Published June 21, 2019

Meat and Muscle Biology™

Longissimus Muscle Composition and Palatability of Grazing Steers Supplemented with Corn Oil or Corn Grain

Enrique Pavan[1,2]* and Susan K. Duckett[3]

[1]Instituto Nacional de Tecnologia Agropecuaria, 7620 Balcarce, Argentina
[2]Facultad Ciencias Agrarias, Universidad Nacional de Mar del Plata, 7620 Balcarce, Argentina
[3]Department of Animal and Veterinary Science, Clemson University, Clemson, SC 29634, USA
*Corresponding author. Email: pavan.enrique@inta.gob.ar (E. Pavan).

Abstract: Twenty-eight Angus (289 ± 3.8 kg) steers were used to evaluate the effect of isocaloric supplementation of 2 different energy sources to steers grazing tall fescue pastures for 197 d on *longissimus* muscle fatty acid profile, shear force, tenderness and color. Steers were supplemented with either corn grain (PC) or soybean hulls plus corn oil (PO). A negative control, pasture only (PA), and positive control, high-concentrate control diets (CONC) were also included in the study. Total *trans*-11 vaccenic acid (TVA) and *cis*-9, *trans*-11 CLA content per serving were similar with PA, PC and CONC and greatest with PO ($P < 0.001$). Muscle total fatty acids, myristic and palmitic contents per serving were similar with PC, PO, and PA and greatest with CONC ($P < 0.001$). Muscle PUFA n-6:n-3 ratio was greater with PC than with PA and lower with PC than with CONC, but it was greatest with PO ($P < 0.001$). Shear force was lower ($P = 0.046$) with CONC than with PA and PC; beef from PO did not differ from any of the other treatments. Sensory panel scores for overall tenderness ($P < 0.001$) were greatest with CONC, greater with PO than with PC, and similar with PA than with PO and PC. Muscle lightness was similar for PO and PC, greater with PO and PC than with PA and lower with PO and PC than with CONC ($P < 0.001$). Treatment by time postmortem interaction was significant for muscle temperature ($P < 0.001$), but not for muscle pH ($P = 0.79$). Temperature decline was fastest with PA and slowest with CONC. Postmortem muscle pH was greater with PA, PC, and PO than with CONC ($P = 0.011$). Overall, fatty acid profile with PC was closer to the fatty acid profile with PA than that with PO or CONC. Finishing systems altered fat deposition, which impacted chilling rate, muscle color and palatability.

Keywords: color, fatty acids, muscle temperature, shear force, tenderness
Meat and Muscle Biology 3(1):181–193 (2019) **doi:10.22175/mmb2018.10.0030**
Submitted 1 Oct. 2018 Accepted 29 Mar. 2019

Introduction

Grass-fed beef has been marketed in different countries as a leaner product, with an altered fatty acid composition. Grass-fed beef has lower proportions of the highly atherogenic myristic and palmitic acids than concentrate-fed beef and greater of the anti-atherogenic and anti-carcinogenic *cis*-9, *trans*-11 conjugated linolenic acid (CLA) and of its precursor, the *trans*-11 vaccenic acid (TVA; Daley et al., 2010). Although the n-6: n-3 ratio from grass-fed beef is always below the maximum dietary threshold of 4, as suggested by the WHO (WHO, 2003), ratios from 3 to 13 have been reported in the literature for feedlot-finished beef (Daley et al., 2010). Increasing corn grain supplementation to grazing steers changes the fatty acid profile toward that observed in feedlot-finished cattle (Garcia et al., 2008), whereas increasing corn oil supplementation to grazing steers has shown to reduce palmitic acid and increase CLA and TVA proportions (Pavan and Duckett, 2007).

In previous studies, we observed that when equal amounts of metabolizable energy (ME) are supplemented to grazing steers with corn grain or corn oil plus soybean hulls, similar improvement of animal performance could be obtained (Pavan and Duckett, 2008). However, the type of energy supplemented had a differential effect on fatty acid metabolism of

© American Meat Science Association.
This is an open access article distributed under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/)

the subcutaneous (s.c.) adipose tissue (Duckett et al., 2009). Relative to non-supplemented steers, fatty acid synthase (FASN) mRNA expression was up-regulated with corn grain supplementation, but not with corn oil; stearoyl-CoA desaturase (SCD) desaturation was up-regulated with both energy types, but to a greater extent with corn grain compared to corn oil.

The leanness and fatty acid profile of grass-fed beef could compromise its organoleptic properties. It has been suggested that a minimum 3% of fat content in beef (Savell and Cross, 1988) and 0.7 cm of dorsal back fat thickness are required to guarantee adequate level of shear-force or tenderness in beef (Tatum et al., 1982). Duckett et al. (2007) and Duckett et al. (2013) did not observe shear force or tenderness differences, despite grass-fed beef fat levels were below the suggested beef fat content and dorsal back fat thresholds; lower beef flavor and greater off-flavor intensities were reported for grass-fed beef in both studies. Furthermore, associated with greater ultimate pH level, grass-fed beef presented a darker red color than feedlot-finished beef (Duckett et al., 2007; Duckett et al., 2013). Therefore, the objective of this study was to evaluate the effect of supplementing iso-caloric levels of corn grain or corn oil plus soybean hulls to grazing cattle on the *longissimus* muscle fatty acid composition, shear-force, sensory attributes in comparison to negative, pasture only control and positive, feedlot-finished control diets.

Materials and Methods

The experimental procedures were reviewed and approved by the University of Georgia Animal Care and Use Committee (A2004–10067-C2).

Twenty-eight yearling Angus steers (288.7 ± 3.8 kg) were randomly assigned to 1 of 4 dietary treatments. Dietary treatments included 2 isocaloric supplementation treatments to steers grazing endophyte-free tall fescue [corn grain (0.52% of LW, DM basis; PC) or corn oil plus soybean hulls (SBH; 0.10 and 0.45% of LW, respectively; PO)], no supplementation to steers grazing endophyte-free tall fescue (PA), or a high-concentrate diet (85% concentrate:15% bermudagrass hay on a DM basis; CONC). Corn oil and SBH were mixed daily on an individual basis before feeding. The concentrate used in the CONC treatment was formulated to contain 94.11% rolled corn, 2.91% soybean meal, 1.50% limestone, 0.95% urea, and 0.53% of trace minerals (DM basis).

Steers assigned to the PO and PC treatments were trained to use Calan gate feeders (American Calan Inc., Northwood, NH) for 21 d before the beginning of the trial, and in the last 5 d, steers were adapted to supplements. During adaptation, steers assigned to the grazing treatments (PA, PO, and PC) were allowed to graze the same pasture that was used for the experimental period. Steers assigned to the CONC treatment were fed the high-concentrate diet during the last 92 d of the trial (d 105 to 197), before which they grazed endophyte-free tall fescue pastures and trained to use Calan gates feeders (American Calan Inc., Northwood, NH) for 21 d. Additional information on the experimental design, diet in vivo digestibility steer performance, and steer carcass quality was reported previously by Pavan and Duckett (2008); whereas information on subcutaneous fatty acid composition and lipogenic gene expression was in Duckett et al. (2009).

Sample collection

Animals were slaughtered after an overnight feed withdrawal at the University of Georgia (UGA) Meat Science Technology Center; a captive bolt pistol was used for stunning animals prior to slaughter. Carcasses were chilled at –1°C; pH and temperature of the M. *longissimus thoracis* (LM) between the 12th and 13th ribs were measured at 6, 12, and 24 h postmortem using a portable pH-meter (Sper Scientific, Scottsdale, AZ, model 850081) with a temperature penetration probe and a pH penetration probe type 13 (Testo 06500245; Testo SE & Co. KGaA; Germany).

After 24 h of chilling, the 9 to 12th rib section was removed from the left side of each carcass and allowed to bloom for at least 30 min for muscle color determination. The LM was removed from the rib section and cut into 2.5 cm-thick steaks. Steaks were vacuum packaged (5 mmbar) in Cryovac BB2800 bags (O_2 permeability 6,000 to 8,000 cc/m^2 per 24 h and CO_2 permeability 19,000 to 22,000 cc/m^2 per 24 h at 22.8°C and 1 atm) using a Multivac A 300/16 vaccum packager (Multivac, Germany) and assigned to future analysis; the first steak (from caudal to cranial) was assigned for subsequent fatty acid analysis, the following 5 steaks for Warner-Bratzler shear-force (WBSF) evaluation, and the last one for trained sensory panel evaluation. All external fat and connective tissue were removed from the steaks collected for FA analysis. Steaks for FA analysis were not aged whereas steaks for WBSF evaluation were randomly aged for 1, 3, 7, 14, or 28 d at 2°C, and steaks for trained sensory panel evaluation were aged for 14 d. At the end of each aging period, steaks were frozen and stored at –20°C until subsequent analysis.

