expressed as a percentage of total fatty acids, concentrations of linolenic acid were higher ($P < 0.05$) on d 84 than d 28. The higher concentrations of linolenic acid in ruminal fluid from pasture-finished steers were probably a result of the considerably higher linolenic acid in the pasture forage samples, when compared to the high-concentrate diets (Tables 5 and 7). The average linolenic acid concentration of the pasture forages were 72.9, 63.9, and 61.55 % of total fatty acids, while the linolenic acid concentrations of the high-concentrate diets averaged 3.06, 2.19, and 1.33 % of total fatty acids, for periods 1, 2, and 3, respectively. Dhiman et al. (1999b), French et al. (2000), Scollan et al. (2001) observed that linolenic acid was the primary fatty acid in forages.

Sackmann et al. (2000) observed an increase in the flow of linolenic acid to the duodenum in cannulated steers fed increasing levels of forage in the diet. The authors

observed duodenal flows of 1.08, 1.52, and 1.85 g/d in the 12, 24, and 36 % (of DM) forage treatments, respectively. Intakes of linolenic acid were 15.62, 23.00, and 25.21 g/d, for the 12, 24, and 36 % forage diets. Griinari et al. (1998) observed increased concentrations (0.19 versus 0.27 % of total fatty acids) of linolenic acid in milk from cows fed low- and high-forage diets, respectively. LeDoux et al. (2004) observed linolenic acid concentrations of 0.27 and 0.38 in milk obtained from goats fed alfalfa hay at 30 and 60% (of DM), respectively. The concentrations of linolenic acid in milk fat would presumably reflect the content of linolenic acid in the diets and ruminal fluid.

In the current study, observations were made for other *n*-3 (22:5 and 22:6, DPA and DHA, respectively) fatty acids in ruminal fluid. Concentrations (% of total fatty acids) of DPA were higher ($P < 0.05$) in the ruminal fluid obtained from the pasture-finished steers (1.13 and 1.18 % of total fatty acids) than the high-concentrate finished steers (0.16 and 0.20 % of total fatty acids) on d 28 and 84, respectively (Table 12). On d 28 and 140, concentrations (% of total fatty acids) of DHA were higher ($P < 0.05$) in the pasture finishing treatment (0.35 and 0.28 % of total fatty acids, respectively) than high-concentrate finishing treatment (0.11 and 0.12 % of total fatty acids, respectively). These two fatty acids were not detected in the high-concentrate diets. The higher amounts of DPA and DHA in the ruminal fluid from pasture-finished steers is presumably due to their presence in pasture forages (Table 7). Average DPA concentration of the pasture forages were 0.51, 0.75, and 0.84 % of total fatty acids, for periods 1, 2, and 3, respectively. Concentrations of DHA in pasture forages averaged 1.11, 1.25, and 1.56 % of total fatty acids, for periods 1, 2, and 3, respectively. Studies evaluating these long chain omega-3 fatty acids in ruminal fluid or digesta are not known.

Concentrations (mg/g DM) of 20:2 *n*-6 in ruminal fluid obtained from high-concentrate finished steers were higher ($P < 0.05$) than the pasture-finished steers on d 28, 84, and 140, while the opposite effect was observed for this fatty acid when expressed as a percentage of total fatty acids (on d 84 and 140). Again, these discrepancies may be a result of the water content of the sample, since water content would have an effect on the extent of dilution of fatty acids within the samples.

The concentrations (mg/g DM) of 22:2 *n*-6 were higher ($P < 0.05$) in pasture-finished steers and increased ($P < 0.05$) from d 0 to 28, then remained constant. When expressed as a percentage of total fatty acids, 22:2 *n*-6 in the pasture-finished steers increased ($P < 0.05$) from d 0 to 28, then declined ($P < 0.05$) from d 28 to d 84. These results may be attributed to the dietary fatty acid concentrations. No detectable amounts of 22:2 *n*-6 were observed in the high-concentrate diets or in the ruminal fluid from steers in the high-concentrate finishing treatment on d 28, 84, and 140. Fluctuations observed in 22 *n*-6 in ruminal fluid in the pasture finishing treatment may be attributed to changes in dietary fatty acid concentration in the forages over time (Table 7). An increase of 22:2 *n*-6 (% of total fatty acids) in the pasture forages was observed from period 1 (d 0 to 28) to 2 (d 28 to 84), then a decrease from period 2 to 3 (d 84 to 140). Studies evaluating these long chain omega-6 fatty acids in ruminal fluid or digesta are not known.

Dietary content of 20:2 *n*-6 and 22:2 *n*-6 may have contributed to these differences between treatments. Concentrations of these fatty acids were higher in the pasture forages than the high-concentrate diets. Concentrations of 20:2 *n*-6 and 22:2 *n*-6 in the pasture forages ranged from 0.21 to 0.27 and 0.18 to 0.30 mg/g DM, respectively.

Concentrations of 20:2 *n*-6 in the high-concentrate diets ranged from 0.04 to 0.15 mg/g DM, while 22:2 *n*-6 was not detected.

Serum fatty acids. The saturated fatty acid (SFA) myristic acid (14:0) and pentadecylic acid (15:0) concentrations (µg/mL and % of total fatty acids) were higher ($P < 0.05$) in the serum obtained from pasture-finished steers than the high-concentrate finished steers on d 28, 84, and 140 (Table 13). Concentrations (µg/mL) of palmitic acid (16:0), margaric acid (17:0), and stearic acid (18:0) were higher ($P < 0.05$) in the serum obtained from pasture-finished steers than the high-concentrate finished steers on d 28. However, when expressed as a percentage of total fatty acids, palmitic acid was higher ($P < 0.05$) and margaric acid was lower ($P < 0.05$) in the serum obtained from pasture-finished steers than the high-concentrate finished steers on d 84, while no differences between treatments were observed for stearic acid.

Serum concentrations of SFA did not reflect the values observed in ruminal fluid in the current study. In general, the SFA in ruminal fluid and serum did not have consistent trends in the data. On some sampling dates ruminal fluid values of SFA (myristic acid and margaric acid) were higher ($P < 0.05$) in the high-concentrate finishing treatment and serum values of these same fatty acids were higher ($P < 0.05$) in the pasture finishing treatment. With palmitic acid, the opposite effect was observed. One consistency was observed, which was that concentrations (% of total fatty acids) of pentadecylic acid were higher ($P < 0.05$) in the pasture-finished steers than high-concentrate finished steers, in both ruminal fluid and serum. These inconsistencies may be a result of the small differences between the SFA content of the pasture forages versus

Table 13. The effect of high-concentrate or pasture finishing treatments on fatty acid composition of serum

	High-concentrate finishing				Pasture finishing				
	Time of sampling								
Fatty acid	d 0	d 28	d 84	d 140	d 0	d 28	d 84	d 140	SE
No. of samples	12	12	12	12	12	12	12	12	
	----------µg/mL----------								
Myristic (14:0)	10.55[be]	5.39[a]	5.08[ad]	8.00[a]	10.78[ef]	13.33	14.55	14.10	0.3420
Myristoleic (14:1)	11.74[bef]	4.56[a]	3.93[a]	4.49[a]	11.15[bef]	16.47	17.09	15.55	0.3462
Pentadecylic acid (15:0)	12.06[bef]	4.16[a]	5.87[a]	7.22[a]	11.16	12.16	11.33	12.79	0.2788
Palmitic (16:0)	142.11[be]	80.88[a]	97.82[d]	125.30	140.43[e]	133.82	114.41	125.96	2.8670
Palmitoleic(16:1)	18.32[bef]	11.22[a]	9.85[a]	12.76[a]	19.86	19.29	20.66	18.71	0.5838
Margaric (17:0)	12.19[b]	6.24[ac]	10.59	11.26	11.72[e]	9.82	9.27	10.50	0.2809
17:1	6.84[bef]	4.13[a]	3.08[a]	4.39[a]	7.67	7.72	8.62	7.32	0.1892
Stearic (18:0)	169.50[b]	108.19[a]	138.94[d]	187.82	164.35	196.38[c]	151.30[d]	188.62	4.1342
Total fatty acids[g]	1005.21	548.51	906.60	1055.97	999.15	1045.56	889.50	1046.71	
	----------% of total fatty acids----------								
Myristic (14:0)	1.06[ef]	0.96[ac]	0.55[ad]	0.73[a]	1.06[bef]	1.27[c]	1.55[d]	1.34	0.0216
Myristoleic (14:1)	1.14[bef]	0.78[ac]	0.44[a]	0.41[a]	1.08[bef]	1.59[c]	1.86[d]	1.50	0.0233
Pentadecylic acid (15:0)	1.18[bef]	0.71[a]	0.62[a]	0.65[a]	1.11[f]	1.17	1.22	1.24	0.0162
Palmitic (16:0)	14.17[ef]	14.12[c]	10.53[a]	11.44	13.95[ef]	12.95	12.36	12.24	0.1974
Palmitoleic(16:1)	1.84[ef]	1.98[c]	1.11[a]	1.19[a]	1.99	1.87	2.25	1.80	0.0579
Margaric (17:0)	1.21[f]	1.09	1.15[a]	1.03	1.16[bef]	0.95	1.00	1.00	0.0186
17:1	0.69[ef]	0.71[c]	0.33[a]	0.41[a]	0.78[e]	0.74[c]	0.93[d]	0.70	0.0155
Stearic (18:0)	16.80	18.49[c]	15.19[d]	17.25	16.16[b]	18.99[c]	16.34	18.04	0.2588

[a]Within date, high-concentrate and pasture finishing treatments differ ($P < 0.05$).
[b]Contrast: within treatment, d 0 and d 28 differ ($P < 0.05$).
[c]Contrast: within treatment, d 28 and d 84 differ ($P < 0.05$).
[d]Contrast: within treatment, d 84 and d 140 differ ($P < 0.05$).
[e]Contrast: within treatment, d 0 and d 84 differ ($P < 0.05$).
[f]Contrast: within treatment, d 0 and d 140 differ ($P < 0.05$).
[g]Includes the fatty acids measured.

high-concentrate diets. Additionally, lipid metabolism by various tissues within the steers may have influenced the results.

Studies comparing the blood fatty acid profiles of ruminants consuming forage or high-concentrate based diets are not known. Although not entirely analogous, researchers have evaluated the effects of oil supplements on plasma fatty acid profiles. Gaynor et al (1994) evaluated plasma from cows abomasally infused with *cis* or *trans* isomers of 18:1, compared to an uninfused control. The cows were fed a diet consisting primarily of corn, corn silage, soybean meal, and alfalfa hay, at 30.3, 22.9, 23.0, and 17.5 % (of DM), respectively. Concentrations of myristic acid, palmitic acid and stearic acid (0.5, 10.2, 13.4 % of total fatty acids, respectively) in the plasma from the control cows were similar to the serum fatty acid values observed in the current study in the high-concentrate finishing treatment, specifically on d 84. Similar values were observed by Loor et al. (2002b) in plasma obtained from control cows fed a comparable diet consisting of 31.0, 30.7, 10.7, and 17.5 % (of DM) corn, corn silage, soybean meal, and alfalfa haylage, respectively. In their study, the treatments consisted of the control diet supplemented (at 3.3 %) with canola oil, canolamide, or a canola/canolamide mixture. The authors reported myristic, palmitic, margaric and stearic acid values, in blood plasma from cows fed the control diet, of 0.2, 2.2, 8.0, and 13.4 % of total fatty acids, respectively. Feeding the canola supplements resulted in decreases in myristic and palmitic acids, and an increase in stearic acid in plasma. Canola supplementation had no effect on pentadecylic and margaric acids. Loor and Herbein. (2003a) also observed similar plasma values of these SFA when cows were fed a basal diet consisting of 27.0, 19.8, 34.5, and 4.7 % (of DM) corn, corn silage, alfalfa haylage, and soybean meal,

respectively. The treatments in their study consisted of soybean or canola oil supplemented at 3.0 % of DM, with or without a mixture of CLA. Concentrations of myristic, palmitic, and stearic acids in plasma were 4.2, 110, and 125 μg/mL, respectively. Oil supplementation resulted in numeric increases in all of these fatty acids.

In the current study, concentrations (μg/mL) of all serum SFA decreased ($P < 0.05$) from d 0 to 28, in the serum from high-concentrate finished steers. The SFA concentrations (μg/mL) within the high-concentrate finishing treatment generally were lower on d 84 or 140, compared to d 0 values. Myristic acid (μg/mL) decreased ($P < 0.05$) from d 0 to 28, and increased ($P < 0.05$) from d 84 to 140. Also, concentrations (μg/mL) of myristic acid were higher ($P < 0.05$) on d 0 than 84. Concentrations (μg/mL) of pentadecylic acid were higher ($P < 0.05$) on d 0 than all other sampling dates. On d 0, palmitic acid concentrations (μg/mL) were higher ($P < 0.05$) on d 0 than on d 28 and 84, and concentrations on d 84 were lower ($P < 0.05$) than on d 140. Concentrations (μg/mL) of margaric acid decreased ($P < 0.05$) from d 0 to 28, and increased ($P < 0.05$) from d 28 to 84. Ruminal fluid concentrations of stearic acid were higher ($P < 0.05$) on d 0 than 28, and lower ($P < 0.05$) on d 84 than 140.

When expressed as a percentage of total fatty acids, additional variations over time were observed. Concentrations (% of total fatty acids) of myristic acid in the serum obtained from the high-concentrate finished steers were higher ($P < 0.05$) on d 0 than d 84 and 140, and decreased ($P < 0.05$) from d 28 to 84, then increased ($P < 0.05$) from d 84 to 140. Serum concentrations of pentadecylic acid (% of total fatty acids) decreased ($P < 0.05$) from d 0 to 28 and remained low, as values were higher ($P < 0.05$) on d 0 than 28, 84, and 140. Concentrations (% of total fatty acids) of palmitic acid were higher ($P <$

0.05) on d 0 than 84 and 140, and values on d 28 were higher ($P < 0.05$) than on d 84. The only difference observed for margaric acid concentrations (% of total fatty acids) was that values on d 0 were higher ($P < 0.05$) than on d 140. Concentrations (% of total fatty acids) of stearic acid decreased ($P < 0.05$) from d 28 to 84, then increased ($P < 0.05$) from d 84 to 140.

Within the pasture finishing treatment, myristic acid concentrations (μg/mL) on d 0 were lower ($P < 0.05$) than on d 84 and 140, while concentrations (μg/mL) of palmitic acid and margaric acid on d 0 were higher ($P < 0.05$) than on d 84. Concentrations (μg/mL) of stearic acid increased over time, since concentrations on d 28 were lower ($P < 0.05$) than on d 84, and values on d 84 were lower ($P < 0.05$) than on d 140.

When expressed as a percentage of total fatty acids, myristic acid concentrations in the pasture finishing treatment increased ($P < 0.05$) from d 0 to 28 and 84, then decreased ($P < 0.05$) from d 84 to 140. Concentrations (% of total fatty acids) of palmitic acid decreased ($P < 0.05$) from d 0 to 28 and 84. Margaric acid was higher ($P < 0.05$) on d 0 than all other sampling dates. Concentrations (% of total fatty acids) of stearic acid increased ($P < 0.05$) from d 0 to 28, then decreased ($P < 0.05$) from d 28 to 84.

Similar to ruminal fluid, palmitic acid and stearic acid comprised the greatest proportion of SFA observed in serum. Serum values of SFA were generally consistent with ruminal fluid SFA concentrations, in that there was an overall decrease after d 0. Additionally, fluctuations over time within the SFA in serum reflected some of the fluctuations observed in ruminal fluid. These fluctuations again may have been a result of the fluctuations in ruminal fluid biohydrogenation and changes in the diet ingredient composition or fatty acid content of the diets. However, the fluctuations in SFA over

time observed in serum were not identical to those observed in ruminal fluid. The discrepancies may be due to alterations in fatty acids postruminally.

The MUFA myristoleic acid (14:1) , palmitoleic acid (16:1), 17:1, and oleic acid (18:1 *cis*-9) (μg/mL) were higher ($P < 0.05$) in serum obtained from pasture-finished steers than feedlot finished steers on d 28, 84, and 140 (Tables 13 and 14). However, when expressed as a percentage of total fatty acids, this effect was not consistent, as palmitoleic acid, 17:1, and oleic acid were higher ($P < 0.05$) in the pasture finishing than the high-concentrate finishing treatment only on d 84 and 140.