Instrumental color

Instrumental color measurements were recorded for L* (measures darkness to lightness; lower L* indicates a darker color), a* (measures redness and grenness; greater a* value indicates a redder color), and b* (measures yellowness and blueness; greater b* value indicates a more yellow color) using a Minolta chromameter (CR-310; Minolta Inc., Osaka, Japan) with a 50-mm-diameter measurement area using a D65 illuminant, which was calibrated using the white ceramic disk provided by the manufacturer. Color readings were determined at 24 h postmortem on the exposed LM at the posterior (12th rib) of the rib and s.c. fat covering the posterior rib. Values were recorded from 3 locations of exposed lean and s.c. fat to obtain a representative reading.

Warner-Bratzler shear force

Steaks (2.5-cm thick) were thawed for 24 h at 4°C and broiled on Farberware (Bronx, NY) electric grills to an internal temperature of 71°C (American Meat Science Association, 2016). Steaks were allowed to cool to room temperature before six 1.27-cm-diameter cores were removed from each steak parallel to the longitudinal orientation of the muscle fibers. All cores were sheared perpendicular to the long axis of the core using a Warner-Bratzler shear machine (G-R Manufacturing, Manhattan, KS).

Trained sensory panel evaluation

Steaks were thawed for 24 h at 4°C and broiled on Farberware electric grills to an internal temperature of 71°C (American Meat Science Association, 2016). Steaks were immediately cut into 2.54 cm × 1.27 cm × 1.27 cm cubes and served warm to an 8-member sensory panel (American Meat Science Association, 2016). Potential panelists were recruited verbally and selected based on willingness to serve at scheduled times and interest in evaluation of beef steaks. A total of twelve panelists were screened and trained following the Research Guidelines for Cookery, Sensory Evaluation and Instrumental Tenderness Measurements of Fresh Meat (American Meat Science Association, 2016). Briefly, potential panelists were screened on several steak samples and chosen to serve based on their abilities to discriminate known differences in tenderness, juiciness, and flavor. Selected panelists (8) were trained in six 1 h sessions in the 10 d immediately before the evaluation. Steak samples from concentrate-fed cattle representing a wide range of tenderness, juiciness and flavor traits were used in each training session; steaks from M. *semitendinosus*, M. *psoas major*, M. *longissimus lumborum* cooked to different degree of doneness (rare, 60°C, medium, 71°C, and wel-done, 77°C). Each panelist evaluated 2 cubes from each sample for juiciness, initial tenderness, overall tenderness, and beef flavor intensity using an 8-point scale (1 = extremely dry, tough, and bland to 8 = extremely juicy, tender, and intense). Off-flavor scores were also recorded on a 9-point scale (0 = none, 1 = extremely slight off-flavor to 8 = extremely intense off-flavor).

Fatty acid composition

LM steak samples were submerged in liquid nitrogen (–196°C), pulverized and stored anaerobically at –20°C. Total lipid extracts were obtained from the pulverized samples following the chloroform–methanol procedure of Folch et al. (Folch et al., 1957), modified by using a 10:1 ratio of chloroform-methanol to sample. Extracts containing approximately 4 mg of total lipids were transmethylated according to the method of Park and Goins (Park and Goins, 1994). Fatty acid methyl esters (FAME) were analyzed using a HP6850 (Hewlett-Packard, San Fernando, CA) gas chromatograph equipped with a HP7673A (Hewlett-Packard) automatic sampler. Separations were accomplished using a 100-m SP2560 (Supelco, Bellefonte, PA) capillary column (0.25-mm i.d. and 0.20-μm film thickness). Column oven temperature increased from 150 to 160°C at 1°C per min, from 160 to 167°C at 0.2°C per min, from 167 to 225°C at 1.5°C per min, and then held at 225°C for 16 min. The injector and detector were maintained at 250°C. Sample injection volume was 1μL. Hydrogen was the carrier gas at a flow rate of 1 mL per min. Individual FA were identified by comparison of retention times with standards [Conjugated linoleic acid (O-5507), Sigma-Aldrich, St. Louis, MO; F.A.M.E. mix (18920) and PUFA N°3 (47085-U) Supelco, Bellefonte, PA; Methyl 9(Z),11(E)-octadecadienoate (1255), Methyl 10(E),12(Z)-octadecadienoate (1254) and octadecenoic acid (trans-11) (1262) Matreya, Pleasant Gap, PA). The FA were quantified by incorporating 0.5 mg of an internal standard, methyl heptacosanoic (C27:0) acid, into each sample during methylation and expressed as a percentage of total FA.

Statistical analysis

All data were analyzed using the MIXED procedure of SAS (SAS Inst. Inc., Cary, NC). Fatty acid and color data were analyzed as a complete randomized model with dietary treatment as fixed effect. A similar model was used for sensory data adding panelist

as random effect. Muscle pH, temperature, and shear force data were analyzed as a Split Plot Design using repeated measurements analyses and selecting the covariance model with the BIC criterion (lower is better); the unstructured, compound symmetry, first-order autoregressive, and the Toeplitz covariance models were evaluated. Dietary treatments were randomly assigned to animals (subjects) on which repeated measures across aging periods were taken, aging periods were randomly assigned to steaks within animal. The individual animal was considered the experimental unit. When F-test was significant ($P < 0.05$) for main or interaction effects, least-square means were separated using the PDIFF option from PROC MIXED LSMEAN statement. Statistical significance was set at $P < 0.05$.

The relationship between fatty acids was determined with principal component analysis (Destefanis et al., 2000) using ONES as prior communality estimates with the FACTOR procedure of SAS, and using the principal axis method to extract the components.

Results and Discussion

One of the major objectives of the present study was to evaluate the effect of different type of energy supplementation on *longissimus* muscle fatty acid composition as compared to non-supplemented grazing steers or concentrate-finished steers. An overview of general dietary treatment effects on *longissimus* muscle fatty acid profile can be observed on the scoring plot (Fig. 1) where the steers sorted into three main groups. Two groups of steers were differentiated based on the first component and a third group, intermediate in the first component, was differentiated based on the second component. One of the first 2 groups contains concentrate-finished steers (CONC) and the other grazing steers supplemented with corn oil (PO). The group containing CONC was characterized by having the greatest proportions of fatty acids from synthesis *de novo* (C14:0 and C16:0) and endogenous desaturation fatty acids (C16:1 *cis*-9, C18:1 *cis*-9) and lowest proportions of those fatty acids derived from complete or partial ruminal biohydrogenation of dietary linoleic acid contain in the corn oil (C18:0, C18:1 *trans*-11 and CLA *cis*-9, *trans*-11). In contrast, the group containing PO was characterized by having the lowest proportions of fatty acids from *de novo* and endogenous desaturation and the greatest proportions of fatty acids derived from dietary linoleic acids. The third group, containing PA and PC, was characterized by having a lower n-6: n-3 ratio as compare to the other 2 groups. The scoring plot suggests that overall fatty acid profile from corn grain supplemented steers is closer to the fatty acid profile of non-supplemented grazing steers than that from steers finished on a high-concentrate diet.

Longissimus muscle total fatty acid content (mg FA/100 g fresh tissue; $P < 0.001$; Table 1) was 2-times greater in CONC than in grazing treatments; in turn no differences were detected between grazing treatments. This is in agreement with the observed difference in marbling reported in a companion manuscript by Pavan and Duckett (2008). Several studies reported greater total FA content for cattle finished on concentrate than on forage diets (Realini et al., 2004; Duckett et al., 2007; Duckett et al., 2013). Lack of supplementation effect with corn grain on total FA content was also observed by Wright et al. (2015) and Pouzo et al. (2015) when supplemented corn grain to grazing steers with 0.75% of LW for the last 102 d of finishing or with 0.70% of LW for the last 70 d, respectively. Total *longissimus* muscle lipid content was not affected by increasing the level (0, 0.075 or 0.15% of LW) of corn oil supplementation to grazing steers throughout the last 116 d of fattening (Pavan and Duckett, 2007) or when increasing the level of whole-flaxseed (0, 0.125 or 0.25% of LW) added to the corn grain (0.7% of LW) supplemented to grazing steers (Pouzo et al., 2015). It is noteworthy to mention that the lack of corn grain or corn oil supplementation effect on total fatty acid content or marbling in the LM observed in the present study and in the studies of Wright et al. (2015), Pouzo et al. (2015), and Pavan and Duckett (2007), where steers were slaughtered at similar time end-point, contrast with the greater subcutaneous fat thickness reported with supplementation in all 3 studies. In contrast, when slaughtered at similar degree of finishing estimated by visual evaluation, Latimori et al. (2008) observed that increasing corn grain supplementation (0, 0.7 or 1% of LW) reduced the fattening period and increased total FA content in the *longissimus* muscle.

The proportion of total SFA ($P = 0.047$), and the individual proportions of myristic ($P < 0.001$), palmitic ($P < 0.001$) and stearic ($P < 0.001$) acids were affected by dietary treatments (Table 1). Total SFA proportion was greatest with CONC and PO and least with PA, whereas the proportion with PC did not differ from any of the other dietary treatments. Nonetheless, the proportion of individual SFA differed between beef from CONC and PO; beef from CONC had the greatest proportions of myristic (C14:0) and palmitic (C16:0) acids and least of stearic acid (C18:0) of all 4 dietary treatments. In contrast, beef from PO had the lowest proportions of myristic and palmitic acids, but the greatest of stearic acid. Myristic and palmitic acids proportions with PC and PA did not differ from those with PO; however, palmitic acid proportion was greater with PC than with PA. Stearic acid

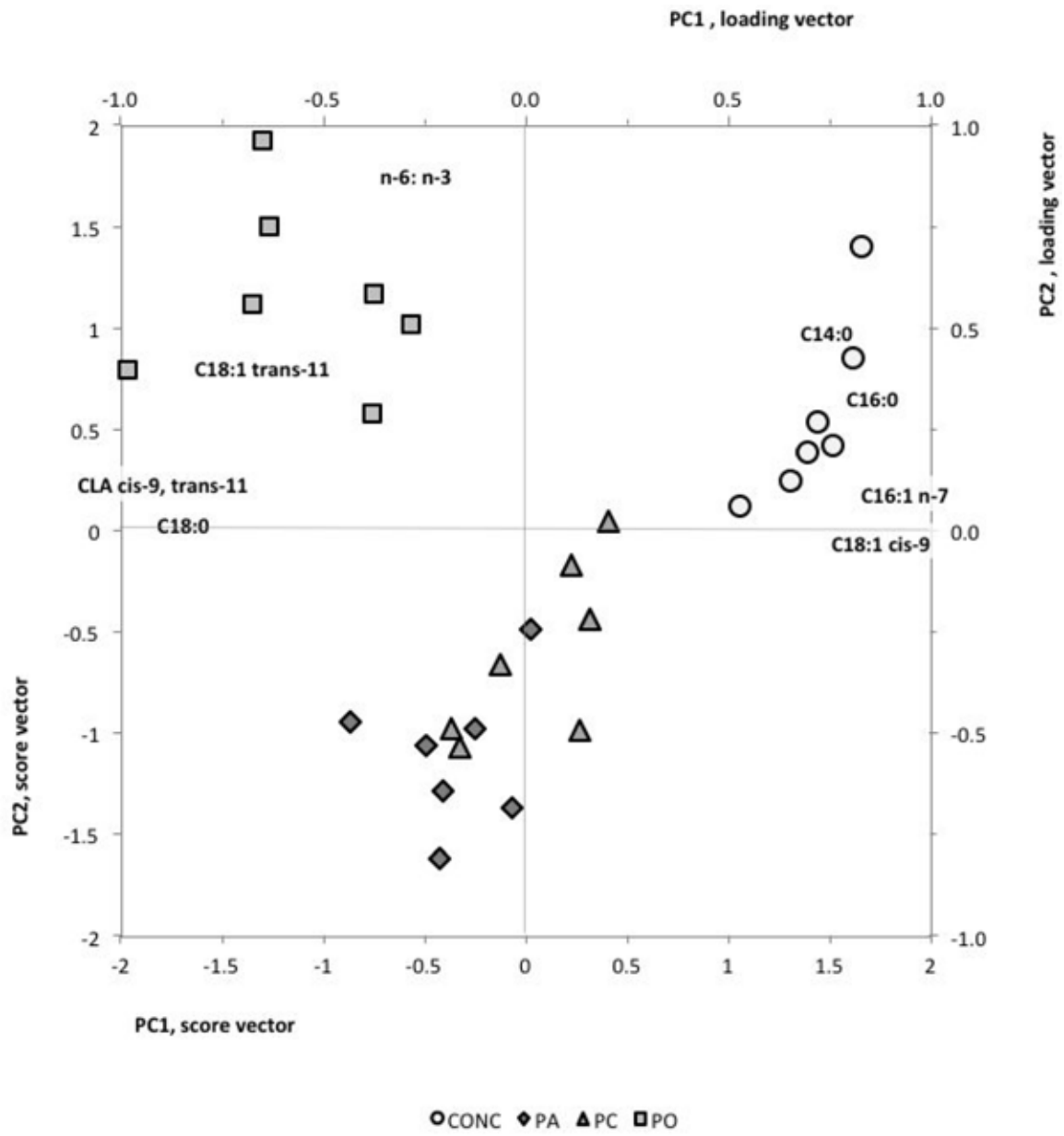

Figure 1. Plot of the 2 principal components score vectors (principal axis) and loading vectors (secondary axis) of main fatty acid proportions (C14:0, C16:0, C18:0, C18:1 cis-9, C18:1 *trans*-11, CLA *cis*-9, *trans*-11 g/100 g of total FA) and the n-6: n-3 ratio from the *longissimus* muscle from grazing steers supplemented with either corn oil plus soybean hulls (PO) or corn grain (PC) during 197 d as compared to no-supplemented grassing steers (PA) or concentrate finished steers (90 d, CONC). Both principal components explained 83.6% of the total variance (PC1, 66.3% and PC2, 17.3%).

proportion with PC and PA were similar, but greater than with CONC and lower than with PO. Similar results were observed by Duckett et al. (2009) in a three year study (n = 198) when comparing fatty acid profile from concentrate- and grass-finished steers. In addition, in a literature review, Daley et al. (2010) observed that total SFA was greater in concentrate-fed than in grass-fed cattle in one out of seven (1/7) studies reviewed, whereas no differences were observed in four of the seven (4/7) studies reviewed. In the studies reviewed by Daley et al. (2010) when different, myristic and palmitic acids were greater in concentrate-fed (4/7), whereas stearic acid was greater in grass-fed (5/7). In agreement with our results, when supplementing with increasing corn oil levels to grazing steers, myristic and palmitic acid decreased and stearic acid increased linearly (Pavan and Duckett, 2007). Noci et al. (2007) observed that proportions of all three fatty acids decline when grazing heifers were supplemented with concentrates enriched with flaxseed or soybean oils. Pouzo et al. (2015) observed an increase in stearic acid proportion but no effect on myristic and palmitic acid proportions when 0.125% LW of flaxseed were added to the corn grain supplemented to grazing steers; no effects were observed when flaxseed level was increased to

Table 1. Fatty acids (FA) composition (g/100 g of total FA) from the *longissimus* muscle from grazing steers supplemented with either corn oil plus soybean hulls (PO) or corn grain (PC) during 197 d as compared to no-supplemented grassing steers (PA) or concentrate finished steers (90 d, CONC)