Similar to the results of the SFA, the differences observed in MUFA in serum did not correspond to the differences observed in ruminal fluid. Overall, concentrations (μg/mL) of SFA were higher ($P < 0.05$) in ruminal fluid, but lower ($P < 0.05$) in the serum from the high-concentrate finishing treatment, as compared to the pasture finishing treatment. These discrepancies in the concentrations of MUFA, when comparing ruminal fluid to serum, may again be due to fatty acid metabolism in various tissues within the animal. For instance, the enzyme Δ^9 desaturase has the ability to add a double bond to SFA, and liver, mammary, and adipose tissues are known to have this enzyme (Wahle, 1974; Pollard et al., 1980; Adlof et al., 2000; Santora et al., 2000). The lower concentrations of MUFA in serum may possibly be an indicator of lower Δ^9 desaturase activity in the high-concentrate finished steers, compared to pasture-finished steers. Yang et al. (1999) compared the Δ^9 desaturase activity of subcutaneous adipose tissue in pasture-finished and grain-fed cattle. The Δ^9 desaturase activity of adipose tissue from pasture-finished cattle (1.48 nmol·mg protein^{-1}·min^{-1}) was greater than grain-finished cattle (approximately 0.85 nmol·mg protein^{-1}·min^{-1}). Loor and Herbein (1998) and

Table 14. The effect of high-concentrate or pasture finishing treatments on conjugated linoleic acid and 18:1 fatty acid isomers in serum

	High-concentrate finishing				Pasture finishing				
	Time of sampling								
Fatty acid	d 0	d 28	d 84	d 140	d 0	d 28	d 84	d 140	SE
No. of samples	12	12	12	12	12	12	12	12	
	µg/mL								
Oleic (18:1 *cis*-9)	158.80[bef]	101.95[a]	77.31[a]	107.78[a]	176.32	188.16	181.81	167.58	4.6992
18:1 *trans*-10	7.76[bef]	4.27[ac]	14.67[ad]	11.33[a]	8.04[bef]	-	-	-	0.3239
Vaccenic (18:1 *trans*-11)	7.95	5.71[a]	5.09[a]	5.00[a]	7.88[bef]	36.93[c]	25.28	29.23	0.5592
Conjugated linoleic,									
18:2 *cis*-9, *trans*-11	7.82[bef]	3.70[a]	1.99[a]	2.33[a]	9.07	9.84	9.84	8.12	0.2281
18:2 *trans*-10, *cis*-12	0.48[ef]	0.42[c]	0.98[a]	1.06[a]	0.54[bef]	0.21	0.15	0.16	0.0257
18:12 *cis*-9, *cis*-11	25.11	13.69	38.29	0.77	1.32	2.31	1.89	2.09	5.7741
18:12 *trans*-9, *trans*-11	5.39[bef]	1.69[a]	1.17[a]	1.46[a]	5.24[bef]	15.20[c]	12.02	13.56	0.2572
Total fatty acids[g]	1005.21	548.51	906.60	1055.97	999.15	1045.56	889.50	1046.71	
	% of total fatty acids								
Oleic (18:1 *cis*-9)	15.82[ef]	17.73[c]	8.30[a]	9.84[a]	17.32	17.91	19.55[d]	15.78	0.3032
18:1 *trans*-10	0.72[ef]	0.72[ac]	1.58[ad]	1.03[a]	0.75[bef]	-	-	-	0.0265
Vaccenic (18:1 *trans*-11)	0.82[f]	1.04[ac]	0.55[a]	0.46[a]	0.79[bef]	3.60[c]	2.72	2.86	0.0395
Conjugated linoleic,									
18:2 *cis*-9, *trans*-11	0.80[ef]	0.67[ac]	0.21[a]	0.21[a]	0.91	0.96	1.06[d]	0.80	0.0201
18:2 *trans*-10, *cis*-12	0.05[bef]	0.08[ac]	0.11[a]	0.10[a]	0.05[bef]	0.02	0.02	0.01	0.0028
18:12 *cis*-9, *cis*-11	2.05	2.02	2.83	0.07	0.13	0.23	0.21	0.21	0.4784
18:12 *trans*-9, *trans*-11	0.54[bef]	0.29[ac]	0.13[a]	0.14[a]	0.52[bef]	1.47[c]	1.29	1.31	0.0169

[a]Within date, high-concentrate and pasture finishing treatments differ ($P < 0.05$).
[b]Contrast: within treatment, d 0 and d 28 differ ($P < 0.05$).
[c]Contrast: within treatment, d 28 and d 84 differ ($P < 0.05$).
[d]Contrast: within treatment, d 84 and d 140 differ ($P < 0.05$).
[e]Contrast: within treatment, d 0 and d 84 differ ($P < 0.05$).
[f]Contrast: within treatment, d 0 and d 140 differ ($P < 0.05$).
[g]Includes the fatty acids measured.

Chouinard et al. (1999a, 1999b) observed increased ratios of SFA to MUFA in milk obtained from cows with depressed milk fat as compared to control cows with normal milk fat production. Milk fat depression has been linked to feeding a high-concentrate diet to cows (Gaynor et al., 1995).

In the current study, within the high-concentrate finishing treatment, myristoleic acid, palmitoleic acid, 17:1, and, oleic acid (μg/mL) decreased ($P < 0.05$) from d 0 to d 28. When expressed as a percentage of total fatty acids, myristoleic acid decreased ($P < 0.05$) until d 84. Concentrations (% of total fatty acids) of palmitoleic acid, 17:1, and oleic acid were higher ($P < 0.05$) on d 0 than 84 and 140, and were also higher ($P < 0.05$) on d 28 than 84.

Within the pasture finishing treatment, d 0 myristoleic acid concentrations (μg/mL) were lower ($P < 0.05$) than on d 28, 84, and 140, while no differences between sampling dates were observed in palmitoleic acid and 17:1. As a percentage of total fatty acids, serum concentrations within the pasture finishing treatment, myristoleic acid and 17:1 increased ($P < 0.05$) until d 84, and d 84 values were higher ($P < 0.05$) than the other sampling dates. The oleic acid levels were higher ($P < 0.05$) for d 84 than d 140.

Overall, the variations over time in MUFA within ruminal fluid and serum were not consistent. Generally, there was more variation observed within the high-concentrate than pasture finishing treatment, presumably due to shifts in dietary ingredients (Table 1). These shifts in dietary ingredients perhaps led to alterations in Δ^9 desaturase activity, as high-concentrate diets lead to reduced Δ^9 desaturase activity (Yang et al., 1999).

The MUFA 18:1 *trans*-10 (μg/mL and % of total fatty acids) was higher ($P < 0.05$) in the high-concentrate fed cattle on d 28, 84, and 140, than pasture-finished cattle,

and was observed in serum in the pasture finishing treatment only on d 0 (0.75 % of total fatty acids) (Table 14). Concentrations of 18:1 *trans*-10 in the serum of high-concentrate finished steers were 0.72, 0.72, 1.58, and 1.03 % of total fatty acids on d 0, 28, 84, and 140, respectively.

Within the high-concentrate finishing treatment, 18:1 *trans*-10 values (µg/mL and % of total fatty acids) fluctuated and values on d 84 were higher ($P < 0.05$) than any other sampling date. These results are similar to those observed for ruminal fluid. Ruminal fluid concentrations (mg/g DM and % of total fatty acids) of 18:1 *trans*-10 were higher ($P < 0.05$) in the high-concentrate than pasture finishing treatment on d 84. The amounts of 18:1 *trans*-10 in ruminal fluid of pasture-finished steers were very small (0.01 to 0.06 mg/g DM), and as a result were not detectable in serum.

Although it appears that no studies have been conducted to evaluate the effects of a pasture-based diet on 18:1 *trans*-10 in blood, dietary effects on the concentrations of this fatty acid in digesta or milk may be analogous. Piperova et al. (2000) and LeDoux et al. (2002) observed increased 18:1 *trans*-10 in milk when ruminants were fed high-concentrate diets. Additionally, Griinari et al. (1998) observed increased concentrations of 18:1 *trans*-10 in milk in response to both decreased forage level and inclusion of unsaturated fatty acids. Loor et al. (2004) and Sackmann et al. (2003) observed increased duodenal flows of 18:1 *trans*-10 as a result of feeding high-concentrate diets and oil supplementation. Loor et al. (2003a) observed increased (0.3 versus 3.8 to 5.4 µg/mL) 18:1 *trans*-10 in plasma from cows supplemented with canola and soybean oil with or without CLA, compared to the control.

In the current study, serum concentrations (µg/mL and % of total fatty acids) of vaccenic acid (18:1 *trans*-11) were higher ($P < 0.05$) in the serum of pasture-finished steers than high-concentrate finished steers on d 28, 84, and 140 (Table 14). Serum concentrations of vaccenic acid were 0.79, 3.60, 2.72, and 2.86 % of total fatty acids on d 0, 28, 84, and 140, respectively, within the pasture-fed steers. Serum obtained from the high-concentrate finished steers contained 0.82, 1.04, 0.55, and 0.46 % of total fatty acids of vaccenic acid, on d 0, 28, 84, and 140, respectively.

Within the pasture finishing treatment, serum concentrations (µg/mL and % of total fatty acids) of vaccenic acid increased ($P < 0.05$) from d 0 to 28, 84, and 140 but decreased ($P < 0.05$) from d 28 to 84. These changes in vaccenic acid amounts in serum generally reflect the vaccenic acid content of the ruminal fluid. Pasture-finished steers contained higher ($P < 0.05$) vaccenic acid in both ruminal fluid and serum, compared to high-concentrate finished steers, which peaked on d 28 of the current study. This peak on d 28 in vaccenic acid in serum (and also in ruminal fluid) from the high-concentrate finished steers may be attributed to dietary changes. Prior to the start of the study, the steers had been consuming timothy hay-based diets supplemented with soybean hulls and soybean meal. In the current study, during period 1 (d 0 to 28), the steers on the high-concentrate diet consumed a diet consisting primarily of corn silage (average 88.77 % of DM). These differing diet ingredients (and their fiber and fatty acid contents) may have resulted in the higher ($P < 0.05$) content of vaccenic acid in ruminal fluid and serum on d 28 than on d 0, within the high-concentrate finishing treatment.

The higher ($P < 0.05$) levels of vaccenic acid in ruminal fluid and serum from pasture-finished steers may be attributed to the biohydrogenation of the fatty acids in the

pasture forages. A main precursor of vaccenic acid is linolenic acid (Kellens et al., 1986). French et al. (2000), Rhee et al. (2000), and Dewhurst et al. (2001) observed that linolenic acid is a major component of the fatty acids found in pasture forages. In the current study, the linolenic acid concentrations in the pasture forages that the steers grazed declined sharply after d 28 and remained low, as compared to the first 28 d (Table 7). In the current study, concentrations of linolenic acid were 72.90, 63.90, and 61.55 % of total fatty acids in periods 1, 2, and 3, respectively.

Serum concentrations (μg/mL and % of total fatty acids) of 18:2 *cis*-9, *trans*-11 CLA were higher ($P < 0.05$) in the pasture-finished steers than the high-concentrate finished steers on d 28, 84, and 140 (Table 14). Within the high-concentrate finishing treatment, 18:2 *cis*-9, *trans*-11 CLA (μg/mL and % of total fatty acids) decreased ($P < 0.05$) from d 0 to 28. Within the pasture finishing treatment, 18:2 *cis*-9, *trans*-11 CLA concentrations (% of total fatty acids) were higher ($P < 0.05$) on d 84 than 140. Overall, the differences of CLA concentrations in serum reflect those observed in ruminal fluid. Concentrations of 18:2 *cis*-9, *trans*-11 CLA were small in both ruminal fluid and serum, and were higher ($P < 0.05$) in the pasture-finished than high-concentrate finished steers on d 84 and 140, when expressed as a percentage of total fatty acids. The serum concentrations of 18:2 *cis*-9, *trans*-11 CLA were lower than its precursor vaccenic acid, indicating the importance of *de novo* synthesis. Endogenous (adipose/mammary tissue) synthesis is the primary mechanism by which 18:2 *cis*-9, *trans*-11 CLA is produced (Griinari et al., 2000, Corl et al., 2001, Kay et al., 2004). In the current study, 18:2 *cis*-9, *trans*-11 CLA concentrations in serum from the pasture-finished steers ranged from 0.80

to 1.06 % of total fatty acids, while the vaccenic acid concentrations ranged from 0.79 to 3.60 % of total fatty acids.

The concentrations (μg/mL) of 18:2 *trans*-10, *cis*-12 CLA were higher ($P < 0.05$) in serum from high-concentrate finished steers than pasture-finished steers on d 84 and 140 (Table 14). When expressed as a percentage of total fatty acids, 18:2 *trans*-10, *cis*-12 CLA was also higher ($P < 0.05$) on d 28 in the high-concentrate finishing treatment. Concentrations of 18:2 *trans*-10, *cis*-12 CLA in serum from high-concentrate finished steers were 0.05, 0.08, 0.11, and 0.10 % of total fatty acids on d 0, 28, 84, and 140, respectively. Within the pasture finishing treatment, serum concentrations of 18:2 *trans*-10, *cis*-12 CLA were 0.05, 0.02, 0.02, and 0.01 % of total fatty acids on d 0, 28, 84, and 140, respectively.

Within the high-concentrate finishing treatment, 18:2 *trans*-10, *cis*-12 CLA (μg/mL) was higher ($P < 0.05$) on d 84 and 140 than on d 0 and 28. When expressed as a percentage of total fatty acids, 18:2 *trans*-10, *cis*-12 CLA increased ($P < 0.05$) up to d 84. Within the pasture finishing treatment, 18:2 *trans*-10, *cis*-12 CLA was not detected in any of the ruminal fluid samples, and only in the last two sampling dates in the high-concentrate finishing treatment. This fatty acid was detected in serum from steers in both treatments, on all sampling dates. However, the same effect of 18:2 *trans*-10, *cis*-12 CLA being higher ($P < 0.05$) in the high-concentrate than pasture finishing treatment was observed in both ruminal fluid and serum. The appearance of 18:2 *trans*-10, *cis*-12 CLA only in serum, in some instances, may be a result of the differences in the analytical procedures used to analyze the samples, rather than a greater relative abundance of 18:2 *trans*-10, *cis*-12 CLA in serum. Due to the sensitivity of the gas chromatographic

analysis, a much smaller amount of ruminal fluid was injected onto the column as compared to serum. Additionally, the serum injection was splitless while the ruminal fluid was split at a ratio of 70:1.

The higher ($P < 0.05$) concentrations of 18:2 *trans*-10, *cis*-12 CLA in serum from steers in the high-concentrate finishing treatment, compared to pasture finishing treatment may be attributed to the altered ruminal biohydrogention of CLA associated with high-concentrate diets. Kim et al. (2002) isolated a strain of *Megasphaera elsdenii*, which produces significant amounts of 18:2 *trans*-10, *cis*-12 CLA, from the ruminal fluid of cows fed a high-concentrate diet. Sackmann et al. (2003) and Kucuk et al. (2001) observed increased duodenal flows of 18:2 *trans*-10, *cis*-12 CLA in ruminants with decreasing dietary forage levels. Loor et al. (2003a) observed increased 18:2 *trans*-10, *cis*-12 CLA outflow from continuous culture fermenters fed forages with increasing levels of corn supplementation.

In the current study, no differences in concentrations (µg/mL and % of total fatty acid) of 18:12 *cis*-9, *cis*-11 CLA were observed (Table 14). Serum concentrations (µg/mL and % of total fatty acid) of 18:12 *trans*-9, *trans*-11 CLA were higher ($P < 0.05$) in the serum obtained from pasture-finished steers than high-concentrate finished steers on d 28, 84, and 140 (Table 14). Within the pasture finishing treatment, 18:12 *trans*-9, *trans*-11 CLA concentrations (µg/mL and % of total fatty acid) increased ($P < 0.05$) from d 0 to 28, then decreased ($P < 0.05$) from d 28 to 84. Also, values on d 0 were lower ($P < 0.05$) than on d 84 and 140. Within the high-concentrate finishing treatment, 18:12 *trans*-9, *trans*-11 CLA concentrations (µg/mL) were higher ($P < 0.05$) on d 0 than on d 28, 84, and 140. When expressed as a percentage of total fatty acids, 18:12 *trans*-9, *trans*-11

CLA concentrations were higher ($P < 0.05$) on d 0 than on d 28, 84, and 140, and were higher ($P < 0.05$) on d 28 than 84.

Concentrations (µg/mL) of linoleic acid (18:2 *n*-6) and homogamma linolenic acid (20:3 *n*-6) fatty acids were higher ($P< 0.05$) in the serum obtained from the high-concentrate finished steers than pasture-finished steers on d 84 and 140 (Table 15). When expressed as a percentage of total fatty acids, these fatty acids were higher ($P < 0.05$) on d 28, 84, and 140 in the high-concentrate finishing treatment. Serum concentrations (µg/mL) of arachidonic acid (20:4 *n*-6) were higher ($P < 0.05$) in the high-concentrate finishing treatment on d 140, and when expressed as a percentage of total fatty acids, this fatty acid was also higher ($P < 0.05$) on d 28, than the pasture finishing treatment. The 20:2 *n*-6 concentrations (µg/mL) were lower ($P < 0.05$) in serum from the steers in the high-concentrate finishing treatment than the pasture finishing treatment on d 58, 84, and 140. As a percentage of total fatty acids, the values for the high-concentrate finished steers were lower ($P < 0.05$) than the pasture-finished steers only on d 84 and 140. Additionally, 22:2 *n*-6 concentrations (µg/mL) were lower ($P < 0.05$) in the high-concentrate finishing treatment than pasture finishing treatment on d 0, 28, and 84, and as a percentage of total fatty acids on d 84. The *n*-6 fatty acid 22:4 (µg/mL and % of total fatty acids) was higher ($P < 0.05$) in serum obtained from high-concentrate finished steers than pasture-finished steers
on d 84 and 140.

Within the high-concentrate finishing treatment, linoleic acid serum concentrations (µg/mL) decreased ($P < 0.05$) from d 0 to 28, and 140 increased ($P < 0.05$) from d 28 to 84, then remained high after d 84. However, as a percentage of total fatty

Table 15. The effect of high-concentrate or pasture finishing treatments on *n*-3 and *n*-6 fatty acids in serum

	High-concentrate finishing				Pasture finishing				
	Time of sampling								
Fatty acid	d 0	d 28	d 84	d 140	d 0	d 28	d 84	d 140	SE
No. of samples	12	12	12	12	12	12	12	12	
	µg/mL								
Linoleic (18:2 *n*-6)	236.39[bef]	132.49[c]	425.06[a]	481.60[a]	238.44[be]	153.97	114.97[d]	204.47	8.4308
Linolenic (18:3 *n*-3)	67.33[bef]	7.94[a]	6.28[a]	8.48[a]	71.27[bef]	137.20	116.35	138.16	2.9442
20:2 *n*-6	1.52[bef]	0.85[a]	0.82[a]	0.87[a]	1.30	1.30	1.10	1.27	0.0312
20:3 *n*-3	0.39[be]	0.24[a]	0.23[a]	0.24[a]	0.44	0.53	0.55	0.42	0.0183
Homogamma-linolenic, (20:3 *n*-6)	21.27[bf]	11.17[c]	20.39[ad]	27.19[a]	22.19[be]	15.43	11.64[d]	18.97	0.6775
Arachidonic (20:4 *n*-6)	29.15[be]	15.45	19.93[d]	27.18[a]	27.51[bef]	19.92	16.28	17.85	0.8148
22:2 *n*-6	0.56[abef]	0.30[a]	0.23[a]	0.27	0.36[b]	0.59	0.52	0.37	0.0234
22:3 *n*-3	20.42[bef]	4.33[a]	1.83[a]	2.03[a]	20.00[b]	27.84[c]	23.06	22.76	0.5265
22:4 *n*-6	2.87[ef]	2.70[c]	6.67[a]	7.81[a]	2.75	2.08	1.90	2.59	0.1563
DPA (22:5 *n*-3)	20.53[bef]	11.20[a]	7.43[a]	6.63[a]	20.93	19.32	19.32	20.98	0.4768
DHA (22:6 *n*-3)	8.16[bef]	5.66[c]	3.09[a]	2.72[a]	8.45[bef]	5.74	5.61	4.59	0.1367
Total fatty acids[g]	1005.21	548.51	906.60	1055.97	999.15	1045.56	889.50	1046.71	
	% of total fatty acids								
Linoleic (18:2 *n*-6)	22.58[ef]	22.10[ac]	46.00[a]	43.91[a]	23.10[be]	14.65	12.35[d]	19.35	0.5456
Linolenic (18:3 *n*-3)	6.68[bef]	1.35[a]	0.68[a]	0.78[a]	7.06[bef]	12.88	12.37	13.12	0.1379
20:2 *n*-6	0.15[ef]	0.16[c]	0.09[a]	0.08[a]	0.13	0.13	0.12	0.12	0.0034
20:3 *n*-3	0.04[ef]	0.04[c]	0.02[a]	0.02[a]	0.04	0.05	0.06[d]	0.04	0.0019
Homogamma-linolenic, (20:3 *n*-6)	2.03[f]	1.87[a]	2.19[a]	2.46[a]	2.17[bef]	1.48	1.27[d]	1.79	0.0434
Arachidonic (20:4 *n*-6)	2.83[e]	2.61[ac]	2.07	2.44[a]	2.67[bef]	1.87	1.77	1.69	0.0535
22:2 *n*-6	0.06[ef]	0.06[c]	0.03[a]	0.03	0.04	0.06	0.06	0.04	0.0033
22:3 *n*-3	2.09[bef]	0.78[ac]	0.20[a]	0.19[a]	2.01[be]	2.65	2.50[d]	2.16	0.0358
22:4 *n*-6	0.27[bef]	0.45[ac]	0.70[a]	0.71[a]	0.26	0.20	0.21	0.24	0.0101
DPA (22:5 *n*-3)	2.04[ef]	1.98[c]	0.81[a]	0.62[a]	2.05	1.84	2.07	2.01	0.0324
DHA (22:6 *n*-3)	0.82[bef]	0.99[ac]	0.34[a]	0.25[a]	0.85[bef]	0.56	0.61[d]	0.45	0.0154

[a]Within date, high-concentrate and pasture finishing treatments differ ($P < 0.05$).
[b]Contrast: within treatment, d 0 and d 28 differ ($P < 0.05$).
[c]Contrast: within treatment, d 28 and d 84 differ ($P < 0.05$).
[d]Contrast: within treatment, d 84 and d 140 differ ($P < 0.05$).
[e]Contrast: within treatment, d 0 and d 84 differ ($P < 0.05$).
[f]Contrast: within treatment, d 0 and d 140 differ ($P < 0.05$).
[g]Includes the fatty acids measured.

acids, linoleic acid concentrations increased ($P < 0.05$) from d 0 and 28 to 84, and remained high after d 84. Concentrations (µg/mL) of 20:2 *n*-6 decreased ($P < 0.05$) from d 0 to 28, and remained low. As a percentage of total fatty acids, 20:2 *n*-6 decreased ($P < 0.05$) from d 28 to d 84 and 140. Serum concentrations (µg/mL) of homogamma linolenic acid decreased ($P < 0.05$) from d 0 to 28, then increased ($P < 0.05$) from d 28 through 140, while as a percentage of total fatty acids, the value was lower ($P < 0.05$) only for d 0, compare to d 140.

Within the high-concentrate finishing treatment, arachidonic acid serum concentrations (µg/mL) decreased ($P < 0.05$) from d 0 to 28, and increased ($P < 0.05$) from d 84 to 140. However, as a percentage of total fatty acids, only values on d 0 and 28 were higher ($P < 0.05$) than on d 84. Concentrations of 22:2 *n*-6 (µg/mL) decreased ($P < 0.05$) from d 0 to 28, and then remained low. As a percentage of total fatty acids, concentrations of 22:2 *n*-6 decreased ($P < 0.05$) from d 0 to d 84 and 140, and d 28 to 84, and remained low after d 84. The 22:4 *n*-6 fatty acid serum concentrations (µg/mL) within the high-concentrate finishing treatment increased ($P < 0.05$) from d 28 to 84. When expressed as a percentage of total fatty acids, concentrations increased ($P < 0.05$) from d 0 to 28 and 84.

Within the pasture finishing treatment, serum concentrations (µg/mL and % of total fatty acids) of linoleic acid and homogamma linolenic acid decreased ($P < 0.05$) from d 0 to d 28 and 84, and increased ($P < 0.05$) from d 84 to 140. There were no differences among sampling dates within the pasture finishing treatment for 20:2 *n*-6. Concentrations (µg/mL and % of total fatty acids) of arachidonic acid in serum from pasture-finished steers decreased ($P < 0.05$) from d 0 to d 28, and remained lower ($P <$

0.05) than d 0 values for the remainder of the study. Serum values (μg/mL) for 22:2 *n*-6 were lower ($P < 0.05$) on d 0 than 28, and when expressed as a percentage of total fatty acids, there were no differences among sampling dates within the pasture finishing treatment. Among sampling dates, no differences in serum 22:4 *n*-6 concentrations were observed in the pasture finishing treatment.

The fatty acids, linoleic acid, 20:2 *n*-6, and 22:2 *n*-6 were observed in both ruminal fluid and serum. Lack of detection of homogamma linolenic acid, arachidonic acid, and 22:4 *n*-6 in the diets or ruminal fluid from steers in either treatment may again be due to analytical technique. Serum values of these fatty acids were small, and a larger amount of the fatty acids from the serum samples were injected onto the gas chromatograph column in comparison to diet and ruminal fluid samples (splitless versus split injections, respectively). Overall the omega-6 (*n*-6) fatty acids in serum reflected the ruminal fluid and diets. Concentrations of linoleic acid were generally higher in both ruminal fluid and serum in the high-concentrate finished steers than pasture-finished steers, which may be attributed to the greater content of this fatty acid in the diets of the high-concentrate finished steers, compared to pasture-finished steers. The linoleic acid content of the high-concentrate finishing diet averaged 58.39, 57.05, and 56.74 % of total fatty acids in periods 1 (d 0 to 28), 2 (d 28 to 84), and 3 (d 84 to 140), respectively. The linoleic acid concentration of the pasture forages averaged 6.92, 9.41, and 10.13 % of total fatty acids for periods 1, 2, and 3, respectively (Table 7).

Concentrations of the fatty acids 20:2 *n*-6 and 22:2 *n*-6 tended to be lower in both ruminal fluid and serum of the high-concentrate finished than pasture-finished steers. The fatty acid 22:2 *n*-6 was not detected in ruminal fluid of the high-concentrate finished

steers on d 28, 84, and 140. Dietary content of these fatty acids may have contributed to these differences between treatments. Concentrations of 20:2 *n*-6 and 22:2 *n*-6 were higher in the pasture forages than the high-concentrate diets. Concentrations of 20:2 *n*-6 and 22:2 *n*-6 in the pasture forages ranged from 0.21 to 0.27 and 0.18 to 0.30 mg/g DM, respectively. Concentrations of 20:2 *n*-6 in the high-concentrate diets ranged from 0.04 to 0.15 mg/g DM, while 22:2 *n*-6 was not detected. Generally, the effects of sampling date on omega-6 fatty acids in ruminal fluid and serum from the high-concentrate finishing treatment may be attributed to dietary fluctuations of these fatty acids.

Serum concentrations (μg/mL) of the omega-3 (*n*-3) fatty acids linolenic (18:3 *n*-3) and 22:3 *n*-3 were higher ($P < 0.05$) in the pasture-finished than the high-concentrate finished steers on d 28, 84, and 140 (Table 15). Serum concentrations (μg/mL) of 20:3 *n*-3 and DPA (22:5 *n*-3) were higher ($P < 0.05$) in the pasture-finished steers than the high-concentrate finished steers on d 28, 84, and 140 (Table 15). Concentrations (μg/mL) of DHA (22:6 *n*-3) were higher ($P < 0.05$) in the pasture finishing than high-concentrate finishing treatment on d 84 and 140.

When expressed as a percentage of total fatty acids, linolenic acid and 22:3 *n*-3 were higher ($P < 0.05$) in the pasture finishing system on d 28, 84, and 140. Within the pasture finishing treatment, serum concentrations of linolenic acid were 7.06, 12.88, 12.37, and 13.12 % of total fatty acids on d 0, 28, 84, and 140, respectively. In the serum from the high-concentrate finished steers, concentrations of linolenic acid were 6.68, 1.35, 0.68, and 0.78 % of total fatty acids on d 0, 28, 84, and 140, respectively. Serum concentrations of 20:3 *n*-3 and DPA were higher ($P < 0.05$) in the pasture-finished steers

than the high-concentrate finished steers only on d 84 and 140. Values for DHA were higher ($P < 0.05$) in the pasture finishing treatment on d 28 (Table 15).

Overall, concentrations of omega-3 fatty acids were higher in both the ruminal fluid and serum from the pasture-finished steers, compared to the high-concentrate finished steers. These results may be attributed to the higher omega-3 content of the pasture forages, as compared to the high-concentrate diet (Tables 5 and 7). The average linolenic acid concentration of the pasture forages were 72.9, 63.9, and 61.55 % of total fatty acids, while the linolenic acid concentrations of the high-concentrate diets averaged 3.06, 2.19, and 1.33 % of total fatty acids, for periods 1, 2, and 3, respectively. Sackmann et al. (2000) observed an increase in the flow of linolenic acid to the duodenum in cannulated steers fed increasing levels of forage in the diet. Griinari et al. (1998) and LeDoux et al. (2004) observed increased concentrations of linolenic acid in milk when ruminants were fed increased levels of forages.

Within the high-concentrate treatment, serum concentrations (μg/mL and % of total fatty acids) of linolenic acid decreased ($P < 0.05$) from d 0 to d 28, and remained low after d 28, as concentrations on d 0 were higher ($P < 0.05$) than on d 84 and 140. Fatty acids 20:3 *n*-3, 22:3 *n*-3, and DPA (μg/mL) decreased ($P < 0.05$) in serum from the high-concentrate finished steers from d 0 to 28, and were lower ($P < 0.05$) on d 84 and 140 than d 0. When expressed as a percentage of total fatty acids, these fatty acids decreased ($P < 0.05$) until d 84, as values on d 0 were higher ($P < 0.05$) than all others. Concentrations (μg/mL) of DHA decreased ($P < 0.05$) in the high-concentrate fed steers from d 0 through 140. However, when expressed as a percentage of total fatty acids, DHA increased ($P < 0.05$) from d 0 to 28, then decreased ($P < 0.05$) from d 28 to d 84.

Within the pasture finishing treatment, serum concentrations (µg/mL and % of total fatty acids) of linolenic acid and DHA increased ($P < 0.05$) from d 0 to 28, and remained high throughout the study, with the exception of DHA (% of total fatty acids), which decreased ($P < 0.05$) from d 84 to 140. There were no sampling date differences in 20:3 *n*-3, except that values on d 84 were higher ($P < 0.05$) than d 140, as a percentage of total fatty acids, but the difference was small. Concentrations (µg/mL) of 22:3 *n*-3 increased ($P < 0.05$) from d 0 to 28, and decreased ($P < 0.05$) from d 28 to 84. When expressed as a percentage of total fatty acids, serum concentrations of 22:3 *n*-3 fluctuated over time, as values on d 0 were lower ($P < 0.05$) than on d 28 and 84. Concentrations of 22:3 *n*-3 were higher ($P < 0.05$) on d 84 than 140. Among sampling dates, no differences in serum DPA concentrations were observed in the pasture finishing treatment.

Studies comparing the effects of high-concentrate versus pasture finishing on ruminal fluid, serum or milk long chain (C20 or greater) omega-3 and omega-6 fatty acids are limited. Ward et al. (2003) evaluated plasma cholesterol content of these long chain fatty acids. However, the authors did not distinguish between the omega-3 and omega-6 fatty acid isomers, for example 20:3 *n*-3 versus *n*-6, in their article. Additionally, the diets contained tallow supplementation. Researchers (Loor et al., 2002b; Loor and Herbein, 2003a) have investigated the effects of oil supplementation on blood plasma and milk fatty acids. Therefore, the results of these studies are not very comparable to the current study. Loor et al. (2002b) reported plasma 20:3 *n*-3, arachidonic acid, and 20:5 *n*-3 concentrations, from cows fed the control diet, of 3.9, 2.1, and 0.6 % of total fatty acids, respectively. Canola supplementation resulted in a small decrease in 20:3 *n*-3, and no changes in arachidonic acid, and 20:5 *n*-3. Loor and

Herbein (2003a) reported plasma 20:3 *n*-3, arachidonic acid, and 20:5 *n*-3 concentrations of 18, 38, and 22 μg/mL, respectively, in cows fed the control diets. Oil supplementation resulted in increases in all of these fatty acids.

In general, differences between sampling dates within treatments, in both ruminal fluid and serum samples, may be attributed to the hydration status of the steers. Hydration status may have an influence on the amounts of fatty acids, expressed as mg/g ruminal fluid DM or as μg/mL of serum, since a dehydrated animal would most likely have more concentrated ruminal fluid and serum. The day prior to the initiation of the study, the steers were shipped to the finishing locations, a potential stressor. Additionally, the steers may have needed to adapt to finding new sources of feed and water, and perhaps learn how to use the water facilities present in the feedlot. All of these factors may have resulted in some amount of dehydration in the steers. Although hydration status was not quantified in this study, it was noted that ruminal fluid samples were difficult to obtain on d 0, and it was not always possible to obtain the desired 200 mL volume of rumen fluid (as described in the experimental protocol). Possible dehydration in the steers may have been reflected in the results. For many of the fatty acids, a decrease from d 0 to d 28 was observed in the absolute concentrations (mg/g DM or μg/mL). However, when expressed as a percentage of total fatty acids, no difference between d 0 and 28 was observed. Therefore, presenting the data as a percentage of total fatty acids may be a valuable tool in fatty acid research, since the data would not be biased by hydration status of the animals, since the overall ratios of fatty acids within a sample would not change due to differences in the amount of water in the sample.

Adipose tissue fatty acids. There was no effect of treatment or sampling date on lauric acid (12:0) (Table 16), and values ranged from 0.14 to 0.33 % of total fatty acids. There were no differences among sampling dates for lauric acid concentrations in adipose tissue, in either finishing treatment. French et al. (2002) observed no differences in beef fatty acid content of lauric acid due to pasture finishing, high-concentrate finishing, or supplementing pasture-fed cattle with grain. The authors observed concentrations of lauric acid ranging from 0.8 to 0.9 % of total fatty acids.

In the current study, the adipose tissue obtained from the high-concentrate finished steers contained lower ($P < 0.05$) myristic acid (14:0) (mg/g tissue) than the pasture-finished steers on d 0 and 28 (Table 16). However, when expressed as a percentage of total fatty acids, no treatment effect was observed, and values ranged from 1.28 to 2.77 % of total fatty acids. In general, patterns in ruminal fluid and serum SFA were not very consistent and did not relate well to the SFA in adipose tissue. Concentrations of myristic acid were higher ($P < 0.05$) in ruminal fluid from the high-concentrate than pasture-finished steers, but only on some sampling dates. In the serum, myristic acid concentrations were lower ($P < 0.05$) in the high-concentrate than pasture-finished steers, on d 28, 84, and 140. Adipose tissue concentrations of myristic acid were lower ($P < 0.05$) in the high-concentrate than pasture-finished steers only on d 0 and 28.

Results of previous research regarding SFA have been inconsistent. French et al (2000) observed no difference in intramuscular myristic acid concentrations due to grain- versus pasture finishing, or supplementation of pasture-fed cattle with grain. The authors observed myristic acid values ranging from 2.34 to 2.76 % of total fatty acids. Rhee et al. (2000) and Yang et al. (2002b) also observed no differences in myristic acid

Table 16. The effect of high-concentrate or pasture finishing treatments on fatty acid composition of subcutaneous adipose tissue in steers

	High-concentrate finishing				Pasture finishing				
	Time of sampling								
Fatty acid	d 0	d 28	d 84	d 140	d 0	d 28	d 84	d 140	SE
No. of samples	12	12	12	12	12	12	12	12	
	mg/g tissue								
Lauric (12:0)	1.34	1.22	1.10	1.22	1.28	1.21	1.12	1.20	0.0315
Myristic (14:0)	16.35[abe]	12.37[a]	10.45	12.91	21.73[ef]	18.29[c]	12.43	12.90	0.4773
Myristoleic (14:1)	3.86[f]	4.80	3.64[d]	5.35	5.23[e]	4.81	3.67	4.47	0.1749
Pentadecylic acid (15:0)	4.17[be]	2.81[a]	2.96[a]	3.43	4.96	5.22	4.57	4.12	0.1510
Palmitic (16:0)	221.02[f]	256.06	275.48	306.44	289.53	280.15	243.24	251.52	9.4078
Palmitoleic(16:1)	20.62[bef]	39.45	34.73	40.80	29.99	34.71	31.52	35.18	1.2733
Margaric (17:0)	6.50[ef]	5.95[ac]	11.90[a]	12.95[a]	7.62	8.89	7.64	7.92	0.3317
17:1	3.39[ef]	4.63[c]	10.03[ad]	12.35[a]	3.85	4.37	4.34	4.92	0.2303
Stearic (18:0)	129.60	100.64[a]	104.87[a]	94.55[a]	152.04	182.09	157.84	142.79	5.8763
Oleic (18:1 *cis*-9)	239.77[ef]	283.60[c]	396.67[a]	440.94[a]	275.52	319.15	284.80	291.50	13.8415
Vaccenic (18:1 *trans*-11)	22.58	13.20[a]	22.13[a]	26.97[a]	30.56[bef]	68.44	67.67	62.38	2.4657
Linoleic (18:2 *n*-6)	5.68[ef]	6.48[c]	11.74[ad]	14.45[a]	6.79	6.73	5.26	4.93	0.2913
CLA 18:2 *cis*-9, *trans*-11)	7.44[ef]	5.26[ac]	2.16[a]	2.17[a]	9.99	12.80	10.40	9.91	0.3612
Linolenic (18:3 *n*-3)	3.71[a]	2.68[a]	2.70[a]	2.48[a]	5.22[b]	6.83[c]	5.16	5.82	0.1863
Total fatty acids[g]	686.01	739.11	890.55	976.98	844.32	953.70	839.66	839.56	
	% of total fatty acids								
Lauric (12:0)	0.28	0.19	0.14	0.14	0.33	0.15	0.17	0.16	0.0238
Myristic (14:0)	2.58[bef]	1.72	1.28	1.39	2.77[bef]	2.09	1.62	1.65	0.0606
Myristoleic (14:1)	0.60	0.68[c]	0.45	0.57	0.61	0.55	0.47	0.57	0.0220
Pentadecylic acid (15:0)	0.68[bef]	0.41[a]	0.37[a]	0.37	0.58	0.60	0.61	0.54	0.0230
Palmitic (16:0)	32.60	34.71[ac]	31.52	31.74	33.95[bef]	29.10	29.39	30.28	0.3390
Palmitoleic(16:1)	2.89[bef]	5.52[ac]	4.02	4.21	3.26[f]	3.73	3.75	4.20	0.0960
Margaric (17:0)	1.01[ef]	0.84[c]	1.42[a]	1.37[a]	0.86	1.00	0.96	1.00	0.0387
17:1	0.54[ef]	0.67[c]	1.17[a]	1.29[a]	0.45	0.49	0.57	0.61	0.0269
Stearic (18:0)	19.30[bef]	14.01[a]	11.89[a]	9.88[a]	17.79	19.11	18.94	17.02	0.3650
Oleic (18:1 *cis*-9)	33.86[ef]	37.53[ac]	43.07[a]	44.34[a]	33.58	33.24	32.93	34.11	0.5240
Vaccenic (18:1 *trans*-11)	3.14[b]	1.73[a]	2.72[a]	2.75[a]	3.20[bef]	7.03	7.91	7.22	0.1651
Linoleic (18:2 *n*-6)	0.84[ef]	0.92[c]	1.40[a]	1.50[a]	0.74	0.72	0.67	0.63	0.0294
CLA (18:2 *cis*-9, *trans*-11)	1.17[bef]	0.72[ac]	0.26[a]	0.21[a]	1.25	1.41	1.32	1.23	0.0429
Linolenic (18:3 *n*-3)	0.50[f]	0.35[a]	0.30[a]	0.24[a]	0.64	0.80	0.71	0.78	0.0320

[a]Within date, high-concentrate and pasture finishing treatments differ ($P < 0.05$).
[b]Contrast: within treatment, d 0 and d 28 differ ($P < 0.05$).
[c]Contrast: within treatment, d 28 and d 84 differ ($P < 0.05$).
[d]Contrast: within treatment, d 84 and d 140 differ ($P < 0.05$).
[e]Contrast: within treatment, d 0 and d 84 differ ($P < 0.05$).
[f]Contrast: within treatment, d 0 and d 140 differ ($P < 0.05$).
[g]Includes the fatty acids measured.

concentrations in ruminants (goats or cattle, respectively) finished on high-grain or on pasture. Rhee et al. (2000) observed concentrations of 1.78 % of total fatty acids in goat muscle finished on either a high-concentrate diet or on range. Yang et al.(2002b) observed myristic acid concentrations of 1.15 and 2.01 % of total fatty acids extracted from beef finished on pasture or concentrate, respectively. In contrast, Realini et al. (2004) observed myristic acid concentrations of 2.17 % of total fatty acids in cattle finished on high-concentrate diet, as compared to 1.64 % of total fatty acids in pasture-finished cattle.