	Dietary treatments[1]					
Fatty acids	CONC	PO	PC	PA	SEM	*P*-value
Total FA, g/100g LM	4.00^{a}	2.21^{b}	1.71^{b}	1.56^{b}	0.266	< 0.001
C12:0	0.02	0.04	0.01	0.02	0.012	0.54
C14:0	2.85^{a}	2.03^{b}	1.98^{b}	1.95^{b}	0.132	< 0.001
C14:1	0.74^{a}	0.47^{b}	0.38^{b}	0.35^{b}	0.063	< 0.001
C15:0	0.48^{a}	0.44^{a}	0.45^{a}	0.61^{b}	0.023	< 0.001
C16:0	26.60^{a}	22.15^{bc}	23.17^{b}	21.71^{c}	0.483	< 0.001
C16:1	3.63^{a}	2.31^{c}	2.74^{b}	2.67^{b}	0.109	< 0.001
C17:0	1.26^{a}	0.71^{c}	0.87^{b}	1.00^{b}	0.053	< 0.001
C18:0	13.29^{c}	18.12^{a}	16.21^{b}	16.02^{b}	0.447	< 0.001
C18:1 trans-9	nd^{b1}	0.38^{a}	nd^{b}	0.04^{b}	0.038	< 0.001
C18:1 trans-10	0.52^{a}	0.42^{a}	0.08^{b}	0.08^{b}	0.084	< 0.01
C18:1 trans-11	0.95^{d}	5.40^{a}	2.04^{c}	2.83^{b}	0.231	< 0.001
C18:1 cis-9	38.67^{a}	27.87^{c}	33.30^{b}	30.23^{c}	1.009	< 0.001
C18:1 cis-11	1.51^{a}	0.98^{c}	1.20^{b}	1.20^{b}	0.045	< 0.001
C18:2 cis-9, cis-12	2.77^{c}	6.95^{a}	4.59^{b}	4.08^{bc}	0.521	< 0.001
C18:3 cis-9, cis-12, cis-15	0.46^{d}	0.73^{c}	0.97^{b}	1.56^{a}	0.056	< 0.001
C20:4 n-6	0.77^{b}	1.93^{a}	1.94^{a}	2.14^{a}	0.221	< 0.001
C20:5 n-3	0.18^{c}	0.37^{bc}	0.58^{b}	1.11^{a}	0.084	< 0.001
C22:5 n-3	0.40^{c}	0.62^{c}	0.93^{b}	1.30^{a}	0.094	< 0.001
C22:6 n-3	0.05^{c}	0.08^{c}	0.13^{b}	0.19^{a}	0.017	< 0.001
Total CLA	0.43^{c}	1.23^{a}	0.70^{b}	1.05^{a}	0.064	< 0.001
CLA cis-9, trans-11	0.36^{d}	1.14^{a}	0.62^{c}	0.92^{b}	0.061	< 0.001
CLA cis-11, trans-13	0.03^{a}	< 0.01^{b}	0.02^{a}	0.03^{a}	0.003	< 0.001
CLA trans-10, cis-12	< 0.01^{b}	0.01^{a}	< 0.01^{b}	< 0.01^{b}	0.002	< 0.001
CLA cis, cis	0.03^{c}	0.08^{b}	0.06^{b}	0.09^{a}	0.005	< 0.001
CLA trans, trans	< 0.01	n.d.	n.d.	< 0.01	0.04	0.51
SFA	42.76^{a}	42.34^{a}	41.38^{ab}	39.69^{b}	0.778	0.047
MUFA	43.04^{a}	30.64^{c}	36.42^{b}	33.25^{c}	1.065	< 0.001
PUFA	4.63^{b}	10.66^{a}	9.15^{a}	10.38^{a}	0.928	< 0.001
Odd FA	1.74^{a}	1.15^{b}	1.33^{b}	1.61^{a}	0.070	< 0.001
Unidentified FA	4.43^{c}	6.79^{b}	7.70^{b}	9.87^{a}	0.740	< 0.001
n-6	3.54^{c}	8.78^{a}	6.53^{b}	6.22^{b}	0.728	< 0.001
n-3	1.08^{d}	1.79^{c}	2.61^{b}	4.16^{a}	0.240	< 0.001
n-6:n-3	3.27^{b}	4.95^{a}	2.49^{c}	1.49^{d}	0.151	< 0.001
PUFA:SFA	0.10^{b}	0.25^{a}	0.22^{a}	0.26^{a}	0.025	< 0.001

$^{a–d}$Within a row means without a common superscript letter differ ($P < 0.05$).

[1]n.d., not detected.

0.25% of LW. *Longissimus* muscle proportions of myristic and palmitic acid were also increased when Wright et al. (2015) supplemented grazing steers with 0.75% LW of corn grain or when French et al. (2003) increased concentrate supplementation (0, 2.5 and 5 kg fresh weight/head) to grazing steers receiving a low forage allowance and found no changes in SFA with supplementation. In contrast, when increasing corn grain supplementation level (0, 0.7 or 1% LW) to grazing cattle, Garcia et al. (2008) did not observe changes in LM myristic and palmitic acid proportions but a reduction in stearic acid proportion. Pouzo et al. (2015) did not observe differences in these three saturated fatty acids, nor in total SFA proportions when grazing steers were supplemented with 0.7% of LW.

As for the saturated fatty acids, total monounsaturated fatty acids (MUFA) and the individual proportions of myristoleic, palmitoleic, oleic acids were affected by dietary treatments ($P < 0.001$); all proportions were greatest with CONC. Among grazing treatments, total MUFA was greater for beef from PC than from PO and PA, which did not differ. Corn oil plus SBH supplementation reduced palmitoleic proportion as compared with PC and PA; whereas corn grain supplementation increased oleic acid proportion as compared with PO and PA. Duckett et

al. (2009) also observed greater proportions of total and individual MUFA with concentrate- than with pasture-finished steers. In addition, in 6 of the 7 studies reviewed by Daley et al. (2010), total MUFA were also greater in beef from concentrate than from grass-fed cattle. Total or individual MUFA proportions were not affected when Pavan and Duckett (2007) or Pouzo et al. (2015) increased the level of corn oil or whole-flaxseed being supplemented to grazing steers. Palmitoleic acid proportion was not affected when Noci et al. (2005a) supplemented grazing heifers with concentrates that contain flaxseed or sunflower oil, but sunflower oil supplementation reduced myristoleic acid proportion, and supplementation with either type of oil reduced oleic acid proportion. In agreement with the results of the present study, Garcia et al. (2008) and Wright et al. (2015) observed greater MUFA proportion when supplementing grazing steers with corn grain as compare to non-supplemented steers. These greater proportions were associated with greater proportion of oleic acid (Garcia et al., 2008) or trends toward greater proportions of palmitoleic and oleic acids (Wright et al., 2015) in beef from supplemented steers. In contrast, Pouzo et al. (2015) did not observe any change in total or individual MUFA when supplemented with 0.7% of corn grain to grazing steers throughout the last 70 d of finishing.

In agreement with the results reported here for the *longissimus* muscle fatty acid profile, we (Duckett et al., 2009) found that the relative expression of the enzyme fatty acid synthase in the subcutaneous fat was up-regulated by 9- and fivefold in concentrate finished and in grain supplemented steers, but no change was observed with oil supplementation. In addition, subcutaneous fat stearoyl CoA desaturase (SCD) mRNA expression relative to PA was increased by 7-, 18- and 46-fold in PO, PC and CONC, respectively (Duckett et al., 2009). Joseph et al. (2010) observed that the effect of oil supplementation on lipogenic enzyme gene expression is depended on the level of oil supplemented. As compere to non-supplemented grazing steers, supplementation with 0.075%LW of corn oil up-regulated gene expression of key lipogenic enzymes in subcutaneous fat; but increasing corn oil supplementation to 0.15%LW downregulated gene expression of lipogenic enzyme responsible for *de novo* fatty acid synthesis and desaturation.

Proportion of total and individual PUFA in the *longissimus* muscle were also affected by dietary treatments ($P < 0.001$). The proportion of total and individual PUFA were greater in the LM from any of the grazing treatments than in CONC. As suggested by Scollan et al. (2006), these differences between grazing treatments and CONC would be mainly attributed to the greater LM total fatty acid content in the latter. However, despite similar total FA content among grazing treatments proportion of individual PUFA were affected by supplementation and by type of supplement. Total n-6 PUFA and C18:2 n-6 proportions were greater in the LM from corn oil supplemented steers than in the LM from corn grain supplemented or from non-supplemented steers. The greater C18:2 n-6 proportions with PO are in agreement with the greater C18:2n-6 intake observed with corn oil supplementation than with the other 2 grazing treatments and with the results from Noci et al. (2005b) when supplemented grazing heifers with a concentrate containing sunflower oil. In a previous study, Pavan and Duckett (2007) did not observe an increase in C18:2 n-6 nor in total n-6 PUFA proportions when increasing corn oil supplementation up to 0.15% LW to steers grazing the same tall fescue pasture used in the present study. In agreement with the observation of Pouzo et al. (2015), differences in pasture fiber content between studies (Pavan et al., 2007; Pavan and Duckett, 2008) may have altered ruminal biohydrogenation and hence the effect of supplementation on LM fatty acid profile.

In contrast to n-6 proportions, total n-3 and all individual PUFA proportions, except C20:5 n-3, were greater in the LM form non-supplemented than in the LM from supplemented grazing steers, and in the LM form corn grain supplemented than in that form corn oil supplemented steers. Although a similar trend was observed for eicosapentanoic acid, its proportion with PO did not differ from that with CONC or PC. Differences in total and individual n-3 PUFA between grazing treatments could be the result of sum of small nonsignificant differences in daily linolenic acid intake. Reduction of n-3 fatty acid proportions in the LM from grazing cattle were also observed by Noci et al. (2005b) when supplemented with a concentrate containing sunflower oil or by French et al. (2003), Garcia et al. (2008), Wright et al. (2015) and Pouzo et al. (2015) when supplemented with corn grain. In contrast, as with n-6 PUFA, Pavan and Duckett (2007) did not observe any effect on n-3 PUFA with increasing corn oil supplementation level.

Polyunsaturated n-6: n-3 ratio was affected by dietary treatments ($P < 0.001$); it was lowest with non-supplemented grazing steers. As compare to non-supplemented grazing steers, corn grain supplementation increased the ratio by 67% and corn oil supplementation by 232%. Nonetheless, the ratio remained below the threshold of 4 recommended by the WHO to prevent cardiovascular diseases when corn grain was use as supplement but not when corn oil was supplemented. Finishing steers for 90 d on high-concentrate diet after being back-grounded on pasture with no-supplementation generated greater n-6:

n-3 ratios than when finished on pasture without supplementation or supplemented with corn grain, but lower than when supplemented with corn oil; being below the threshold of 4. As suggested by Scollan et al. (2006) and as grazing steers were on the same diet throughout their fattening period (weaning to slaughter), *longissimus* muscle n-6: n-3 ratio for grazing steers was highly associated with the ratio in the diet. Whereas the higher dietary n-6: n-3 ratio in the high concentrate diet used in CONC (last 90 d of the fattening period) may have been counterbalanced by a low ratio in the pasture during the backgrounding phase. Pordomingo et al. (2012) reported dietary backgrounding effects on n-6:n-3 ratio were still evident after 132 d of finishing on pasture. In their review, Daley et al. (2010) reported that *Longissimus* muscle n-6: n-3 ratio form grazing cattle varied from 1.44 to 3.72, whereas in concentrate-finished cattle it varied from 3.00 to 13.6. Lower ratios in concentrate-finished cattle could be obtained if, as in the present study, cattle are backgrounded on high-quality pastures without supplementation or if, as shown by Duckett et al. (1993), are finished on high-concentrate diets for short periods.

As expected, dietary treatments affected *trans*-11 vaccenic acid and CLA *cis*-9, *trans*-11 proportions ($P < 0.001$). In agreement with others (Realini et al., 2004; Duckett et al., 2009; Duckett et al., 2013) both the proportions of these 2 fatty acids were lower in the LM from concentrate finished cattle than in the LM from grazing treatments. Both fatty acids were also lower in the LM from steers supplemented with corn grain as compere to the LM from non-supplemented ones (Garcia et al., 2008; Pouzo et al., 2015; Wright et al., 2015). According to Duckett et al. (2009), this negative effect on *trans*-11 vaccenic acid and CLA *cis*-9, *trans*-11 proportions is the result of a reduced ruminal *trans*-11 vaccenic outflow when corn grain is fed as main component of the diet or as supplement for grazing cattle. In contrast, *trans*-11 vaccenic acid was 91% greater with PO than with PA and CLA *cis*-9, *trans*-11, 24% greater. The 3 times greater increase in *trans*-11 vaccenic acid than in CLA *cis*-9, *trans*-11 proportion in the LM with corn oil supplementation is in agreement with our previous observation (Duckett et al., 2009) that corn oil supplementation downregulates SCD gene expression in the subcutaneous fat of grazing as compared to non-supplemented grazing steers. Joseph et al. (2010) observed that the effect of lipid supplementation to grazing steers on gene expression of depends on level of lipid supplemented; SCD and other lipogenic enzymes gene expression were downregulated when steers were supplemented with 0.15% LW of corn oil, but were up-regulated with 0.075% LW as compared to no-supplemented steers.

Dietary treatment influenced ($P < 0.001$) total fatty acids, myristic, palmitic, *trans*-11 vaccenic acid and CLA *cis*-9, *trans*-11, and total SFA, MUFA, PUFA, n-6 and n-3 content per serving of *longissimus* muscle (85.5 g fresh tissue; Table 2). Daily intake of *trans*-11 vaccenic acid and CLA *cis*-9, *trans*-11 per serving can be increased by oil-supplementation of grazing steers, whereas similar intakes per serving can be obtained from beef of non-supplemented or corn-grain supplemented from grazing steers or even from beef of high-concentrated finished steers. However, a serving from beef of high-concentrated finished cattle contains twice as much total fatty acids than a serving from any of the grazing treatments and more than three times as much of 2 highly atherogenic saturated fatty acid (Ulbricht and Southgate, 1991). Total PUFA consumption would be greatest when cattle are supplemented with corn oil and lowest with either non-supplemented or corn grain supplemented grazing steers. The WHO recommends to increase dietary consumption of PUFA, but n-3 in particular (WHO, 2003). Beef has been suggested as an important dietary source of n-3 fatty acids in human diet, especially in countries with high levels of beef consumption (Howe et al., 2006). Furthermore, despite the low conversion rate of dietary linolenic acid to long-chain n-3 PUFA (Webb and O'Neill, 2008), replacing concentrate-finished beef by grass-finished beef had shown to increase plasma concentration of long-chain n-3 PUFA (McAfee et al., 2011). The different n-3 fatty acid content per serving of beef observed with the different dietary treatments suggests that consumer plasma concentration of long-chain n-3 PUFA could be greater when consumers eat beef from non-supplemented grazing cattle as compare to any of the other dietary treatments. Supplementing grazing cattle with corn oil would reduce n-3 PUFA consumption more than any other treatment, hence potentially lowering plasma long-chain n-3 PUFA content below that obtained with beef from concentrate-fed cattle.

On the other hand, it has been demonstrated that ground beef rich in oleic acid may reduce risk factors for cardiovascular disease (Adams et al., 2010; Gilmore et al., 2011; Gilmore et al., 2013). However, in those studies, even when ground beef palmitic acid content was similar between treatments, positive correlations were observed between consumer plasma palmitic acid concentration and risk factors for cardiovascular disease. Therefore, the potential health benefits of a greater consumption of oleic acid with a steak from CONC than with one from grazing treatments could be counterbalanced by a greater consumption of palmitic acid. It has to be mentioned that, in the present study, steaks from grazing steers had not only sim-

Table 2. Total and main fatty acids content per serving (mg/85.5-g serving) of *longissimus* muscle from grazing steers supplemented with either corn oil plus soybean hulls (PO) or corn grain (PC) during 197 d as compared to no-supplemented grassing steers (PA) or concentrate finished steers (90 d, CONC)

	Dietary treatments					
Fatty acid, mg per serving, broiled	CONC	PO	PC	PA	SEM	*P*-value
Total	4621[a]	2524[b]	1950[b]	1730[b]	294.7	< 0.001
C14:0	132[a]	52[b]	40[b]	34[b]	8.7	< 0.001
C16:0	1230[a]	564[b]	458[b]	381[b]	77.7	< 0.001
C18:1 *trans*-11	44[b]	138[a]	41[b]	49[b]	12.3	< 0.001
CLA *cis*-9, *trans*-11	17 [b]	29[a]	12[b]	16[b]	2.7	< 0.001
SFA	1982[a]	1077[b]	815[b]	698[b]	139.5	< 0.001
MUFA	1998[a]	799[b]	712[b]	588[b]	130.5	< 0.001
PUFA	209[b]	245[a]	171[c]	164[c]	7.2	< 0.001
n6	160[b]	203[a]	122[c]	98[d]	6.2	< 0.001
n3	49[b]	41[c]	49[b]	66[a]	1.9	< 0.001

[a–d]Within a row means without a common superscript letter differ ($P < 0.05$).

ilar or lower proportions of total SFA than did steaks from concentrate-finished steers, but also a greater stearic to palmitic acid ratio. According to Crupkin and Zambelli (2008), it is clear that stearic acid does not have the same detrimental effect on human health as do other saturated fatty acids, and some literature suggests that its impact on human health is, in many ways, similar to the impact of oleic and linolenic acids.

Tenderness is the main characteristic defining beef organoleptic quality. Different studies (Bowling et al., 1977; Hedrick et al., 1983; Williams and Bennett, 1995) had reported lower tenderness or shear force levels in beef from grazing than from concentrate finished cattle, though others found no differences (Realini et al., 2004; Duckett et al., 2007; Latimori et al., 2008; Duckett et al., 2013). Duckett et al. (2013) suggested that differences occur when cattle are slaughtered at similar weight or fatness due to age differences, but not when cattle are slaughter at similar ages. Nonetheless, Latimori et al. (2008) slaughtered cattle at similar end point, different ages, and did not observe differences and, in the current study, cattle were slaughtered at a similar age and differences were observed between treatments in initial ($P < 0.001$) or overall ($P < 0.001$) tenderness and in shear-force ($P = 0.046$; Table 3 and Table 4). Initial and overall tenderness scores were greater with CONC than with all three grazing treatments (PO, PC, and PA); no differences were observed for initial tenderness scores between grazing treatment, whereas overall tenderness scores were greater with PO than with PC, and intermediate with PA. Shear force was lower with CONC than with PA and PC, and intermediate with PO not differing from any of the other dietary treatments. Furthermore, dietary treatment differences were observed for the shear force coefficient of variation within each steak ($P = 0.014$); the coefficient of variation was lower with CONC and PO than with PA, and intermediate with PC not differing from any of the other dietary treatments.