In the current study, concentrations (mg/g tissue and % of total fatty acids) of myristic acid decreased ($P < 0.05$) in adipose tissue from d 0 to 28 and 84 (Table 16). Concentrations (mg/g tissue) of myristic acid in adipose tissue from pasture-finished steers were higher ($P < 0.05$) on d 0 than on d 84 and 140, and concentrations were higher ($P < 0.05$) on d 28 than 84. When expressed as a percentage of total fatty acids, a decrease ($P < 0.05$) in myristic acid was observed from d 0 to 28, 84, and 140.

There were inconsistencies in sampling date effects when relating ruminal fluid, serum, and adipose tissue myristic acid content. Concentrations of myristic acid (% of total fatty acids) in ruminal fluid were higher ($P < 0.05$) on d 0 than all other sampling dates within both the high-concentrate and pasture finishing treatments. Serum concentrations of myristic acid generally decreased in the high-concentrate finishing treatment, while increasing in the pasture finishing treatment. Adipose tissue concentrations of myristic acid were also higher ($P < 0.05$) in both treatments on d 0, as compared to all other sampling dates. Studies comparing the changes in fatty acid composition of adipose tissue from cattle finished on grain versus pasture, over time, are

not known. Duckett et al. (1993) observed increases in myristic acid as cattle were finished on a high-concentrate diet. The authors observed myristic acid concentrations of 2.25, 2.68, 3.15, and 3.56 % of total fatty acids, after 0, 28, 84, and 140 d on feed. In contrast, Yang et al. (1999) observed no differences in myristic acid concentrations (3.3 to 3.4 % of fresh tissue weight) in cattle finished on a high-concentrate diet for 0, 100, 200, or 300 d.

Adipose tissue concentrations (mg/g tissue and % of total fatty acids) of pentadecylic acid (15:0) were lower ($P < 0.05$) in the high-concentrate finishing treatment than pasture finishing treatment, on d 28 and 84 (Table 16). Ruminal fluid, serum, and adipose tissue concentrations (% of total fatty acids) of pentadecylic acid were lower ($P < 0.05$) in the high-concentrate than pasture finishing treatment. Similarly, Yang et al. (2002b) observed lower concentrations of pentadecylic acid in beef (0.19 versus 0.48) from grain-finished cattle, compared to pasture-finished cattle. In contrast, French et al. (2000) observed no difference due to dietary treatment in beef pentadecylic acid concentrations (0.58 to 0.66% of total fatty acids).

Concentrations (mg/g tissue and % of total fatty acids) of pentadecylic acid decreased ($P < 0.05$) in adipose tissue from d 0 to 28 and 84, in the high-concentrate finished steers. Within the pasture finishing treatment, there was no effect of sampling date on pentadecylic acid concentrations (mg/g tissue or % of total fatty acids). Ruminal fluid concentrations of pentadecylic acid in the high-concentrate and pasture finishing treatments were higher ($P < 0.05$) on d 0, compared to all other sampling dates. However, serum concentrations of pentadecylic acid in the high-concentrate finishing treatment were higher ($P < 0.05$) on d 0 than all other sampling dates, while in the pasture

finishing treatment, concentrations on d 0 were lower ($P < 0.05$) than on d 140. In adipose tissue, concentrations of pentadecylic acid in the high-concentrate finishing treatment were higher ($P < 0.05$) on d 0 than all other sampling dates, while no sampling date effect was observed in the pasture finishing treatment. In contrast to the current study, Duckett et al. (1993) observed increases in pentadecylic acid concentrations in beef over time, on a high-grain diet. The authors observed pentadecylic acid concentrations of 0.66, 0.86, 0.85, and 0.98 % of total fatty acids, after 0, 28, 84, and 140 d on feed. Yang et al. (1999) observed no differences in pentadecylic acid concentrations (0.4 to 0.7 % of fresh tissue weight) when cattle were fed for 0, 100, 200, or 300 d.

There was no treatment effect on adipose tissue palmitic acid (16:0) concentrations when expressed as mg/g tissue (Table 16). When expressed as a percentage of total fatty acids, the level was higher ($P < 0.05$) on d 28 for the high-concentrate-fed steers. Differences in concentrations of palmitic acid were not consistent among ruminal fluid, serum and adipose tissue samples. Ruminal fluid concentrations (% of total fatty acids) were lower ($P < 0.05$) in the high-concentrate finished steers, than pasture-finished steers, on d 84 and 140. Serum concentrations of palmitic acid were lower ($P < 0.05$) in the high-concentrate finished steers only on d 84. In contrast, adipose tissue concentrations of palmitic acid were higher ($P < 0.05$) in the high-concentrate than pasture-finished steers on d 28 (34.71 versus 29.10 % of total fatty acids). French et al. (2000), Yang et al. (2002b), and Realini et al. (2004) observed higher palmitic acid concentrations in grain-fed, as compared to pasture-fed beef. French et al. (2000) observed palmitic acid concentrations of 22.8 and 24.7 % of total fatty acids in pasture- and grain-fed beef, respectively. In pasture-finished and grain-finished cattle, Yang et al.

(2002b) observed palmitic acid concentrations of 22.7 and 27.3 % of total fatty acids, respectively. In contrast, Rhee et al. (2000) observed no effect of range- or grain-finishing on palmitic acid concentrations in goats (20.5 and 20.99 % of total fatty acids, respectively).

Concentrations (mg/g tissue) of palmitic acid on d 0 were lower ($P < 0.05$) than on d 140, within the high-concentrate finishing treatment (Table 16). When expressed as a percentage of total fatty acids, the levels on d 28 were higher ($P < 0.05$) than on d 84. Within the pasture finishing treatment, concentrations of palmitic acid were higher ($P < 0.05$) on d 0 than all other sampling dates. Sampling date effects were also inconsistent among ruminal fluid, serum, and adipose tissue. Ruminal fluid concentrations (% of total fatty acids) of palmitic acid were higher ($P < 0.05$) on d 0 than all other sampling dates, in both the high-concentrate and pasture finishing treatments. However, serum concentrations of palmitic acid were higher ($P < 0.05$) on d 0 than 84 and 140, in both treatments. Within the high-concentrate finishing treatment, a small decrease in adipose tissue palmitic acid concentrations from d 28 to 84 was observed, while in the pasture finishing treatment, concentrations were higher ($P < 0.05$) on d 0 than all other sampling dates. Duckett et al. (1993) observed a small increase in palmitic acid in cattle adipose tissue, from 0 to 28 d on a high-grain diet, and concentrations of palmitic acid remained higher ($P < 0.05$) than d 0 throughout the remainder of the study. Concentrations of palmitic acid in beef in their study were 24.84, 26.97, 27.66, and 26.70 % of total fatty acids, after 0, 28, 84, and 140 d on feed, respectively. Similar results were observed by Yang et al. (1999) in cattle after 0, 100, 200, and 300 d on feed. The authors observed

palmitic acid concentrations of 23.4, 26.2, 26.3, and 26.7 % (of fresh tissue weight), respectively.

Concentrations (mg/g tissue) of margaric acid (17:0) were lower ($P < 0.05$) in the high-concentrate finished steers than the pasture-finished steers on d 28, and were higher ($P< 0.05$) compared to the pasture-finished cattle on d 84 and 140 (mg/g tissue and % of total fatty acids) (Table 16). Concentrations of margaric acid were not entirely consistent among the samples (ruminal fluid, blood, and adipose) obtained in the current study. Generally, margaric acid concentrations (% of total fatty acids) were lower ($P < 0.05$) in the high-concentrate finishing treatment, compared to the pasture finishing treatment, on d 0, 28, and 84. However, serum and adipose tissue concentrations of margaric acid were higher ($P < 0.05$) in the high-concentrate finishing treatment than pasture finishing treatment on d 84. Adipose tissue concentrations of margaric acid were higher ($P < 0.05$) in the high-concentrate finishing treatment than pasture finishing treatment on d 84 and 140. Similar to the results of the current study, Rhee et al. (2000) observed lower margaric acid (1.29 versus 1.75 % of total fatty acids) in goats finished on range than on a high-grain diet. In contrast to the current study, Yang et al. (2002b) observed higher concentrations of margaric acid (1.10 versus 0.70 % of total fatty acids) in beef finished on pasture than on grain. French et al. (2000) observed no difference in margaric acid concentrations in beef finished on pasture or grain, and values ranged from 1.17 to 1.22 % of total fatty acids.

There was an increase ($P < 0.05$) in margaric acid concentrations in adipose tissue obtained from high-concentrate finished steers from d 0 to d 84 and 140 (Table 16). Within the pasture finishing treatment, there was no effect of sampling date on margaric

acid concentrations (mg/g tissue or % of total fatty acids). Yang et al. (1999) observed no effect of sampling date (0, 100, 200, or 300 d on a high-grain diet) on margaric acid beef content. The authors observed values ranging from 0.9 to 1.9 % (of fresh tissue weight). In contrast, Duckett et al. (1993) observed a gradual increase in margaric acid in beef finished on a high-concentrate diet, over time. The authors reported margaric acid concentrations of 1.28, 1.69, 2.10, and 2.33 % of total fatty acids, after 0, 28, 84, and 140 d, respectively.

The high-concentrate finished steers had lower ($P < 0.05$) stearic acid (18:0), expressed as mg/g tissue and percentage of total fatty acids, in adipose tissue on d 28, 84, and 140 than pasture-finished steers (Table 16). Treatment effects on ruminal fluid and serum stearic acid concentrations did not correspond to adipose tissue. Ruminal fluid stearic acid concentrations (%of total fatty acids) were higher ($P < 0.05$) in the high-concentrate than pasture finishing treatment, while there were no treatment effects on serum content of stearic acid. In contrast, adipose tissue concentrations of stearic acid were lower ($P < 0.05$) in the high-concentrate than pasture-finished cattle. Rhee et al. (2000) observed greater stearic acid concentrations in goats finished on range than on a high-grain diet (16.27 versus 10.24 % of total fatty acids). Realini et al. (2004) also observed higher stearic acid concentrations in beef finished on pasture, compared to a high-grain diet. The authors observed stearic acid concentrations of 17.74 and 15.77 % of total fatty acids in pasture- and grain-finished beef, respectively. However, Yang et al. (2002b) and French et al. (2000) observed no differences in stearic acid concentrations in beef between pasture and grain-finished cattle. Yang et al. (2002b) observed stearic acid values of 16.3 and 15.0 % of total fatty acids in the *longissimus dorsi* muscles from

pasture- and grain-fed cattle, respectively. French et al. (2000) observed values of 15.95, 14.72, and 16.13 % of total fatty acids in cattle finished on grain, pasture, or pasture supplemented with grain, respectively.

There was no effect of sampling date on stearic acid concentrations in adipose tissue from the high-concentrate finishing treatment, when presented as mg/g tissue (Table 16). When expressed as a percentage of total fatty acids, stearic acid decreased ($P < 0.05$) from d 0 to 28, 84, and 140, and no other differences among sampling dates were observed. Within the pasture finishing treatment, there was no effect of sampling date on stearic acid concentrations (mg/g tissue or % of total fatty acids). Ruminal fluid and serum concentrations of stearic acid generally increased in both treatments after d 0. In contrast, there was no change in serum content of stearic acid over time in the high-concentrate finishing treatment.

Within the pasture finishing treatment, stearic acid concentrations in serum were lower ($P < 0.05$) on d 0 than d 28. Therefore, ruminal fluid and serum did not relate well with adipose tissue content of stearic acid, as on d 0 it was higher ($P < 0.05$) than all other sampling dates within the high-concentrate finishing treatment, and there was no change over time with the pasture finishing treatment. Results of previous research on the effects of time on feed on stearic acid have been inconsistent. Similar to the results of the current study, Duckett et al. (1993) observed a gradual decrease in stearic acid content of grain-fed beef over time, as concentrations on d 140 were lower than on d 0 and 28. The authors observed stearic acid values of 17.38, 17.38, 15.72, and 14.29 % of total fatty acids for d 0, 28, 84, and 140. In contrast, Yang et al. (1999) observed fluctuations in stearic acid content of beef over time. The authors observed stearic acid concentrations

of 11.1, 13.7, 12.5, and 13.3 % (of fresh tissue weight), in beef after 0, 100, 200, or 300 d of finishing on a high-grain diet.

There was no effect of treatment on adipose myristoleic acid (14:1) concentrations (Table 16), and values ranged from 0.45 to 0.68 % of total fatty acids. However, ruminal fluid and serum tissue concentrations of myristoleic acid were generally lower in the high-concentrate finishing treatment than pasture finishing treatment. Yang et al. (2002b) and French et al. (2000) observed no differences in beef myristoleic acid content as a result of pasture or grain finishing. Yang et al. (2002b) observed myristoleic acid concentrations of 0.14 and 0.30 % of total fatty acids in pasture- and grain-finished beef, respectively. French et al. (2000) observed values ranging from 0.59 to 0.66 % of total fatty acids in beef finished on grain, pasture, or pasture with grain supplementation. In contrast, Realini et al. (2004) and Rhee et al. (2000) observed increased myristoleic acid as a result of grain finishing. Realini et al. (2004) observed myristoleic acid values of 0.23 and 0.41 % of total fatty acids in pasture-fed and grain-fed beef, respectively. Rhee et al. (2000) observed myristoleic acid concentrations of 0.30 and 0.43 % of total fatty acids in goats finished on range or a high-grain diet, respectively.

Within the high-concentrate finishing treatment, myristoleic acid concentrations (mg/g tissue) were higher ($P < 0.05$) on d 140 than d 0 and 84 (Table 16). However, when expressed as a percentage of total fatty acids, values on d 28 were higher ($P < 0.05$) than on d 84. Within the pasture finishing treatment, adipose tissue concentrations (mg/g tissue) of myristoleic acid decreased ($P < 0.05$) from d 0 to 84. When expressed as a percentage of total fatty acids, there were no differences among sampling dates. Ruminal

fluid and serum did not correspond to these differences in myristoleic acid concentrations as a result of sampling date. Concentrations of myristoleic acid in ruminal fluid and serum were higher ($P < 0.05$) on d 0 than all other sampling dates. With regards to time on feed, Duckett et al. (1993) observed no effect on myristoleic acid concentrations after 0, 28, 84, or 140 d on a high-grain diet. The authors observed values ranging from 0.69 to 0.91 % of total fatty acids. Yang et al. (1999) observed myristoleic acid concentrations to be lower after 100 d on feed, compared to 0, 200, or 300 d on feed. The authors observed myristoleic acid concentrations of 1.5, 0.8, 1.2, and 1.2 % (of fresh tissue weight) after 0, 100, 200, and 300 d on a high-grain diet, respectively.

There was no effect of treatment on adipose tissue palmitoleic acid (16:1) concentrations when presented as mg/g tissue; however, when expressed as a percentage of total fatty acids, the palmitoleic acid concentrations in the high-concentrate finished cattle were higher ($P < 0.05$) than the pasture-finished cattle on d 28 (Table 16). Ruminal fluid and serum content of palmitoleic acid did not reflect these differences due to treatment. Ruminal fluid palmitoleic acid concentrations (% of total fatty acids) on d 84 were lower ($P < 0.05$) in steers fed the high-concentrate than on the pasture finishing treatment. The same effect was observed in serum on d 84 and 140. French et al. (2000) observed no differences in palmitoleic acid content of beef due to pasture- or grain-finishing. The authors observed values ranging from 0.59 to 0.66 % of total fatty acids. In contrast, Rhee et al. (2000), Yang et al. (2002b), and Realini et al. (2004) observed higher palmitoleic acid concentrations as a result of grain finishing, compared to forage finishing. Rhee et al. (2000) observed palmitoleic acid concentrations of 1.62 and 2.71 % of total fatty acids in goats finished on range or a high-concentrate diet, respectively.

Yang et al. (2002b) observed content of palmitoleic acid in pasture-fed and grain-fed beef of 1.65 and 2.65 % of total fatty acids, respectively. Realini et al. (2004) found higher palmitoleic acid concentrations (3.38 versus 2.5 % of total fatty acids) in grain-finished cattle, compared to pasture-finished cattle.