Treatment differences in tenderness and shear-force could be explained by their differences in marbling score, total FA content or ultimate pH. Total FA content in steaks from concentrate-finished steers was above the threshold proposed by Savell and Cross (1988) to guarantee tenderness and overall palatability (3% of total fat); whereas in steaks from grazing finished steers was below it. The greater ultimate pH in the LM from grazing steers than from concentrate finished ones (5.74 ± 0.10 vs. 5.47 ± 0.08) would also contribute to their greater toughness by reducing postmortem protease activity (Watanabe et al., 1996a; Watanabe et al., 1996b). However, if this was the case, the lack of dietary treatment by aging period interaction observed on LM shear force and tenderness suggests that the effect of ultimate pH on protease activity took place within the first 3 d after harvest.

The other factor that may have influence meat shear-force and tenderness between dietary treatments in the current study could have been their differences in rates of muscle pH and temperature decline during the onset of rigor mortis (Thompson, 2002; Savell et al., 2005). No interaction ($P = 0.795$) between dietary treatments and time postmortem, but main effects were observed for muscle pH (dietary treatment, $P = 0.011$) and time postmortem ($P = 0.028$; Fig. 2). Muscle pH was greater in all three grazing treatments (5.77 ± 0.09) than in CONC (5.47 ± 0.07) and declined from 6 to 12 h postmortem, but not from 12 to 24 h postmortem. In contrast, main effects interaction was observed for muscle temperature ($P < 0.001$); muscle temperature was always higher in CONC than in any of the grazing treatments; whereas

Table 3. Shear force (kg and coefficient of variation with each steak) of *longissimus* muscle from grazing steers supplemented with either corn oil plus soybean hulls (PO) or corn grain (PC) during 197 d as compared to no-supplemented grassing steers (PA) or concentrate finished steers (90 d, CONC)

	Dietary treatments					*P*-value		
Shear force	CONC	PO	PC	PA	*SEM*	Diet	AP	Treat × AP
Kg	4.21[b]	4.87[ab]	6.05[a]	5.63[a]	0.46	0.046	< 0.001	0.605
CV, %	22.3[a]	23.8[a]	26.8[ab]	32.6[b]	2.15	0.014	0.115	0.758

[a,b]LSmeans in the same row followed by different superscripts differ at $P < 0.05$.

muscle temperature was lower in PA than in PO and tended ($P < 0.07$) to be lower than in PC at 6 and 12 h. Rapid muscle temperature decline would increase muscle contraction; Thompson (2002) suggested that severe cold shortening would occur if at the onset of rigor (pH = 6), muscle temperature is under 12°C. In the current study, pH differences were observed between dietary treatments when the muscle reached 12°C ($P = 0.016$); pH at 12°C was greater in PA (5.94 ± 0.11) and PC (5.76 ± 0.09) than in CONC (5.46 ± 0.08); pH at 12°C in PO was similar to PA and PC and tended ($P = 0.054$) to be greater than in CONC. Therefore, differences in muscle shortening associated with different relative rate of pH and temperature decline may explain, to some extent, observed differences in shear-force and tenderness between dietary treatments. Faster rates of temperature decline are in agreement with smaller rib eye areas and thinner dorsal back fat reported by Pavan and Duckett (2008). Tatum et al. (1982) suggested that to maximize tenderness dorsal back fat thickness should be greater than 0.70 cm; back fat thickness reported by Pavan and Duckett (2008) were 0.26, 0.41, 0.53, and 1.23 for PA, PC, PO, and CONC, respectively. In addition, the greater REA and HCW reported by Pavan and Duckett (2008) for CONC than for the pasture-finished treatment could have also contributed to the slower chilling rate observed in CONC. Bowling et al. (1977) observed that the greater shear-force values in pasture- than in concentrate-finished cattle was associated with shorter sarcomeres (1.70 and 2.07 μm, respectively) and less subcutaneous fat thickness (4,1 and 8,4 mm). They also observed that when half-carcass from pasture-finished cattle was chilled at higher temperatures than at the conventional chilling temperature (0°C), sarcomere length increased (1.92 μm) and shear-force decreased.

Dietary treatments affected *Longissimus* muscle L*- ($P < 0.001$) and b* ($P < 0.001$) values, but not a*-value ($P = 0.094$; Table 5). In agreement with the observed differences in ultimate pH, *longissimus* muscle color was ligher (greater L*) with CONC than with any of the grazing treatments and was lighter with the supplemented treatments than with PA. The association of brighter color in the LM from grain-finished cattle with lower ultimate pH values than in the LM from grass-fed beef had also been reported by others (Realini et al., 2004; Duckett et al., 2007; Duckett et al., 2013). Bidner et al. (1981) observed similar color differences between pasture-fed cattle and cattle finished on feedlot, but the difference were not due to muscle pH; color difference was attributed to the older age of pasture-fed cattle that were slaughtered at similar weight as cattle finished on feedlot. Corn grain supplementation to grazing steers did not generate LM color differences when supplemented during the last 100 d of fattening at 0.75% LW (Wright et al., 2015), neither when supplemented at 0.7 or 1% LW through the fattening period (Latimori et al., 2008). Nonetheless, meat

Table 4. Sensory panel scores for juiciness, initial and overall tenderness, beef flavor and off-flavors of *longissimus* muscle from grazing steers supplemented with either corn oil plus soybean hulls (PO) or corn grain (PC) during 197 d as compared to non-supplemented grass-fed steers (PA) or concentrate-finished steers (90 d, CONC)

	Dietary treatments					
Panel rating[1]	CONC	PO	PC	PA	SEM	*P*-value
Juiciness	4.4	4.1	4.1	4.6	0.18	0.130
Initial tenderness	5.9[a]	4.9[b]	4.7[b]	4.8[b]	0.23	< 0.001
Overall tenderness	6.1[a]	5.0[b]	4.4[c]	4.8[bc]	0.32	< 0.001
Beef flavor	4.7[a]	4.0[b]	3.9[b]	4.2[b]	0.21	< 0.001
Off flavor	1.4[c]	2.0[bc]	2.1[b]	2.7[a]	0.29	< 0.001

[a–c]LSmeans in the same row followed by different superscripts differ at $P < 0.05$.

[1]For juiciness, 1 = extremely dry and 8 = extremely juicy; for initial and overall tenderness, 1 = extremely tought and 8 = extremely tender; for beef flavor, 1 = extremely bland and 8 extremely intense; for off flavor, 0 = none and 8 extremely intense.

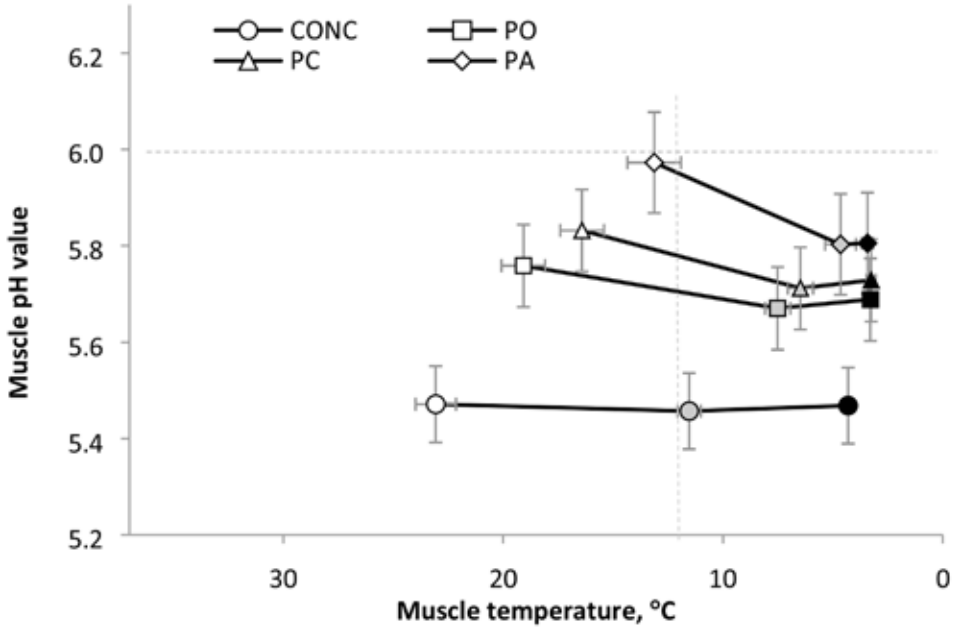

Figure 2. Post-mortem *longissimus* muscle temperature and pH decline from grazing steers supplemented with either corn oil plus soybean hulls (squares) or corn grain (triangles) during 197 d as compared to no-supplemented grassing steers (diamonds) or concentrate finished steers (circles). Symbols of similar color across lines represent similar sampling time; white, 6 h postmortem, gray, 12 h postmortem, black, 24 h post-mortem. Vertical error lines represent muscle pH standard errors and horizontal error lines, muscle temperature standar errors.

was brighter when supplemented at 1% LW throughout the fattening period (Bidner et al., 1981). *Longissimus* muscle b* values were highest with CONC, greater with PO than with PA, being PC intermediate among the last 2 and non differing from any of them. It has been suggested that LM differences in b* value may indicate differences in the relative rate of pH and temperature decline (Wulf et al., 1997) as observed in the present study.