Adipose tissue concentrations (mg/g tissue) of palmitoleic acid increased ($P < 0.05$), within the high-concentrate finishing treatment, from d 0 to 28, and remained higher ($P < 0.05$) for the other sampling dates than d 0 (Table 16). In contrast, when expressed as a percentage of total fatty acids, a decrease ($P < 0.05$) in palmitoleic acid was observed, when comparing d 28 and 84. Also, levels on d 0 were lower ($P < 0.05$) than for all the other dates. Within the pasture finishing treatment, when presented as mg/g tissue, there were no sampling date effects for palmitoleic acid; however, as a percentage of total fatty acids, levels on d 0 were lower ($P < 0.05$) than on d 140. In general, levels of this fatty acid in ruminal fluid and serum did not seem to be related to adipose tissue palmitoleic acid concentrations. Content of palmitoleic acid (% of total fatty acids) was higher ($P < 0.05$) in ruminal fluid on d 0 than all other sampling dates. However, this was not the case with serum and adipose tissue. There were some differences between sampling dates, within serum and adipose tissue, however these differences were not consistent. Duckett et al. (1993) observed no differences in palmitoleic acid concentrations of beef finished 0, 28, 84, or 140 d on feed, and values ranged from 3.01 to 3.66 % of total fatty acids. In contrast, Yang et al. (1999) observed that beef content of palmitoleic acid was higher on d 0, compared to 100, 200, or 300 d on a high-grain diet. The authors observed palmitoleic acid concentrations of 5.5, 3.2, 4.1, and 3.8 % (of fresh tissue weight), respectively.

On d 84 and 140, 17:1 concentrations (mg/g tissue and % of total fatty acid) were higher ($P < 0.05$) in adipose from the high-concentrate finished steers than the pasture-finished steers (Table 16). In the ruminal fluid, concentrations of 17:1 were higher ($P < 0.05$) in the high-concentrate finishing treatment, but only on d 84. In contrast, serum concentrations of 17:1 were higher ($P < 0.05$) in the pasture-finished steers on d 84 and 140, while the opposite effect was seen in adipose tissue. Yang et al. (2002b) observed no difference in 17:1 concentrations due to pasture or grain finishing (0.85 and 0.50 % of total fatty acids, respectively). Rhee et al. (2000) observed lower 17:1 concentrations (0.94 versus 2.32 % of total fatty acids) in range-finished goats, compared to goats finished on grain.

There was an overall increase of 17:1 (mg/g tissue and % of total fatty acids) in the high-concentrate finishing treatment, as values on d 0 were lower ($P < 0.05$) than on d 84 and 140, and values on d 28 were lower ($P < 0.05$) than on d 84 (Table 16). Additionally, concentrations (mg/g tissue) observed on d 84 were lower ($P < 0.05$) than on d 140. There were no effects of sampling date on adipose tissue concentrations (mg/g tissue or % of total fatty acids) of 17:1, within the pasture finishing treatment. Ruminal fluid concentrations of 17:1 were lower ($P < 0.05$) on d 0 than all other sampling dates, within both treatments. However this effect was not observed in serum or adipose tissue, and differences due to sampling date were not consistent among these samples. Duckett et al. (1993) observed a gradual increase in 17:1 concentrations, over time, in beef from cattle fed a high-concentrate diet. In their study, the concentrations of 17:1 were 0.63, 0.89, 1.20, and 1.42 % of total fatty acids after 0, 28, 84, and 140 d on feed. Yang et al.

(1999) observed no differences in 17:1 content of beef after 0, 100, 200, or 300 d on feed, and values ranged from 0.8 to 1.3 % (of fresh tissue weight).

Concentrations of oleic acid (18:1 *cis*-9) were higher ($P < 0.05$) in the high-concentrate finishing treatment on d 28, 84, and 140 when expressed as a percentage of total fatty acids (Table 16). Adipose oleic acid concentrations in high-concentrate finished steers were 33.86, 37.53, 43.07, and 44.34 % of total fatty acids on d 0, 28, 84, and 140, respectively. Within the pasture finishing treatment, oleic acid concentrations were 33.58, 33.24, 32.93, and 34.11 % of total fatty acids on d 0, 28, 84, and 140, respectively. In contrast, serum content of oleic acid was higher ($P < 0.05$) in the pasture finishing treatment, on d 84 and 140, while there were no differences due to treatment on ruminal fluid oleic acid concentrations. In contrast to the results of the current study, French et al. (2000) observed no differences in the oleic acid content of grain- versus pasture-finished beef, and values ranged from 38.62 to 40.58 % of total fatty acids. Rhee et al. (2000) observed lower concentrations of oleic acid in goats finished on range than on grain (42.43 versus 51.00 % of total fatty acids). Similar to the results of the current research, Realini et al. (2004) observed lower concentrations of oleic acid in beef finished on pasture, as compared to grain-fed beef. The authors observed values of 31.54 and 37.28 % of total fatty acids in the pasture and grain finishing treatments, respectively. Similar results were observed by Yang et al. (2002b), who found content of oleic acid was lower in pasture-finished beef, compared to grain-finished, as values were 27.20 and 32.10 % of total fatty acids, respectively.

Adipose tissue concentrations of oleic acid were lower ($P < 0.05$) on d 0 than on d 84 and 140, and on d 28 than 84, within the high-concentrate finishing treatment (Table

16). There were no effects of sampling date on adipose tissue concentrations (mg/g tissue or % of total fatty acids) of oleic acid, within the pasture finishing treatment. In contrast, ruminal fluid concentrations oleic acid were higher ($P < 0.05$) on d 84 than all other sampling dates, within the pasture finishing treatment, while in the high-concentrate finishing treatment, oleic acid was higher ($P < 0.05$) on d 84 than 28. This effect was not observed in serum oleic acid content. Within the high-concentrate finishing treatment, serum oleic acid content was higher ($P < 0.05$) on d 0 and 28 than on d 84 and 140. The opposite effect was observed in adipose tissue. With regards to the effects of time on feed, Duckett et al. (1993) observed a gradual increase in oleic acid over time, similar to the results of the current study. The authors observed oleic acid concentrations of 34.95, 36.40, 38.04, and 40.31 % of total fatty acids in grain-finished beef after 0, 28, 84, and 140 d on feed. In contrast, Yang et al. (1999) observed no effect of time on feed on oleic acid content of beef. In their study, values ranged from 41.2 to 43.6 % (of fresh tissue weight).

Vaccenic acid (18:1 *trans*-11) (mg/g tissue and % of total fatty acids) was higher ($P < 0.05$) in the adipose tissue obtained from pasture-finished steers than high-concentrate finished steers on d 28, 84, and 140 (Table 16). Concentrations of vaccenic acid in the adipose from the pasture-finished steers were 3.20, 7.03, 7.91, and 7.22 % of total fatty acids on d 0, 28, 84, and 140, respectively. Within the high-concentrate finishing treatment, vaccenic acid concentrations were 3.14, 1.73, 2.72, and 2.75 % of total fatty acids on d 0, 28, 84, and 140, respectively. For this fatty acid, ruminal fluid and serum concentrations were consistent with the differences observed in adipose tissue due to treatment. In ruminal fluid, serum, and adipose tissue, concentrations of vaccenic

acid were considerably higher ($P < 0.05$) in the pasture-finished steers on d 28, 84, and 140, compared to the high-concentrate finished steers. Unfortunately, limited research has been conducted comparing concentrations of the 18:2 *cis*-9, *trans*-11 CLA precursor, vaccenic acid, in adipose of pasture- versus grain-finished cattle. Yang et al. (2002b) observed no difference in total lipid content of vaccenic acid in pasture- and grain-finished cattle. The authors observed values of 1.86 and 2.86 % of total fatty acids in the pasture-finished and grain-finished beef, respectively.

Concentrations of vaccenic acid (% of total fatty acid), within the high-concentrate finishing treatment, decreased ($P < 0.05$) from d 0 to 28 (Table 16). No other differences among sampling dates were observed. Vaccenic acid concentrations (mg/g tissue and % of total fatty acids) increased ($P < 0.05$) in the pasture-finished steers from d 0 to 28, 84, and 140. Thus, it increased ($P < 0.05$) from d 0 to 28, and remained high throughout the remainder of the study. Similar observations were made for vaccenic acid content of ruminal fluid and serum, which was lower ($P < 0.05$) on d 0 than the remainder of the sampling dates within the pasture finishing treatment. However, concentrations of vaccenic acid concentrations in ruminal fluid and serum increased from d 0 to 28, then decreased, which was not observed in adipose. Yang et al. (1999) observed no effects of time on a high-grain diet on the vaccenic acid content of beef, and values ranged from 2.9 to 3.7 % (of fresh tissue weight).

Concentrations (mg/g DM and % of total fatty acids) of linoleic acid (18:2 *n*-6) were higher ($P < 0.05$) in the high-concentrate than pasture finishing treatment on d 84 and 140 (Table 16). Concentration of linoleic acid in adipose tissue obtained from the high-concentrate finished steers were 0.84, 0.92, 1.40, and 1.50 % of total fatty acids on d

0, 28, 84, and 140, respectively. Within the pasture finishing treatment, concentrations of linoleic acid were 0.74, 0.72, 0.67, and 0.63 % of total fatty acids on d 0, 28, 84, and 140, respectively. This treatment effect was probably due to the considerably higher linoleic acid in the high-concentrate diets, compared to pasture forages. The linoleic acid content of the high-concentrate finishing diet averaged 58.39, 57.05, and 56.74 % of total fatty acids in periods 1 (d 0 to 28), 2 (d 28 to 84), and 3 (d 84 to 140), respectively. The linoleic acid concentration of the pasture forages averaged 6.92, 9.41, and 10.13 % of total fatty acids for periods 1, 2, and 3, respectively. However ruminal fluid concentrations (% of total fatty acids) did not reflect these dietary linoleic acid differences. Serum appeared to be a better indicator of treatment effects on adipose, as serum linoleic acid concentrations were higher ($P < 0.05$) in the high-concentrate than pasture finishing treatment on d 28, 84, and 140. French et al. (2000) and Yang et al. (2002b) observed no differences in linoleic acid concentrations of pasture- versus grain-finished beef. French et al. (2000) observed values ranging from 2.11 to 2.96 % of total fatty acids. Yang et al. (2002b) observed linoleic acid concentrations of 6.99 and 6.36 % of total fatty acids in the pasture- and grain-finished beef, respectively. In contrast Realini et al. (2004) observed higher concentrations of linoleic acid in pasture-finished than grain-finished cattle (3.29 versus 2.84 % of total fatty acids). Similarly, Rhee et al. (2000) observed higher linoleic acid concentrations (7.74 versus 5.74 % of total fatty acids) in range-fed goats, compared to goats that were grain-finished.

There was an overall increase in adipose tissue content of linoleic acid within the high-concentrate finishing treatment (Table 16). Concentrations (mg/g tissue) of linoleic acid were lower ($P < 0.05$) on d 0 than 84 and 140, on d 28 than 84, and on d 84 than 140.

When expressed as a percentage of total fatty acids, concentrations on d 0 were lower ($P < 0.05$) than 84 and 140, and on d 28 than 84. Within the pasture finishing treatment, there were no effects on linoleic acid concentrations due to sampling date. However, there were inconsistencies when comparing the effects of sampling date on ruminal fluid and serum to adipose. Ruminal fluid content of linoleic acid was lower ($P < 0.05$) on d 0 and 28 than 84, within both high-concentrate and pasture finishing treatments. Serum linoleic acid concentrations, within the high-concentrate finishing treatment, were lower ($P < 0.05$) on d 0 than 84 and 140, and on d 28 than 84, indicating an overall increase. The opposite effect was observed in the pasture finishing treatment, as values on d 0 were higher ($P < 0.05$) than on d 84 and 140, and on d 84 than 140. Duckett et al. (1993) observed no effect of time on a high-grain diet on beef linoleic acid content, and values ranged from 3.96 to 6.46 % of total fatty acids. Yang et al. (1999) also observed no differences in linoleic acid content of beef finished 0, 100, 200, or 300 on a high-grain diet, and values ranged from 0.7 to 1.2 % (of fresh tissue weight).

Concentrations (mg/g tissue and % of total fatty acids) of 18:2 *cis*-9, *trans*-11 CLA were higher ($P < 0.05$) in adipose tissue obtained from pasture-finished steers than high-concentrate finished steers on d 28, 84, and 140 (Table 16). Concentrations of 18:2 *cis*-9, *trans*-11 CLA were 1.25, 1.41, 1.32, and 1.23 % of total fatty acids, on d 0, 28, 84, and 140, respectively, within the pasture finishing treatment. Concentrations of 18:2 *cis*-9, *trans*-11 CLA in adipose tissue from high-concentrate finished steers were 1.17, 0.72, 0.26, and 0.21 % of total fatty acids on d 0, 28, 84, and 140, respectively. In relation, serum content of 18:2 *cis*-9, *trans*-11 CLA was also higher ($P < 0.05$) in the pasture-finished steers, compared to high-concentrate finished steers on d 28, 84, and 140.

However in ruminal fluid, concentrations of 18:2 *cis*-9, *trans*-11 CLA in the pasture finishing treatment were higher ($P < 0.05$) only on d 84 and 140.

Within the high-concentrate finishing treatment, there was an overall decline in 18:2 *cis*-9, *trans*-11 CLA adipose tissue concentrations (mg/g tissue and % of total fatty acids), as values on d 0 were higher ($P < 0.05$) than on d 28, 84, and 140 (Table 16). Within the pasture finishing treatment, concentrations (mg/g) of 18:2 *cis*-9, *trans*-11 CLA peaked on d 28 (values on d 0 versus d 28, $P = 0.0549$; d 28 versus d 84 $P = 0.0993$). However, when expressed as a percentage of total fatty acids, 18:2 *cis*-9, *trans*-11 CLA did not differ among sampling dates ($P > 0.10$). Studies investigating the effects of time on feed on CLA content of beef are not known. However, some studies have been conducted investigating the effects of pasture versus grain feeding on CLA. French et al. (2000) observed that with increasing amounts of pasture intake, the amount of CLA in beef increased. The treatment diets were a high-silage diet, a high-concentrate diet, or pasture-based diets with grain supplementation. Grain was supplemented to the steers in decreasing amounts so that pasture intake would increase. The 18:2 *cis*-9, *trans*-11 CLA concentrations were 0.54, 0.66, and 1.08 % of total fatty acids from the steers on pasture supplemented with grain at a rate of 5, 2.5, or 0 kg $\cdot$ head^{-1} $\cdot$ d^{-1}, respectively. The steers on a conventional grain-based diet had the lowest level of CLA (0.37 % of total fatty acids). The fat from steers fed a high-silage diet had an intermediate level of CLA (0.47 % of total fatty acids) and was similar to the steers on pasture supplemented with the highest level of grain.

Steen and Porter (2003) compared the effects of a high-concentrate or a high-forage diet (perennial ryegrass pasture and silage) on the 18:2 *cis*-9, *trans*-11 CLA

composition of beef. The CLA content of *gluteobiceps*, *semimembranosus*, *longissimus dorsi*, *deltoideous*, and subcutaneous fat in the forage finished beef was 1.35, 0.96, 1.07, 1.24, and 2.26 % of total fatty acids, as compared to the CLA content in the grain-finished beef, which was 0.43, 0.33, 0.31, 0.47, and 0.70 % of total fatty acids, respectively.

Realini et al. (2004) compared the 18:2 *cis*-9, *trans*-11 CLA content of forage versus grain-finished beef. The authors observed that the forage finished beef had 18:2 *cis*-9, *trans*-11 CLA concentrations of 0.41 % of total fatty acids, and the grain-finished beef, 0.23 % of total fatty acids. The pasture consisted of a mixture of perennial ryegrass, birdsfoot trefoil, white clover, and tall fescue.

Shantha et al. (1997) observed that muscle tissue from cattle that consumed pasture alone had higher levels of 18:2 *cis*-9, *trans*-11 CLA, compared to cattle on pasture that were allowed a cracked corn supplement. The CLA content of the muscle tissues was 0.77 and 0.52 % of total fatty acids for the pasture only or pasture plus grain supplement groups, respectively.

Endogenous synthesis of 18:2 *cis*-9, *trans*-11 CLA appears to be the primary mechanism of CLA production in ruminant products. Estimates of 64, 78, and 91 % of CLA in milk is of endogenous origin (Griinari et al., 2000, Corl et al., 2001, Kay et al., 2004). Therefore, maintaining a high level of vaccenic acid in ruminal fluid is critical in optimizing CLA production in ruminant products. In the current study, vaccenic acid (in ruminal fluid) and CLA (in adipose) were higher ($P < 0.05$) in pasture-finished steers, compared to high-concentrate finished steers. Ruminal fluid pH did not appear to be a

major factor influencing the biohydrogenation of CLA, as it was lower ($P < 0.05$) in the high-concentrate finishing treatment only on d 84.

Feeding a high-grain diet appears to alter ruminal biohydrogenation and alter the production of C18:1 isomers. Ruminal production of vaccenic acid is reduced, and the production of an alternate isomer (18:1 *trans*-10) is greatly increased with feeding high-grain diets (Piperova et al., 2000; Kucuk et al., 2001; Loor et al., 2003a, 2004; Sackmann et al., 2003). These alterations in ruminal biohydrogenation may be due to shifts in microbial populations due to dietary changes. Fiber degrading bacteria, such as *Butyrivibrio fibrisolvens,* are associated with vaccenic acid production (Kepler et al., 1966; Yokoyama and Davis, 1971; Kemp et al., 1975; Kellens et al., 1986). Recently, Kim et al. (2002) identified a strain of bacteria, *Megasphaera elsdenii* YJ-4, which produces significant amounts of the 18:2 *trans*-10, *cis*-12 isomer of CLA. This bacterium was isolated from the ruminal fluid collected from cows fed a diet consisting of 90 % cracked corn. Perhaps 18:1 *trans*-10 is also produced by this bacterium, or is a product of 18:2 *trans*-10, *cis*-12 CLA breakdown.

Additionally, the 18:2 *trans*-10, *cis*-12 isomer of CLA is known to inhibit Δ^9 desaturase activity (Baumgard et al., 2000, 2001; Choi et al., 2000; Park et al., 2000; Loor and Herbein, 2003b). Increases in 18:1 *trans*-10, and subsequent reductions in vaccenic acid, production in the rumen could also reduce endogenous synthesis of 18:2 *cis*-9, *trans*-11 CLA by the Δ^9 desaturase enzyme, as a result of reduced substrate. Although not measured in the current study, Yang et al. (1999) compared the Δ^9 desaturase activity of subcutaneous adipose tissue in pasture-fed and grain-fed cattle. The Δ^9 desaturase activity of adipose tissue from pasture-finished cattle (1.48 nmol·mg

protein^{-1}·min^{-1}) was greater than grain-finished cattle (approximately 0.85 nmol·mg protein^{-1}·min^{-1}). Increases in the 18:2 *trans*-10, *cis*-12 isomer of CLA, and perhaps 18:1 *trans*-10, in ruminal fluid would, therefore, result in reduced 18:2 *cis*-9, *trans*-11 CLA in adipose tissue in high-concentrate finished cattle, as observed in the current study.

Adipose tissue concentrations (mg/g tissue) of linolenic acid (18:3 *n*-3) were higher ($P < 0.05$) in pasture-finished steers on all sampling dates (Table 16). The difference between treatments observed on d 0 may have been due to a randomization or sampling error. However, when expressed as a percentage of total fatty acids, treatment differences ($P < 0.05$) were observed only on d 28, 84, and 140. Concentrations of linolenic acid in adipose from pasture-finished steers were 0.64, 0.80, 0.71, and 0.78 % of total fatty acids on d 0, 28, 84, and 140, respectively. Within the high-concentrate finishing treatment, concentrations of linolenic acid were 0.50, 0.35, 0.30, and 0.24 % of total fatty acids on d 0, 28, 84, and 140, respectively. Concentrations of linolenic acid were also considerably higher ($P < 0.05$) in ruminal fluid and serum of the pasture-finished steers, compared to the high-concentrate finished steers.

There was no effect of sampling date on linolenic acid concentrations when presented as mg/g tissue. However, when expressed as a percentage of total fatty acids, values on d 0 were higher ($P < 0.05$) than on d 140, which may have indicated a gradual decline in 18:3 in adipose tissue from high-concentrate finished steers. Within the pasture finishing treatment, concentrations of linolenic acid fluctuated over time, as values on d 0 were lower ($P < 0.05$) than on d 28, and values on d 28 were higher ($P < 0.05$) than on d 84. However, there was no effect of sampling date on linolenic acid concentrations within the pasture finishing treatment, when expressed as a percentage of

total fatty acids. Ruminal fluid and serum content of linolenic acid tended to increase in the pasture finishing treatment, and decrease in the high-concentrate finishing treatment, over time. Therefore, changes in adipose tissue content of linolenic acid may be indicated by the changes in ruminal fluid and serum.

The only omega-3 (*n*-3) fatty acid detected in adipose tissue in the current study was linolenic acid, which may have been due to analytical technique and/or perhaps low extraction of adipose tissue samples due to connective tissues. The analysis of fatty acids on the gas chromatograph was optimized for CLA and C18:1 isomers, which may have resulted in the lack of detection of fatty acids longer than C18:3 in adipose tissue. Additionally, the longer chain omega-3 fatty acids are relatively low in concentration, as compared to other fatty acids (Shantha et al., 1997; French et al., 2000; Yang et al., 2002b; Realini et al., 2004). The reduction of DPA (22:5 *n*-3), DHA (22:6 *n*-3), and linolenic acid in the diets, ruminal fluid, and serum of high-concentrate finished steers in the current study may explain why pasture-finished beef contained higher amounts of these fatty acids in beef reported by previous researchers (Shantha et al., 1997; French et al., 2000; Yang et al. 2002b; Realini et al., 2004). Increased intake of pasture resulted in increased concentrations of linolenic acid and 20:5 *n*-3 in beef (French et al., 2000). The authors observed that grain-fed beef contained 0.72 and 0.12 % of total fatty acids of linolenic acid and 20:5 *n*-3, respectively, while the pasture-finished beef contained 1.13 and 0.23 % of total fatty acids of 18:3 and 20:5 *n*-3, respectively. Grass-fed, as compared to grain-supplemented beef also contained higher amounts of linolenic acid and DHA (Shantha et al., 1997). The grass-fed beef contained 0.53 and 0.24 % of total fatty acids of linolenic acid and DHA, respectively, while the grain-supplemented beef contained

0.28 and 0.09 % of total fatty acids of linolenic acid and DHA. Itoh et al. (1999), Rule et al. (2002), Yang et al. (2002b), Steen et al. (2003), Aurousseau et al. (2004), and Realini et al. (2004) also observed higher *n*-3 PUFA in forage-finished beef, compared to grain-finished. Similar differences in the concentrations of linolenic acid, 20:5 *n*-3, DPA, and DHA between lambs finished on grass or grain were observed (Fisher et al., 2000; Santos-Silva et al., 2002).

Duckett et al. (1993) found that as time on a grain-based diet increased, the omega-3 fatty acid content of the beef decreased. The cattle were previously on an all-forage pasture-based diet. The highest omega-3 fatty acid concentrations were observed in beef obtained from steers that served as the grass-fed control, which were harvested at d 0, when the remaining steers were switched to the high-concentrate diet. The authors observed linolenic acid concentrations of 0.93, 0.45, 0.15, and 0.08 % of total fatty acids in beef finished 0, 28, 84, and 140 d on a high-grain diet.

In general, ruminal fluid or serum may be used as an indicator of vaccenic acid, CLA, and linolenic acid metabolism in adipose tissue. Ruminal fluid and serum samples can be collected relatively easily, and are less invasive than subcutaneous adipose tissue or muscle biopsies. Along with biopsies, ruminal fluid and serum samples can be collected over time during finishing, therefore, cattle do not have to be harvested at intervals throughout the study to evaluate changes in the fatty acids resulting from time on feed. This prevents biasing the results as the same number of animals can be maintained throughout the study and individual animal variation can be taken into consideration. However, due to inconsistencies among ruminal fluid, serum, and adipose SFA and MUFA, caution should be used if evaluating these fatty acids.

Ratios of specific fatty acids may also be of interest. The ratios of PUFA:SFA in adipose tissue from the high-concentrate finished steers were 0.04 on all sampling dates, while the ratios in the adipose tissue from the pasture-finished steers were 0.05, 0.06, 0.05, and 0.05 on d 0, 28, 84, and 140, respectively. The n-6:n-3 ratios were also shifted to a healthier ratio as a result of pasture finishing. The n-6:n-3 ratios in adipose tissue from the high-concentrate finished steers were 1.70, 2.65, 4.63, and 6.30, while the ratios in adipose tissue from the pasture-finished steers were 1.16, 0.90, 0.94, and 0.81.

The lack of differences between initial and subsequent sampling dates within the pasture finishing treatment for CLA and linolenic acid may be attributed to the forage-based stockering diet. The stockering diets consisted of timothy hay supplemented with soybean hulls and soybean meal. Although the stockering diets consisted of up to 34.5 % soybean hulls, the soybean hulls were high in fiber (60.72 % NDF; Appendix A), and therefore, the high-fiber content may not have caused a significant disturbance in ruminal function. In the current study, vaccenic acid, 18:2 *cis*-9, *trans*-11 CLA, and linolenic acid concentrations in ruminal fluid were relatively high at the beginning of the study, leading to relatively high levels of these fatty acids in adipose tissue. One proposed future study would be to investigate the effects of supplementing pasture-fed steers with soybean hulls, or a similar high-fiber by-product feed. Soybean hulls could potentially be used as a supplement since they are relatively high in both energy and fiber (80 % TDN, 66.3 % NDF; NRC, 2000).

Although not investigated in the current study, another area of interest may be oil/oilseed supplementation of pasture-fed cattle. Researchers have demonstrated that oil supplementation of high-concentrate diets is detrimental to vaccenic acid and CLA

production in ruminants, and that *trans*-10 18:1 and 18:2 *trans*-10, *cis*-12 CLA are produced at a higher amounts than vaccenic acid and 18:2 *cis*-9, *trans*-11 CLA (Duckett et al., 2002; Kucuk et al, 2004). However, it is unknown if this same effect of oil supplementation will occur in pasture-fed cattle.

In general, cattle do not have to be on a diet for very long for changes in fatty acids to be evident. By d 28, the CLA and linolenic acid concentrations within the high-concentrate finished cattle had decreased. Further reductions were observed until d 84. Concentrations of 18:2 *cis*-9, *trans*-11 CLA in adipose tissue from high-concentrate finished steers were 1.17, 0.72, 0.26, and 0.21 % of total fatty acids on d 0, 28, 84, and 140, respectively. Within the pasture-finished cattle, concentrations of CLA and linolenic acid peaked by d 28, then small numeric decreases were observed. Concentrations of 18:2 *cis*-9, *trans*-11 CLA were 1.25, 1.41, 1.32, and 1.23 % of total fatty acids on d 0, 28, 84, and 140, respectively. Therefore, cattle do not have to be on pasture for very long to optimize CLA and linolenic acid in adipose tissue.

The reduction in adipose tissue CLA and 18:3 in the high-concentrate finishing treatment over time may be an indicator of the time needed to change the concentrations of these fatty acids in adipose tissue (fatty acid turn over in adipose). This may have potential use in future research. Griswold et al. (2003) observed only minimal changes in fatty acids in fattened cattle switched from a high-grain to a corn silage-based diet supplemented with soybean oil, and finished for 42 d. However, corn still comprised a large amount (48 %), of the diet, even with the highest forage level (40% corn silage). Oil supplementation or forage level did not increase CLA content in beef above that of the high-grain control (0.31 % of total fatty acids), and there were only marginal

increases in linolenic acid (0.20 to 0.28 % of total fatty acids). A proposed future study would be an experiment evaluating the CLA and omega-3 fatty acid content of beef cattle finished on a high-concentrate diet followed by a short (28 to 84 d) pasture finishing period. This sequence of finishing regimes would perhaps optimize both the marbling and fatty acid composition of beef.

General Discussion and Implications

Finishing beef cattle on high-grain diets in feedlot is currently the primary method of fattening beef cattle. Usually, feedlot finished cattle gain at a considerably higher rate than pasture-finished cattle. In our study, the rate of gain of the pasture finished steers was about 70 % that of those finished in the feedlot (Table 17). There are, however, concerns regarding excessive intake by consumers of fat, saturated fatty acids (SFA) and inadequate intake of omega-3 polyunsaturated fatty acids (PUFA) (Enser et al., 1988; Simopoulos, 1999; Wood et al., 2003). Recently, interest has increased in the fatty acid composition of pasture-finished beef, compared to grain-fed beef. Pasture-finished beef may be beneficial to consumer health, as it contains less SFA and increased omega-3 fatty acids (French et al., 2000; Steen et al., 2003; Realini et al., 2004). However, the time on pasture needed to optimize fatty acid composition is unknown.

The current study was conducted to evaluate the metabolism of fatty acids, including 18:2 cis-9, trans-11 conjugated linoleic acid (CLA) and omega-3 PUFA, in cattle finished on pasture and on a high-concentrate diet over time. Regarding the adipose tissue SFA evaluated in the current study, results were inconsistent. As a percentage of total fatty acids, lauric, myristic, and palmitic acids generally did not differ due to dietary treatment. Concentrations of pentadecylic acid and oleic acid were lower ($P < 0.05$) in the high-concentrate finished steers, compared to pasture-finished steers. Margaric acid was higher ($P < 0.05$) in the adipose of high-concentrate finished steers than the pasture-finished steers. Results of previous research, comparing individual SFA from pasture- versus grain-finished beef, have also been inconsistent (French et al., 2000; Steen et al., 2003; Realini et al., 2004).

Table 17. The effect of high-concentrate or pasture finishing treatments on body weight and average daily gain in steers[a]

	High-concentrate finishing	Pasture finishing
Number of steers	12	12
Initial weight, kg	297.07	298.31
Final weight, kg	558.68	442.21
ADG, kg/d	1.52	0.90

[a]Source: Dr. J. P. S. Neel, unpublished data.

Additionally, ruminal fluid and serum concentrations of these fatty acids did not reflect dietary treatment effects in adipose tissue. A possible explanation is that each sample contained different forms of fatty acids in various amounts. The primary pool of fatty acids in pasture forages is in the form of phospholipid membranes. Ruminal microbes break down and release fatty acids in the diet, in the form of free fatty acids, which may have undergone biohydrogenation. Serum contains triglycerides, cholesterol, chylomicrons, and free fatty acids. Serum also functions as a transport mechanism for moving the fatty acids absorbed from the digestive tract to various tissues, and from one tissue (such as adipose) to another. Therefore, fatty acids present in the serum have undergone various metabolic processes. Adipose tissue fatty acids are present in the form of triglycerides. Enzymes present in adipocytes have the potential to de novo synthesize, elongate, and desaturate fatty acids.

The primary fatty acid in high-concentrate diets was linoleic acid (approximately 57 % of total fatty acids), while the primary fatty acid in pasture forages was linolenic (approximately 66 % of total fatty acids). This higher content of linolenic acid (18:3 *n*-3) presumably led to higher ($P < 0.05$) omega-3 fatty acids in pasture-finished steers. The linolenic acid concentrations in adipose tissue obtained from pasture-finished steers were 0.64, 0.80, 0.71, and 0.78 % of total fatty acids on d 0, 28, 84, and 140, respectively. In comparison, the adipose tissue of high-concentrate finished steers contained linolenic acid concentrations of 0.50, 0.35, 0.30, and 0.24 % of total fatty acids on d 0, 28, 84, and 140, respectively. Concentrations of linolenic acid were also considerably higher ($P < 0.05$) in ruminal fluid and serum of the pasture-finished steers, compared to the high-concentrate finished steers. Similar increases in linolenic acid content of pasture-fed beef

adipose tissue, compared to grain-fed, were observed by Shantha et al. (1997), French et al. (2000), Yang et al. (2002b), and Realini et al. (2004).

The only omega-3 fatty acid detected in adipose tissue in the current study was linolenic acid. However, the reduction ($P < 0.05$) of DPA, DHA, and linolenic acid in the diets, ruminal fluid, and serum of high-concentrate finished steers in the current study may explain why pasture-finished beef contains higher amounts of these fatty acids, as reported by previous researchers (Shantha et al., 1997; French et al., 2000; Yang et al. 2002b; Realini et al., 2004).

Linolenic acid content of adipose tissue from steers in both finishing treatments were relatively high at the beginning of the study, presumably due to the high forage content of the stockering diet. In the pasture-finished steers linolenic acid concentrations peaked ($P < 0.05$) on d 28, and remained high throughout the study. However, concentrations of linolenic acid gradually decreased ($P < 0.05$) over time within the high-concentrate finished steers. Similar observations were made for linolenic acid in the ruminal fluid and serum. These results agree with those reported by Duckett et al. (1993) who finished cattle on a high-grain diet for up to 196 d.

Concentrations of 18:2 *cis*-9, *trans*-11 CLA in adipose were higher ($P < 0.05$) in the pasture-finished steers than high-concentrate finished steers. In the pasture-finished steers concentrations of 18:2 *cis*-9, *trans*-11 CLA were 1.25, 1.41, 1.32, and 1.23 % of total fatty acids, respectively, on d 0, 28, 84, and 140, respectively. Concentrations of 18:2 *cis*-9, *trans*-11 CLA in adipose tissue from high-concentrate finished steers were 1.17, 0.72, 0.26, and 0.21 % of total fatty acids on d 0, 28, 84, and 140, respectively.

These results are comparable to those observed by Shantha et al. (1997), French et al. (2000), Steen and Porter (2003), and Realini et al. (2004).

Regarding the effect of time on feed, previous studies evaluating 18:2 *cis*-9, *trans*-11 CLA are not known. In the current study, concentrations of 18:2 *cis*-9, *trans*-11 CLA declined in the high-concentrate finished steers ($P < 0.05$) from d 0 to 28 and d 28 to 84, while, in the pasture-finished steers concentrations peaked on d 28, and remained high throughout the duration of the study. Additionally, concentrations of 18:2 *cis*-9, *trans*-11 CLA were relatively high at the initiation of the study, which may have been a result of the previous stockering diet. The stockering diet consisted primarily of timothy hay supplemented with soybean hulls and soybean meal.

It is estimated that between 64 and 91 % of 18:2 *cis*-9, *trans*-11 CLA in ruminant products is produced by endogenous synthesis from vaccenic acid (18:1 *trans*-11) (Griinari et al., 2000, Corl et al., 2001, Kay et al., 2004). Ruminal production of vaccenic acid is optimized by feeding high-forage diets, and is reduced by feeding grain; an alternate isomer (18:1 *trans*-10) is produced as a result of grain feeding (Piperova et al., 2000; Kucuk et al., 2001; Loor et al., 2003a, 2004; Sackmann et al., 2003). Additionally, the 18:2 *trans*-10, *cis*-12 isomer of CLA is known to inhibit endogenous synthesis of 18:2 *cis*-9, *trans*-11 CLA (Baumgard et al., 2000, 2001; Choi et al., 2000; Park et al., 2000; Loor and Herbein, 2003b).

In the current study, concentrations of vaccenic acid were higher ($P < 0.05$) in ruminal fluid obtained from pasture-finished steers than high-concentrate finished steers. Concentrations of vaccenic acid in ruminal fluid from the pasture-finished steers were 2.49, 13.57, 8.97, and 10.07 % of total fatty acids on d 0, 28, 84, and 140, respectively.

In the high-concentrate finished steers concentrations were 2.72, 4.54, 2.07, and 0.86 % of total fatty acids, on d 0, 28, 84, and 140, respectively. Within the high-concentrate finishing treatment, ruminal production of the alternate isomer (18:1 *trans*-10) increased ($P < 0.05$) over time and peaked ($P < 0.05$) on d 84. Concentrations of 18:1 *trans*-10 within ruminal fluid of high-concentrate finished steers were 0.20, 1.10, 13.55, and 3.17 % of total fatty acids, while, in the pasture finishing treatment concentrations of 18:1 *trans*-10 remained low and ranged from 0.05 to 0.41 % of total fatty acids. Additionally, production of 18:2 *trans*-10, *cis*-12 CLA was observed in the ruminal fluid of high-concentrate finished steers on d 84 and 140. In contrast, 18:2 *trans*-10, *cis*-12 CLA was not detected in ruminal fluid from pasture-finished steers. Therefore, pasture finishing may optimize the endogenous synthesis of 18:2 *cis*-9, *trans*-11 CLA in adipose tissue, by providing maximum amounts of the precursor and minimizing inhibitory fatty acids.

Overall, it appears that only a short time is needed to alter the omega-3 and CLA composition of adipose tissue in cattle. By 28 d, reductions were observed in the linolenic acid and 18:2 *cis*-9, *trans*-11 CLA content of adipose tissue in high-concentrate finished steers. Further reductions were observed in these fatty acids, until d 84. In contrast, these fatty acids peaked in adipose tissue of pasture-finished cattle on d 28.