Dietary treatments also influence subcutaneous fat b* (yellowness) value ($P < 0.001$); it was greater with PO and PC than with CONC and PA that were similar among them. Wright et al. (2015) also observed yellower subcutaneous fat in supplemented than in non-supplemented steers; which was attributed to the greater b-carontene content in the LM of supplemented steers. In contrast to what was observed in the present study, several studies observed yellower fat carcasses from pasture-finished than from grain-finished steers (Duckett et al., 2013).

Beef flavor ($P < 0.001$) and off-flavor ($P < 0.001$) were also affected by dietary treatments. As observed by others (Duckett et al., 2007; Duckett et al., 2013), beef flavor scores were lower and off-flavor greater in steaks from non-supplemented grazing steers than in those from concentrate-finished steers. Energy supplementation did not improve (increase) beef flavor as compare to grazing steers, but reduced beef off-flavors. Wright et al. (2015) observed that supplementation of grazing steers with 0.7% LW of corn grain affected dif-

Table 5. *Longissimus* muscle (LM) and subcutaneous (s.c.) fat color from grazing steers supplemented with either corn oil plus soybean hulls (PO) or corn grain (PC) during 197 d as compared to non-supplemented grass-fed steers (PA) or concentrate-finished steers (90 d, CONC)

	Dietary treatments					
Traits	CONC	PO	PC	PA	SEM	*P*-value
LM color						
L	41.1[a]	37.8[b]	37.4[b]	35.9[c]	0.49	< 0.001
a*	24.9	25.0	24.1	23.8	0.42	0.094
b*	10.3[a]	9.4[b]	8.6[bc]	8.3[c]	0.31	< 0.001
s.c. fat color						
L	74.2[c]	77.3[a]	75.7[b]	74.2[c]	0.49	< 0.001
a*	11.1[a]	6.9[b]	6.6[b]	6.5[b]	0.47	< 0.001
b*	16.0[b]	19.3[a]	19.8[a]	17.0[b]	0.64	< 0.001

[a–c]LSmeans in the same row followed by different superscripts differ at $P < 0.05$.

ferent flavor descriptors, reduced leather flavor descriptor, tended to reduce bitter and to increase umami flavor descriptors. They also observed that the effect of corn grain supplementation on beef flavor score was dependent on type of pasture grazed and increased when grazing grasses compared to grazing legumes.

Principal component analysis classified the finishing systems into three groups based on fatty acid composition. Feeding CONC was characterized by having the greatest proportions of fatty acids from synthesis *de novo* (C14:0 and C16:0) and endogenous desaturation fatty acids (C16:1 *cis*-9, C18:1 *cis*-9). Supplementation with corn oil (PO) had there greatest proportions of fatty acids derived from complete or partial ruminal biohydrogenation of dietary linoleic acid contain in the corn oil (C18:0, C18:1 *trans*-11 and CLA *cis*-9, *trans*-11). The third group, containing PA and PC, was characterized by having a lower n-6: n-3 ratio as compare to the other 2 groups. The scoring plot suggests that overall fatty acid profile from corn grain supplemented steers is closer to the fatty acid profile of non-supplemented grazing steers than that from steers finished on a high-concentrate diet. Finishing systems altered fat deposition, which impacted chilling rate, muscle color and palatability. When finishing on pasture, supplementation with corn oil rather than corn grain slight improved muscle color and palatability.

According to our results to provide highly palatable and healthy beef to consumers, the fatty acid profile needs to be improved for concentrate-finished beef and palatability characteristics for pasture-fed beef. Oil supplementation improved palatability of grazing cattle, increased increased C18:1 *trans*-11 and CLA *cis*-9, *trans*-11 content, but reduced n-3 content. The effects of corn grain supplementation to grazing cattle were minor either on palatability and fatty acid profile.

Literature Cited

Adams, T. H., R. L. Walzem, D. R. Smith, S. Tseng, and S. B. Smith. 2010. Hamburger high in total, saturated and trans-fatty acids decreases HDL cholesterol and LDL particle diameter, and increases TAG, in mildly hypercholesterolaemic men. Br. J. Nutr. 103:91–98. doi:10.1017/S0007114509991516

American Meat Science Association. 2016. Research Guidelines for Cookery, Sensory Evaluation, and Instrumental Tenderness Measurements of Meat. 105.

Bidner, T. D., A. R. Schupp, R. E. Montgomery, and J. C. Carpenter. 1981. Acceptability of Beef Finished on All-Forage, Forage-Plus-Grain or High Energy Diets4. J. Anim. Sci. 53. doi:10.2527/jas1981.5351181x

Bowling, R. A., G. C. Smith, Z. L. Carpenter, T. R. Dutson, and W. M. Oliver. 1977. Comparison of Forage-Finished and Grain-Finished Beef Carcasses. J. Anim. Sci. 45:209–215. doi:10.2527/jas1977.452209x

Crupkin, M., and A. Zambelli. 2008. Response from the Authors. Compr. Rev. Food Sci. Food Saf. 7:297–298. doi:10.1111/j.1541-4337.2008.00062_2.x

Daley, C., A. Abbott, P. Doyle, G. Nader, and S. Larson. 2010. A review of fatty acid profiles and antioxidant content in grass-fed and grain-fed beef. Nutr. J. 9:10. doi:10.1186/1475-2891-9-10

Destefanis, G., M. T. Barge, A. Brugiapaglia, and S. Tassone. 2000. The use of principal component analysis (PCA) to characterize beef. Meat Sci. 56:255–259. doi:10.1016/S0309-1740(00)00050-4

Duckett, S. K., J. P. S. Neel, R. M. Lewis, J. P. Fontenot, and W. M. Clapham. 2013. Effects of forage species or concentrate finishing on animal performance, carcass and meat quality. J. Anim. Sci. 91:1454–1467. doi:10.2527/jas.2012-5914

Duckett, S. K., J. P. S. Neel, R. N. Sonon, Jr., J. P. Fontenot, W. M. Clapham, and G. Scaglia. 2007. Effects of winter stocker growth rate and finishing system on: II. Ninth tenth eleventh-rib composition, muscle color, and palatability. J. Anim. Sci. 85:2691–2698. doi:10.2527/jas.2006-734

Duckett, S. K., S. L. Pratt, and E. Pavan. 2009. Corn oil or corn grain supplementation to steers grazing endophyte-free tall fescue. II. Effects on subcutaneous fatty acid content and lipogenic gene expression. J. Anim. Sci. 87:1120–1128. doi:10.2527/jas.2008-1420

Duckett, S. K., D. G. Wagner, L. D. Yates, H. G. Dolezal, and S. G. May. 1993. Effects of time on feed on beef nutrient composition. J. Anim. Sci. 71:2079–2088. doi:10.2527/1993.7182079x

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

French, P., E. G. O'Riordan, F. J. Monahan, P. J. Caffery, and A. P. Moloney. 2003. Fatty acid composition of intra-muscular tricylglycerols of steers fed autumn grass and concentrates. Livest. Prod. Sci. 81:307–317. doi:10.1016/S0301-6226(02)00253-1

Garcia, P. T., N. A. Pensel, A. M. Sancho, N. J. Latimori, A. M. Kloster, M. A. Amigone, and J. J. Casal. 2008. Beef lipids in relation to animal breed and nutrition in Argentina. Meat Sci. 79:500–508. doi:10.1016/j.meatsci.2007.10.019