When evaluating fatty acid metabolism in cattle, the results of the current study indicate that differences observed (due to dietary treatment or time) in SFA and MUFA in ruminal fluid and serum are not consistent with differences observed for these fatty acids in adipose tissue. However, it appears that ruminal fluid and serum concentrations of vaccenic acid, CLA, and omega-3 fatty acids may be indicators of their metabolism in adipose tissue.

The fatty acid content of beef cattle diets is an important factor to consider when finishing cattle. Pasture forages tend to contain primarily linolenic acid, while, high-concentrate diets contain mostly linoleic acid. It seems that this higher content of omega-3 (linolenic acid) in pasture forages will increase the omega-3 fatty acid content of adipose tissue in beef.

Another important factor to consider when finishing cattle is the fiber content of the diet. The 18:2 *cis*-9, *trans*-11 CLA precursor, vaccenic acid (18:1 *trans*-11) production in the rumen may be maximized by pasture feeding (high-fiber diet). Pasture-fed cattle tend to produce less of the fatty acids (18:2 *trans*-10, *cis*-12 CLA and 18:1 *trans*-10) inhibitory to synthesis of 18:2 *cis*-9, *trans*-11 CLA in adipose tissue. These inhibitory fatty acids appear to be produced in greater quantities when low-fiber, high-grain diets are fed. As a result of increased precursor and reduced inhibitors, cattle finished on a high-fiber, pasture-based diet may contain increased levels of 18:2 *cis*-9, *trans*-11 CLA in adipose tissue.

Another factor which may influence the fatty acid composition of adipose tissue in beef cattle is previous diet. The high-fiber, hay-based stockering diet in this study may have influenced the fatty acid metabolism in the cattle at the beginning of the study. Concentrations of 18:2 *cis*-9, *trans*-11 CLA and linolenic acid in adipose tissue were relatively high. The results of the current study indicate that high levels of 18:2 *cis*-9, *trans*-11 CLA and linolenic acid in adipose tissue at the beginning of the study would result in only small increases in these fatty acids when the cattle are finished on pasture. However, it appears that when cattle are stockered on a high-fiber, hay-based diet, followed by finishing on a high-concentrate diet, concentrations of 18:2 *cis*-9, *trans*-11

CLA and linolenic acid in adipose tissue will quickly decrease. Results of the current study suggest that only a short time (28 to 84 d) on feed will be needed to alter the fatty acid composition of adipose tissue in cattle. This may be useful when cattle are fattened on a high-grain diet, then turned out onto pasture to produce a healthier product.

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Appendix A

Chemical composition of diet ingredients fed to steers during stockering and Timothy hay fed to steers in drylot upon arrival at finishing locations on April 21, 2003

		Component[a]				
Ingredient	Location	NDF	ADF	Cellulose	Lignin	CP
		----------%----------				
Timothy hay	Morgantown, WV	66.20	35.35	32.98	3.72	8.08
Soybean meal	Morgantown, WV	13.20	6.60	7.48	0.75	48.87
Soybean hulls	Morgantown, WV	60.72	43.34	41.68	2.90	13.98
Timothy hay	Steeles Tavern, VA	73.13	41.10	37.87	4.71	8.56
Timothy hay	Willow Bend, WV	67.77	37.47	34.65	4.26	6.91

[a]DM basis.

Appendix B

Fatty acid composition of diet ingredients fed to steers during stockering

	Ingredient		
Fatty acid	Timothy hay	Soybean meal	Soybean hulls
	----------mg/g DM----------		
Myristic (14:0)	0.08	0.01	-
Pentadecylic acid (15:0)	1.18	-	-
Palmitic (16:0)	2.78	7.73	3.67
Palmitoleic (16:1)	0.10	0.02	0.08
Stearic (18:0)	0.24	1.67	0.97
Oleic (18:1 *cis*-9)	0.42	8.36	6.40
Linoleic (18:2 *n*-6)	1.96	31.76	17.00
Linolenic (18:3 *n*-)3	5.29	4.15	2.12
20:2 *n*-6	0.20	0.12	0.13
22:2 *n*-6	-	-	-
DPA (22:5 *n*-3)	0.23	-	-
DHA (22:6 *n*-3)	0.21	-	-
Total fatty acids	12.69	53.82	30.37

Appendix C

Fatty acid composition of Timothy hay fed to steers in drylot upon arrival at finishing locations on April 21, 2003

	Finishing Location	
Fatty acid	Steeles Tavern, VA	Willow Bend, WV
	----------mg/g DM----------	
Myristic (14:0)	0.06	0.08
Pentadecylic acid (15:0)	1.08	1.12
Palmitic (16:0)	2.49	3.18
Palmitoleic (16:1)	0.11	0.09
Stearic (18:0)	0.24	0.28
Oleic (18:1 *cis*-9)	1.27	0.53
Linoleic (18:2 *n*-6)	2.24	2.47
Linolenic (18:3 *n*-3)	2.14	4.76
20:2 *n*-6	0.27	0.44
22:2 *n*-6	-	-
DPA (22:5 *n*-3)	0.61	0.53
DHA (22:6 *n*-3)	0.54	0.64

Appendix D

Ingredient composition of high-concentrate diets fed to steers

	Ingredient[ab]				
Date	Silage	Corn	Soybean meal	Limestone	TM salt[c]
	----------	----------	%----------	----------	----------
4/29 to 5/6/03	90.43	-	8.98	0.22	0.37
5/7 to 5/20/03	87.11	3.50	8.81	0.22	0.36
5/21 to 6/3/03	69.43	22.03	8.01	0.20	0.33
6/4 to 6/17/03	44.74	47.94	6.87	0.17	0.28
6/18 to 7/1/03	24.22	69.48	5.91	0.15	0.24
7/2 to 7/16/03	11.41	82.93	5.31	0.13	0.22
7/17 to 7/29/03	16.20	78.01	5.43	0.13	0.22
7/30 to 8/12/03	17.90	76.13	5.61	0.14	0.23
8/13 to 8/27/03	17.87	76.13	5.63	0.14	0.23
8/28 to 9/8/03	17.90	76.12	5.61	0.14	0.23

[a]DM basis.
[b]Vitamin A added to the diet to provide 20,000 IU·head^{-1}·d^{-1}.
[c]Champions Choice, Cargill Inc., Minneapolis, MN.

Appendix E

Dates and forage types that steers grazed at Willow Bend, WV

Dates	Forage type
4/22 to 7/2/03	Cool season grass/legume mixture
7/3 to 7/17/03	Triticale/annual ryegrass
7/18 to 7/31/03	Alfalfa/orchardgrass
8/1 to 8/26/03	Cool season grass/legume mixture
8/27 to 9/8/03	Alfalfa/orchardgrass

Appendix F

Chemical composition of the high-concentrate diet ingredients fed to steers at Steeles Tavern, VA

		Component[a]						
Date	Ingredient	DM	NDF	ADF	Cellulose	Lignin	CP	WSC
		----------	----------	----------	----------	%----------	----------	----------
4/22 to 5/6/03	Silage	42.09	33.72	17.34	16.60	2.45	8.09	47.05
	Soybean meal	90.36	14.19	5.67	6.40	1.00	49.66	-
5/7 to 5/20/03	Silage	41.95	35.88	18.38	17.80	2.13	7.59	53.00
	Corn	87.04	10.56	2.17	3.08	0.68	7.94	-
	Soybean meal	89.87	9.06	4.54	5.47	0.80	50.09	-
5/21 to 6/3/03	Silage	39.99	36.90	18.53	17.57	2.74	8.29	45.99
	Corn	87.08	10.00	2.07	3.14	0.64	7.35	-
	Soybean meal	89.73	8.48	4.58	5.33	0.92	50.93	-
6/4 to 6/17/03	Silage	39.80	39.78	21.59	21.07	2.28	8.98	48.69
	Corn	87.73	9.91	2.05	3.00	0.78	7.02	-
	Soybean meal	88.96	8.25	3.81	4.87	0.69	49.02	-
6/18 to 7/1/03	Silage	41.61	46.33	25.69	24.39	3.07	9.08	39.50
	Corn	87.67	10.22	2.20	3.07	0.88	7.70	-
	Soybean meal	89.39	8.06	3.89	4.97	0.48	52.33	-
7/2 to 7/16/03	Silage	45.17	45.40	26.37	24.83	3.25	10.09	38.81
	Corn	88.80	11.27	2.60	3.41	0.95	8.22	-
	Soybean meal	88.79	8.23	3.95	4.93	0.72	53.31	-
7/17 to 7/29/03	Silage	50.53	47.73	28.14	26.05	3.28	9.91	31.46
	Corn	84.99	11.30	2.35	3.21	1.09	8.52	-
	Soybean meal	89.21	8.86	4.62	5.60	0.72	48.49	-
7/30 to 8/12/03	Silage	45.94	45.68	26.24	24.69	3.35	9.59	25.23
	Corn	85.35	10.18	2.06	3.02	0.96	8.49	-
	Soybean meal	85.86	8.98	4.33	5.25	1.21	51.40	-
8/13 to 8/27/03	Silage	48.12	45.36	26.31	24.96	3.04	9.90	38.09
	Corn	88.15	9.97	1.99	2.94	0.93	8.09	-
	Soybean meal	87.25	8.74	4.39	5.35	0.71	52.22	-
8/28 to 9/8/03	Silage	47.34	52.15	30.20	27.61	3.88	9.54	34.95
	Corn	85.38	8.66	1.66	2.66	1.00	7.10	-
	Soybean meal	87.26	9.73	3.95	4.94	0.76	50.77	-

[a]DM basis.

Appendix G

Lactic acid and volatile fatty acid composition of silage fed to steers at Steeles Tavern, VA

	Component[a]		
Time	Lactate	Acetate	Butyrate
	----------%----------		
4/22 to 5/6/03	2.00	2.31	0.26
5/7 to 5/20/03	2.51	2.08	0.19
5/21 to 6/3/03	2.07	2.65	0.32
6/4 to 6/17/03	2.30	2.53	0.11
6/18 to 7/1/03	1.45	2.11	0.14
7/2 to 7/16/03	0.79	1.00	0.09
7/17 to 7/29/03	0.80	0.65	-
7/30 to 8/12/03	1.40	1.19	-
8/13 to 8/27/03	1.25	0.75	-
8/28 to 9/8/03	0.84	0.51	-

[a]DM basis.

Appendix H

Calcium and phosphorus composition of the mineral supplements fed to steers at Steeles Tavern, VA

	Component[a]	
Date	Ca	P
	----------%----------	
4/22 to 5/6/03	6.31	0.40
5/7 to 5/20/03	5.58	0.43
5/21 to 6/3/03	5.59	0.47
6/4 to 6/17/03	5.67	0.43
6/18 to 7/1/03	6.05	0.41
7/2 to 7/16/03	5.43	0.39
7/17 to 7/29/03	5.14	0.44
7/30 to 8/12/03	4.57	0.44
8/13 to 8/27/03	7.24	0.40
8/28 to 9/8/03	5.47	0.47

[a]DM basis.

Appendix I

Average fatty acid composition of the high-concentrate diets fed to steers at Steeles Tavern, VA

	Fatty acid								
Date	14:0	15:0	16:0	16:1c9	18:0	18:1c9	18:2 *n*-6	18:3	20:2
	mg/g DM								
4/29 to 5/6/03	0.05	0.22	7.55	0.06	0.85	9.23	27.76	1.41	0.16
5/7 to 5/20/03	0.04	0.22	7.54	0.05	0.89	9.81	28.00	1.52	0.15
5/21 to 6/3/03	0.03	0.20	6.52	0.06	0.70	9.30	25.13	0.99	0.12
6/4 to 6/17/03	0.02	0.15	4.79	0.05	0.48	8.40	19.19	1.00	0.08
6/18 to 7/1/03	0.01	0.08	3.51	0.03	0.44	7.31	15.80	0.58	0.05
7/2 to 7/16/03	0.01	0.04	4.03	0.01	0.61	9.41	19.23	0.48	0.03
7/17 to 7/29/03	0.01	0.05	3.36	0.01	0.57	7.71	16.17	0.37	0.04
7/30 to 8/12/03	0.01	0.06	4.87	0.02	0.72	11.27	23.93	0.48	0.04
8/13 to 8/27/03	0.01	0.06	4.25	0.02	0.73	10.57	20.05	0.62	0.04
8/28 to 9/8/03	0.01	0.05	4.10	0.02	0.78	8.95	18.84	0.38	0.04
	% of total fatty acids								
4/29 to 5/6/03	0.10	0.46	15.97	0.12	1.79	19.53	58.71	2.98	0.34
5/7 to 5/20/03	0.09	0.45	15.64	0.11	1.85	20.34	58.08	3.14	0.31
5/21 to 6/3/03	0.08	0.47	15.15	0.13	1.62	21.60	58.37	2.31	0.27
6/4 to 6/17/03	0.05	0.43	14.03	0.14	1.39	24.61	56.20	2.91	0.23
6/18 to 7/1/03	0.04	0.29	12.61	0.10	1.58	26.28	56.83	2.10	0.18
7/2 to 7/16/03	0.02	0.11	11.91	0.04	1.81	27.79	56.81	1.43	0.08
7/17 to 7/29/03	0.03	0.17	11.87	0.05	2.01	27.25	57.17	1.30	0.14
7/30 to 8/12/03	0.02	0.15	11.76	0.04	1.74	27.21	57.80	1.17	0.10
8/13 to 8/27/03	0.02	0.17	11.70	0.05	2.00	29.09	55.18	1.69	0.10
8/28 to 9/8/03	0.02	0.15	12.37	0.06	2.35	26.98	56.80	1.16	0.11

Appendix J

Fatty acid composition of the high-concentrate diet ingredients fed to steers at Steeles Tavern, VA

		Fatty acid								
Date	Ingredient	14:0	15:0	16:0	16:1c9	18:0	18:1c9	18:2 *n*-6	18:3	20:2
		mg/g DM								
4/22 to 5/6/03	Silage	0.05	0.24	7.56	0.06	0.80	9.67	27.39	1.25	0.17
	Soybean meal	-	-	7.95	0.02	1.36	5.44	33.28	3.12	0.09
5/7 to 5/20/03	Silage	0.05	0.25	7.73	0.06	0.85	10.07	28.50	1.38	0.17
	Corn	-	-	3.99	-	0.52	13.74	26.14	0.37	-
	Soybean meal	-	-	7.56	0.02	1.50	6.28	25.67	3.41	-
5/21 to 6/3/03	Silage	0.05	0.29	8.02	0.08	0.79	10.15	28.40	1.06	0.16
	Corn	-	-	2.12	-	0.31	8.64	16.67	0.26	-
	Soybean meal	-	-	6.10	0.01	1.02	4.32	21.69	2.50	0.06
6/4 to 6/17/03	Silage	0.04	0.33	7.14	0.10	0.52	8.97	23.96	1.64	0.17
	Corn	-	-	2.52	-	0.37	8.54	14.91	0.26	-
	Soybean meal	-	-	5.61	0.02	0.95	4.28	19.20	1.99	0.06
6/18 to 7/1/03	Silage	0.05	0.33	8.07	0.11	0.65	10.14	24.25	1.23	0.20
	Corn	-	-	1.89	-	0.35	6.77	13.15	0.29	-
	Soybean meal	-	-	4.02	0.01	0.65	2.52	13.41	1.41	0.04
7/2 to 7/16/03	Silage	0.06	0.33	6.76	0.11	0.76	9.80	17.23	1.03	0.21
	Corn	-	-	3.54	-	0.56	9.69	19.43	0.30	-
	Soybean meal	-	-	4.48	0.01	0.70	2.82	15.16	1.64	0.04
7/17 to 7/29/03	Silage	0.06	0.29	4.90	0.08	0.77	7.86	14.20	0.58	0.21
	Corn	-	-	2.86	-	0.49	7.92	16.27	0.20	-
	Soybean meal	-	-	6.13	0.02	1.15	4.74	21.72	2.19	0.08
7/30 to 8/12/03	Silage	0.05	0.35	5.88	0.09	0.65	7.46	16.41	0.89	0.22
	Corn	-	-	4.59	-	0.71	12.71	26.18	0.28	-
	Soybean meal	-	-	5.73	0.01	1.12	4.52	18.86	1.98	0.06
8/13 to 8/27/03	Silage	0.05	0.35	6.94	0.09	0.76	9.69	20.63	0.95	0.20
	Corn	-	-	3.45	-	0.67	11.21	19.97	0.40	-
	Soybean meal	-	-	6.81	0.02	1.45	5.35	20.52	2.51	-
8/28 to 9/8/03	Silage	0.04	0.28	6.97	0.10	0.83	9.83	18.23	0.74	0.19
	Corn	-	-	3.36	-	0.76	9.13	19.11	0.18	-
	Soybean meal	-	-	5.34	0.01	0.91	4.28	18.43	2.04	0.05

Appendix K

Chemical composition of pasture forage samples at Willow Bend, WV

	Component[a]					
Date	NDF	ADF	Cellulose	Lignin	CP	TNC[b]
	----------%----------					
4/22/2003	53.29	23.46	22.67	2.31	25.86	8.58
5/6/2003	57.96	29.65	28.37	2.53	19.93	-
5/20/2003	57.80	29.67	28.17	2.99	15.25	11.62
6/3/2003	64.34	35.43	32.12	4.65	12.21	-
6/17/2003	67.18	38.23	34.84	4.34	10.17	-
7/1/2003	62.73	33.56	30.30	4.50	14.21	-
7/16/2003	52.51	28.64	24.17	3.56	14.37	12.39
7/29/2003	58.86	33.01	28.11	6.16	15.85	-
8/12/2003	64.43	34.51	29.76	5.21	15.02	-
8/27/2003	63.87	32.90	27.36	6.28	17.02	-
9/8/2003	60.85	31.88	28.03	4.76	16.23	6.50

[a]DM basis.

[a]Total nonstructural carbohydrates.