Gilmore, L. A., S. F. Crouse, A. Carbuhn, J. Klooster, J. A. E. Calles, T. Meade, and S. B. Smith. 2013. Exercise attenuates the increase in plasma monounsaturated fatty acids and high-density lipoprotein cholesterol but not high-density lipoprotein 2b cholesterol caused by high-oleic ground beef in women. Nutr. Res. 33:1003–1011. doi:10.1016/j.nutres.2013.09.003

Gilmore, L. A., R. L. Walzem, S. F. Crouse, D. R. Smith, T. H. Adams, V. Vaidyanathan, X. Cao, and S. B. Smith. 2011. Consumption of High-Oleic Acid Ground Beef Increases HDL-Cholesterol Concentration but Both High- and Low-Oleic Acid Ground Beef Decrease HDL Particle Diameter in Normocholesterolemic Men1,2. J. Nutr. 141:1188–1194. doi:10.3945/jn.110.136085

Hedrick, H. B., J. A. Paterson, A. G. Matches, J. D. Thomas, R. E. Morrow, W. G. Stringer, and R. J. Lipsey. 1983. Carcass and Palatability Characteristics of Beef Produced on Pasture, Corn Silage and Corn Grain1,2. J. Anim. Sci. 57. doi:10.2527/jas1983.574791x

Howe, P., B. Meyer, S. Record, and K. Baghurst. 2006. Dietary intake of long-chain omega-3 polyunsaturated fatty acids: Contribution of meat sources. Nutrition 22:47–53. doi:10.1016/j.nut.2005.05.009

Joseph, S. J., S. L. Pratt, E. Pavan, R. Rekaya, and S. K. Duckett. 2010. Omega-6 fat supplementation alters lipogenic gene expression in bovine subcutaneous adipose tissue. Gene Regul. Syst. Bio. 2010:91–101.

Latimori, N. J., A. M. Kloster, P. T. García, F. J. Carduza, G. Grigioni, and N. A. Pensel. 2008. Diet and genotype effects on the quality index of beef produced in the Argentine Pampeana region. Meat Sci. 79:463–469. doi:10.1016/j.meatsci.2007.10.008

McAfee, A. J., E. M. McSorley, G. J. Cuskelly, A. M. Fearon, B. W. Moss, J. A. M. Beattie, J. M. W. Wallace, M. P. Bonham, and J. J. Strain. 2011. Red meat from animals offered grass diets increases plasma and patelet n-3 PUFA in healthy consumers. Br. J. Nutr. 105:80–89. doi:10.1017/S0007114510003090

Noci, F., P. French, F. J. Monahan, and A. P. Moloney. 2007. The fatty acid composition of muscle fat and subcutaneous adipose tissue of grazing heifers supplemented with plant oil-enriched concentrates. J. Anim. Sci. 85:1062–1073. doi:10.2527/jas.2006-105

Noci, F., F. J. Monahan, P. French, and A. P. Moloney. 2005a. The fatty acid composition of muscle fat and subcutaneous adipose tissue of pasture-fed beef heifers: Influence of the duration of grazing. J. Anim. Sci. 83:1167–1178. doi:10.2527/2005.8351167x

Noci, F., P. O'Kiely, F.J. Monahan, C. Stanton, and A.P. Moloney. 2005b. Conjugated linoleic acid concentration in M. Longissimus dorsi from heifers offered sunflower oil-based concentrates and conserved forages. Meat Sci. 69:509–518. doi:10.1016/j.meatsci.2004.09.006

Park, P., and R. E. Goins. 1994. In: situ preparation of FAME for analysis of fatty acid composition in food. J. Food Sci. 59:1262–1266. doi:10.1111/j.1365-2621.1994.tb14691.x

Pavan, E., and S. K. Duckett. 2007. Corn oil supplementation to steers grazing endophyte-free tall fescue. II. Effects on longissimus muscle and subcutaneous adipose fatty acid composition and stearoyl-CoA desaturase activity and expression. J. Anim. Sci. 85:1731–1740. doi:10.2527/jas.2006-732

Pavan, E., and S. K. Duckett. 2008. Corn oil or corn grain supplementation to steers grazing endophyte-free tall fescue. I. Effects on in vivo digestibility, performance, and carcass quality. J. Anim. Sci. 86:3215–3223. doi:10.2527/jas.2007-0703

Pavan, E., S. K. Duckett, and J. G. Andrae. 2007. Corn oil supplementation to steers grazing endophyte-free tall fescue. I. Effects on in vivo digestibility, performance, and carcass traits. J. Anim. Sci. 85:1330–1339. doi:10.2527/jas.2006-623

Pordomingo, A. J., T. P. García, and G. Volpi Lagreca. 2012. Effect of feeding treatment during the backgrounding phase of beef production from pasture on: II. Longissimus muscle proximate composition, cholesterol and fatty acids. Meat Sci. 90:947–955. doi:10.1016/j.meatsci.2011.11.038

Pouzo, L., N. Fanego, F. J. Santini, A. Descalzo, and E. Pavan. 2015. Animal performance, carcass characteristics and beef fatty acid profile of grazing steers supplemented with corn grain and increasing amounts of flaxseed at two animal weights during finishing. Livest. Sci. 178. doi:10.1016/j.livsci.2015.05.034

Realini, C. E., S. K. Duckett, G. W. Brito, M. Dalla Rizza, and D. De Mattos. 2004. Effect of pasture vs. concentrate feeding with or without antioxidants on carcass characteristics, fatty acid composition, and quality of Uruguayan beef. Meat Sci. 66:567–577. doi:10.1016/S0309-1740(03)00160-8

Savell, J. W., and H. R. Cross. 1988. The role of fat in the palatability of beef, pork, and lamb. In: N. R. C. Committee on Technological Options to Improve the Nutritional Attributes of Animal Products, editor. Designing Foods: Animal Product Options in the Marketplace. National Academies Press, Washington, DC. p. 345–355.

Savell, J. W., S. L. Mueller, and B. E. Baird. 2005. The chilling of carcasses. Meat Sci. 70:449–459. doi:10.1016/j.meatsci.2004.06.027

Scollan, N., J.-F. Hocquette, K. Nuernberg, D. Dannenberger, I. Richardson, and A. Moloney. 2006. Innovations in beef production systems that enhance the nutritional and health value of beef lipids and their relationship with meat quality. Meat Sci. 74:17–33. doi:10.1016/j.meatsci.2006.05.002

Tatum, J. D., G. C. Smith, and Z. L. Carpenter. 1982. Interrelationships between marbling, subcutaneous fat thickness and cooked beef palatability. J. Anim. Sci. 54:777–784. doi:10.2527/jas1982.544777x

Thompson, J. 2002. Managing meat tenderness. Meat Sci. 62:295–308. doi:10.1016/S0309-1740(02)00126-2

Ulbricht, T. L. V., and D. A. T. Southgate. 1991. Coronary heart disease: Seven dietary factors. Lancet 338:985–992. doi:10.1016/0140-6736(91)91846-M

Watanabe, A., C. C. Daly, and C. E. Devine. 1996a. The effects of the ultimate pH of meat on tenderness changes during ageing. Meat Sci. 42:67–78. doi:10.1016/0309-1740(95)00012-7

Watanabe, A., C. Devineb, A. Watanabe, and C. Devine. 1996b. Effect of meat ultimate pH on rate of titin and nebulin degradation. Meat Sci. 42:407–413. doi:10.1016/0309-1740(95)00050-X

Webb, E. C., and H. A. O'Neill. 2008. The animal fat paradox and meat quality. Meat Sci. 80:28–36. doi:10.1016/j.meatsci.2008.05.029

WHO. 2003. Diet, nutrition and the prevention of chronic diseases. (R. of a joint W. expert consultation, editor.). WHO technical report series, Geneva.

Williams, C. B., and G. L. Bennett. 1995. Application of a computer model to predict optimum slaughter end points for different biological types of feeder cattle. J. Anim. Sci. 73:2903–2915. doi:10.2527/1995.73102903x

Wright, A. M., J. G. Andrae, C. F. Rosso, M. C. Miller, E. Pavan, W. Bridges, and S. K. Duckett. 2015. Effect of forage type with or without corn supplementation on animal performance, beef fatty acid composition, and palatability. J. Anim. Sci. 93. doi:10.2527/jas.2015-8939

Wulf, D. M., S. F. O. Connor, J. D. Tatum, and G. C. Smith. 1997. Using objective measures of muscle color to predict beef longissimus tenderness. J. Anim. Sci. 75:684–692. doi:10.2527/1997.753684x