Appendix L

Fatty acid composition of pasture forage samples at Willow Bend, WV

	Date										
Fatty acid	4/22/03	5/6/03	5/20/03	6/3/03	6/17/03	7/1/03	7/16/03	7/29/03	8/12/03	8/27/03	9/8/03
	mg/g DM										
Myristic (14:0)	0.04	0.05	0.05	0.06	0.05	0.05	0.05	0.05	0.04	0.04	0.05
Pentadecylic acid (15:0)	3.72	3.19	2.35	2.08	1.45	1.55	2.36	1.74	1.75	1.68	2.39
Palmitic (16:0)	4.86	4.97	5.39	3.84	2.25	3.70	3.31	3.89	2.31	2.46	3.38
Palmitoleic (16:1)	0.53	0.33	0.21	0.19	0.12	0.09	0.16	0.15	0.10	0.11	0.20
Stearic (18:0)	0.27	0.24	0.26	0.37	0.18	0.23	0.21	0.26	0.18	0.21	0.25
Oleic (18:1 *cis*-9)	0.33	0.49	0.76	0.48	0.50	1.05	0.23	0.32	0.30	0.34	0.46
Linoleic (18:2 *n*-6)	3.04	3.60	4.31	2.98	1.91	3.43	1.91	2.91	1.73	1.96	3.06
Linolenic (18:3 *n*-3)	47.71	40.40	31.34	19.88	9.81	20.08	22.31	18.22	11.22	11.26	18.36
20:2 *n*-6	0.28	0.28	0.24	0.25	0.22	0.14	0.34	0.18	0.20	0.21	0.23
22:2 *n*-6	0.25	0.33	0.31	0.47	0.34	0.18	0.26	0.19	0.20	0.16	0.15
DPA (22:5 *n*-3)	0.31	0.27	0.24	0.22	0.20	0.18	0.18	0.20	0.16	0.18	0.24
DHA (22:6 *n*-3)	0.60	0.67	0.50	0.37	0.36	0.27	0.26	0.34	0.30	0.37	0.40
	% of total fatty acids										
Myristic (14:0)	0.07	0.09	0.12	0.20	0.29	0.16	0.14	0.18	0.24	0.24	0.18
Pentadecylic acid (15:0)	6.09	5.89	5.27	6.68	8.35	5.06	7.46	6.27	9.46	8.84	8.37
Palmitic (16:0)	7.83	9.11	11.50	12.34	12.97	11.90	10.47	13.50	12.53	13.01	11.61
Palmitoleic (16:1)	0.85	0.61	0.47	0.60	0.65	0.31	0.50	0.52	0.55	0.60	0.70
Stearic (18:0)	0.43	0.44	0.56	1.20	1.00	0.76	0.69	0.92	0.97	1.15	0.86
Oleic (18:1 *cis*-9)	0.53	0.92	1.65	1.54	2.88	3.39	0.74	1.11	1.64	1.78	1.63
Linoleic (18:2 *n*-6)	4.89	6.56	9.32	9.51	11.02	11.06	6.04	10.19	9.32	10.36	10.63
Linolenic (18:3 *n*-3)	76.98	73.49	68.23	63.71	56.38	64.85	70.67	64.00	60.62	59.11	62.47
20:2 *n*-6	0.46	0.51	0.54	0.81	1.27	0.46	1.07	0.66	1.10	1.13	0.80
22:2 *n*-6	0.41	0.63	0.69	1.51	1.96	0.59	0.81	0.68	1.08	0.85	0.54
DPA (22:5 *n*-3)	0.51	0.49	0.55	0.71	1.15	0.57	0.58	0.71	0.84	0.98	0.84
DHA (22:6 *n*-3)	0.97	1.25	1.10	1.21	2.07	0.89	0.83	1.27	1.65	1.96	1.37

Appendix M

Freeze dryer programs - FreeZone 12L Freeze Dry System, Labconco Corp

Forage (program 1)

	Segment		
Item	1	2	3
Ramp, ºC/min	1.5	2.5	1.5
Hold, ºC	-34.0	-10.0	10.0
Time, h	5 .0	60.0	48.0

Ruminal fluid (program 2)

	Segment		
Item	1	2	3
Ramp, ºC/min	1.0	1.0	1.0
Hold, ºC	-25.0	-15.0	0.0
Time, h	5.0	24.0	10.0

Adipose tissue (program 3)

	Segment		
Item	1	2	3
Ramp, ºC/min	0.5	1.5	1.5
Hold, ºC	-3.0	-10.0	25.0
Time, h	10.0	48.0	10.0

Appendix N

Sample preparation for freeze drying - FreeZone 12L Freeze Dry System, Labconco Corp

Forages

Forage samples were stored in the freezer at -20ºC. Frozen samples were freeze dried in the same small cloth sample bag that they were placed in when they were collected in the pasture. Four forage samples (on two shelves) were usually dried at one time. The samples were then ground (within 1 wk, 0.5 mm using Wiley mill) and returned to the freezer.

Silages

Silage samples were stored in the freezer at -20ºC in plastic bags. Prior to freeze drying, the silage samples were allowed to thaw overnight in a refrigerator. Silage samples were composited over the 14-d periods by mixing well in a large plastic tub. A subsample (approximately 200 to 400 g) was placed in a preweighed small brown paper bag with the top half removed. The weight of the bag plus wet silage was recorded for later macro DM determination. The top portion of the bag was folded down and secured with rubber bands. The silage samples were then placed in a large plastic bag and returned to the freezer until completely frozen. The samples were then freeze dried in the paper bags using the forage program. When dry, the samples were removed from the freeze dryer, allowed to equilibrate with ambient conditions (approximately 0.5 h), the rubber bands were then removed, and the sample was weighed. Usually six silage samples (on two shelves) were dried at one time. The samples were then ground (within 1 wk, 0.5 mm and 1.0 mm using Wiley mill) and returned to the freezer.

Ruminal Fluid

Ruminal fluid was stored in the ultra-low freezer at -65°C in plastic sample cups (approximately 100-mL volume). Prior to freeze drying, the ruminal fluid samples were allowed to thaw (approximately 2 d) in a refrigerator. One sample cup of the liquid ruminal fluid was then poured into three or four plastic food storage containers (pint size). The lips of the food storage containers had to be trimmed prior to use, so they would fit on all three shelves in the freeze dryer. Cheesecloth was placed over the food storage container and secured with a rubber band. The samples where then placed on metal trays and returned to the freezer until completely frozen. The samples were then freeze dried. When dry, the samples were moved to a shelf-type dessicator (to prevent excessive moisture absorption from the atmosphere) and allowed to return to ambient temperature. The samples were then immediately ground with a mortar and pestle, placed in plastic storage tubes, and returned to the freezer.

Adipose Tissue

Adipose tissue samples were stored in the ultra-low freezer at -65°C, wrapped individually in aluminum foil. The samples were removed from the aluminum foil, excess blood/fluid was blotted off of the exterior of the sample, onto paper towels. The sample was then placed in a preweighed beaker (50-mL size, or smaller) and the weight recorded (for later macro DM determination). The beaker was covered with cheesecloth and secured with a rubber band. The samples were then returned to the freezer until completely frozen. The samples were then freeze-dried. When dry, the samples were removed from the freeze dryer, allowed to equilibrate with ambient conditions (approximately 0.5 h), the rubber band and cheesecloth were then removed, and the dry weight was recorded. The samples were then immediately placed in plastic storage tubes and returned to the freezer.

Appendix O

Modified extraction method of Folch et al. (1957):

Amounts of samples for extractions:
Forage and silage 500 mg
Corn 300 mg
Soybean meal 1.0 g
Soybean hulls 200 mg
Ruminal fluid 500 mg
Adipose tissues 15 to 20 mg
Serum 2 mL

Note: Use of any solvents listed in this procedure required the use of a fume hood.

Samples were weighed into 50-mL (2.5 x 15 cm) screw cap glass tubes (quantity that yielded a maximum of 30 mg lipid).

For forage/feed, ruminal fluid, and serum samples, 15 mL of 2:1 (v:v) chloroform:methanol was added and vortexed well.

For muscle/adipose tissue, 20 mL of 2:1 (v:v) chloroform:methanol was added and homogenized for 0.5 to 1 min at medium to medium-high speed. The tissue was checked for disruption and that the tissue had not been caught in the blades. If tissue was caught in blades, it was gently removed with tweezers and put back in tube. Homogenization was repeated, if needed. Probe was rinsed between samples by homogenizing chloroform:methanol briefly. Rinsing solvent was changed after each sample (done in duplicate).

Tubes were capped tightly and let stand for 1 h. Homogenate was filtered into clean 50-mL (2.5 x 15 cm) screw cap tubes with Whatman filter paper (no 541). Tube were rinsed twice by adding 3.5 mL chloroform:methanol to tube, vortexing, and pouring over residue. Five mL of 0.88% KCl (w:v) (4.4 g/ 500 mL) was added to each tube, capped tightly, and were shaken on a horizontal platform shaker for 10 min at high speed. Caps were removed and tubes were centrifuged at 2200 rpm for 5 min. The upper aqueous layer was discarded. The solvent was evaporated under N_2 in *N*-Evap at 40°C until approximately 2 mL was left in the tube. With glass Pasteur pipettes, the solvent layer was transferred to glass screw cap methylation tubes (1.5 cm x 15 cm). Large tubes were washed twice with 2 mL 2:1 chloroform:methanol, and added to methylation tube. Solvent was evaporated under N_2 in *N*-Evap until tubes were dry. Extracted samples were stored in an ultra-low freezer until methylation step.

Reference:

Folch, J. M. Less, and G. H. Sloane Stanley. 1957. A simple method for the isolation and purification of total lipides from animal tissues. J. Biol. Chem. 226:497-509.

Modified methylation procedure of Park and Goins (1994):

Note: Use of any solvents listed in this procedure required the use of a fume hood.

Added 200 µl dichloromethane (methylene chloride), 500 µl hexane which contained 100 µg/mL 11:1 (free acid form, internal standard undecenoic acid), and 2 mL 0.5N NaOH (9.9993 g/ 500 mL) in methanol to each tube. Tubes were tightly capped and vortexed well. Tubes were placed in a preheated hot water bath (90-95°C) for 10 min. Tubes that leaked and resulted in solvent loss resulted in a loss of fatty acids and needed to be repeated. Tubes were removed from heat and cooled to room temperature. Added 2 mL 14% BF_3 in methanol to each tube. Tubes were capped tightly, vortexed well, and heated in a hot water bath as previously described. Tubes were removed from heat and cooled to room temperature. Added 1 mL deionized water followed by 1 mL hexane to each tube. Tubes were shaken on high setting of platform shaker for 10 min and centrifuged for 5 min at 1500 rpm. Added a small amount of dry sodium sulfate to each screw cap vial. With Pasteur pipette, transferred hexane layer (top layer) to GC vial. Stored methylated samples in an ultra-low freezer until GC analysis.

Reference:

Park, P.W. and R.E. Goins. 1994. In situ preparation of fatty acid methyl esters for analysis of fatty acid composition in foods. J. Food Sci. 59(6):1262-1266.

Appendix P

Standard mixture for adipose tissue, forage, feed and ruminal fluid analysis

Nu-Chek Prep (Elysian, MN) GLC # 463, 100 mg ampule

Added ampule to 10 mL flask = stock
Pipetted 2.5 mL of stock into a 5 mL flask to get a 1:2 dilution
In addition added CLA mixtures to 5 mL flask (see below).

CLA mixtures

Matreya (Pleasant Gap, PA), 25 mg ampules

trans-9, trans-11 CLA catalog #1257
trans-10, cis-12 CLA catalog #1254
cis-9, cis-12 CLA catalog #1256
cis-9, trans-11 CLA catalog # 1255
(Z = cis, E = trans)

2,500 µg/mL CLA stock solution: Added 25 mg ampule to 10 mL flask = stock
Needed a 50 µg/mL in standard mixture (in a 5 mL flask). 50 µg/mL * 5 = 250 µg (in the 5 mL flask).

2,500 µg/1,000 µl = 250 µg/x µl
x = 100 µl

Pipetted 100 µl of each stock solution into 5 mL flask

OR

1,000 µg/mL CLA stock solution: Added 25 mg ampule to 25 mL flask = stock
Needed 50 µg/mL in standard mixture (in a 5 mL flask). 50 µg/mL * 5 = 250 µg (in the 5 mL flask).

1,000 µg/1,000 µl = 250 µg/x µl
x = 250 µl

Pipetted 250 µl of each stock solution into 5 mL flask

Internal standard

Nu-Chek Prep U-31-A, 100 mg ampule

Free fatty acid form added to samples

In the standard mixture there was 50 µg/mL 11:1.

Added 500 µL of 11:1 in hexane to samples, needed to add 2x concentration.
(i.e. wanted to add 50 µg to samples = 500 µL of a 100 µg/mL solution)

50 µg/500 µL = 100 µg/1,000 µL

Added the 100 mg (100,000 µg) ampule to a 10 mL flask = 10,000 µg/mL stock

Needed 100 µg/mL solution (in a 10 mL flask). 100 µg/mL * 10 = 1,000 µg (in the 10 mL flask).

10,000 µg/1,000 µL = 1,000 µg/x µL
x = 100 µL

Pipetted 100 µL of stock solution into 10 mL flask , or 500 µL of stock solution into 50 mL flask

Standard mixture for serum analysis

"Normal" mixture was a 1:2 dilution (for adipose, etc). To get a 1:2 dilution, added 5 mL of stock solution to a 10 mL flask. However, for serum analysis a 1:4 or a 1:8 dilution was needed. Therefore, for a 1:4 dilution added 2.5 mL of stock solution to a 10 mL flask. For a 1:8 dilution, added 1.25 mL of stock solution to a 10 mL flask.

Internal standard: Nu-Chek Prep U-31-M, 100 mg ampule

The internal standard needed to remain constant in the standard mixtures at 50 µg/mL. Remembering to take into account that there was an amount of 11:1 already in the standard mixture. And, the form in the standard mixture needed to be the methylated form, not the free fatty acid form.

Internal standard stock: Added 100 mg ampule to a 10 mL flask.

1:4 standard mixture:
25 µg of internal standard in standard mixture * 10 mL flask = 250 µg total in flask
500 µg needed in flask - 250 µg total in flask = 250 µg needed to add to flask
250 µg * (1 mL/10,000 µL) = 0.025 mL = 25 µL

1:8 standard mixture:
12.5 µg of internal standard in standard mixture * 10 mL flask = 125 µg total in flask
500 µg needed in flask - 125 µg total in flask = 375 µg needed to add to flask
375 µg * (1 mL/10,000 µL) = 0.0375 mL = 37.5 µL

Added 25 µL of internal standard stock solution to the 1:4 dilution and 37.5 µL to the 1:8 dilution.

Additionally, the diluted solutions needed CLA added to them. The 1:4 dilution needed 25 µg/mL of each CLA, and the 1:8 needed 12.5 µg/mL of each CLA.

1:4 standard mixture:
25 µg/mL * 10 mL = 250 µg total needed
250 µg (1 mL/2,500 µg) = 0.1 mL = 100 µL

or
250 µg (1 mL/1,000 µg) = 0.25 mL = 250 µL

1:8 standard mixture:
12.5 µg/mL * 10 mL = 125 µg total needed
125 µg (1 mL/2,500 µg) = 0.05 mL = 50 µL

or
125 µg (1 mL/1,000 µg) = 0.125 mL = 125 µL

Therefore, added 100 µL of each 2,500 µg/mL CLA stock (or 250 µL of each 1,000 µg/mL CLA stock) to the 1:4 dilution. And, added 50 µL of each 2,500 µg/mL CLA stock (or 125 µL of each 1,000 µg/mL CLA stock) to the 1:8 dilution.

Concentrations of fatty acids used in standard mixtures

Fatty acid	µg in ampule	µg/mL in 10 mL hexane	µg/mL (1:2)	µg/mL (1:4)	µg/mL (1:8)
4:0	1000	100	50	25	12.5
5:0	1000	100	50	25	12.5
6:0	1000	100	50	25	12.5
7:0	1000	100	50	25	12.5
8:0	2000	200	100	50	25
9:0	1000	100	50	25	12.5
10:0	2000	200	100	50	25
11:0	1000	100	50	25	12.5
11:1	1000	100	50	25	12.5
12:0	4000	400	200	100	50
12:1	2000	200	100	50	25
13:0	1000	100	50	25	12.5
13:1	1000	100	50	25	12.5
14:0	4000	400	200	100	50
14:1	2000	200	100	50	25
15:0	1000	100	50	25	12.5
15:1	1000	100	50	25	12.5
16:0	4000	400	200	100	50
16:1 t9	1000	100	50	25	12.5
16:1 c9	4000	400	200	100	50
17:0	2000	200	100	50	25
17:1	2000	200	100	50	25
18:0	4000	400	200	100	50
18:1 t9	1000	100	50	25	12.5
18:1 t11	1000	100	50	25	12.5
18:1 c6	1000	100	50	25	12.5
18:1 c9	4000	400	200	100	50
18:1 11	1000	100	50	25	12.5
19:0	1000	100	50	25	12.5
19:1	1000	100	50	25	12.5
18:2 t9t12	2000	200	100	50	25
18:2 c9c12	4000	400	200	100	50
20:0	4000	400	200	100	50
18:3 gamma	1000	100	50	25	12.5
20:1 c5	2000	200	100	50	25
20:1 c8	2000	200	100	50	25
20:1 c11	2000	200	100	50	25
18:3 alpha	4000	400	200	100	50
22:0	2000	200	100	50	25
20:2 *n*-6	2000	200	100	50	25
20:3 *n*-6	2000	200	100	50	25
20:3 *n*-3	1000	100	50	25	12.5
22:1	4000	400	200	100	50
20:4 *n*-6	1000	100	50	25	12.5
22:2 *n*-6	1000	100	50	25	12.5
22:3 *n*-3	2000	200	100	50	25
24:0	2000	200	100	50	25
20:5 *n*-3 (EPA)	2000	200	100	50	25
24:1	1000	100	50	25	12.5
22:4 *n*-6	1000	100	50	25	12.5
22:5 (DHA)	2000	200	100	50	25
22:6 (DPA)	2000	200	100	50	25
CLA:					
18:2 c9,t11	25000	.	50	25	12.5
18:2 t10,12	25000	.	50	25	12.5
18:2 c9,11	25000	.	50	25	12.5
18:2 t9,t11	25000	.	50	25	12.5

VITA

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The author was born on September 20, 1975, in Winchester, Virginia. She is the daughter of John and Elizabeth Fincham, and the wife of Aaron Guay. She grew up on a small family farm in Frederick County, Virginia. She graduated from Sherando High School in 1994. She attended Lord Fairfax Community College for 2 yr, and then transferred to Virginia Polytechnic Institute and State University. She obtained a Bachelor of Science degree in Crop and Soil Environmental Sciences in 1998. In August of 2001, she obtained a Master of Science degree in Crop and Soil Environmental Sciences, also at Virginia Polytechnic Institute and State University. Her Master's research involved the evaluation of the compatibility of Matua prairie grass with legumes. In the fall of 2001, she began working toward a Doctor of Philosophy degree in Animal and Poultry Sciences.