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Fattening performance, metabolic indicators, and muscle composition of bulls fed fiber-rich versus starch-plus-lipid-rich concentrate diets¹

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ABSTRACT: The aim of this study was to compare the responses in fattening performance and meat composition for high-concentrate diets rich in either starch and lipids (especially omega-3 fatty acids) or fibrous by-products. A total of 140 Charolais bulls (initially 319 ± 27 kg BW) were allocated to 3 high-concentrate diets and were fattened for up to 18 mo. The diet treatments included concentrate mixtures rich in either fiber (FR; $n = 56$) or starch plus linseed (diets SL and SLR; $n = 56$ and $n = 28$, respectively) and barley straw. The concentrate mix was offered ad libitum in SL and FR diets but was kept isoenergetic to the FR diet in the SLR diet. Bulls were weighed every 15 d. Feed intake was measured daily. Carcass composition was assessed for all animals slaughtered at 699 ± 65 kg BW. Meat nutritional quality traits (e.g., fat content and fatty acid composition focusing on $n-6$ and $n-3$ polyunsaturated fatty acids) were measured on the longissimus thoracis, rectus abdominis, and semitendinosus muscles.

Metabolic enzyme activity (phosphofructokinase, lactate dehydrogenase, and cytochrome-c oxidase) was measured on these muscles and on liver. The SL diet bulls had greater fattening performance, BW gain ($P = 0.006$), and efficiency for growth ($P = 0.025$) at an energy intake similar to that of FR diet bulls. They also had heavier carcasses with a greater proportion of fat. However, liver samples showed no difference in specific metabolic activity. Compared to bulls fed the SL diet, bulls fed SLR consumed 15% less energy and had lower BW gain ($P < 0.001$) but were slightly more efficient for growth ($P = 0.010$). They had lower carcass weight but a greater muscle-to-fat ratio. Compared to bulls fed the FR diet, SLR bulls had lower than planned NE_g intake and lower BW gain but did not have differences in body composition. Compared to the FR diet, the SL diet led to a greater omega-3 fatty acid content because of a greater supply of dietary linoleic acid, especially in lean muscle.

Key words: bull fattening, carcass composition, energy, fatty acids, metabolism

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INTRODUCTION

Bulls are often fattened using starch-rich diets to yield high BW gain (BWG). However, cereal-fed ruminants are in competition with humans for use of feed resources, and high intakes of starch-rich diets can trigger ruminal acidosis. An alternative strategy may be to feed fiber-rich diets, which give comparable performance if intake is high enough to compensate for the lower energy value, as argued by Bradford and Mullins (2012) for dairy cattle. Alternatively, lipids present the greatest energy value among all feed ingredients and may

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also help to limit acidosis. Several trials have studied the effect of concentrate type on fattening performance, but very few analyzed this effect while dissociating the impact of energy intake from the type of energy source (Mueller et al., 2011). Type of concentrate energy may modify dietary digestive and metabolic efficiency as well as absorbed nutrient profile. As a consequence, type of concentrate may lead to significant differences in performance, muscle metabolism, and carcass composition (Hocquette et al., 2007). Consumers often see beef negatively as high in fats rich in SFA and *trans*-MUFA, which are considered risk factors for human health (Riediger et al., 2009). A moderate incorporation of linseed in the diet can increase the content of beneficial *n*-3 PUFA and reduce SFA in beef (Doreau et al., 2011).

The objectives of this study were 1) to determine the fattening performance and carcass responses of bulls fed high-concentrate diets rich either in a mixture of starch plus linseed or in fibrous by-products while separating the effects of the source and level of energy intake, 2) to relate differences in performance to metabolic activities measured in the liver and 2 muscles at slaughter, and 3) to study the effects of including feeds rich in omega-3 fatty acids (FA) on FA composition in 3 muscles.

MATERIALS AND METHODS

Animals, Experimental Design, and Dietary Treatments

In total, 140 Charolais bulls were used from weaning in a fattening trial repeated over 2 successive years, with 70 bulls of the same genetic origin in each trial. The experiment took place at the INRA experimental farm in Bourges, France. At weaning, the animals averaged 239 ± 9 d old and weighed 319 ± 27 kg. They were assigned to 10 groups of 7 animals of similar initial average BW each year. Each group was housed in a separate pen. Pens were contiguous in the same shed (7 m² per bull) and were bedded with barley straw. Three diets composed of 81% to 87% concentrate were compared: **FR** (based on a fiber-rich concentrate, offered ad libitum), **SL** (based on a starch- and lipid-rich concentrate, offered ad libitum), and **SLR** (based on the same concentrate as SL but offered in restricted amounts to match the NE_g intake [NE_{g,I}] of the FR group). The number of pens receiving the FR, SL, and SLR diets was 4, 4, and 2 each year, respectively. After 3 wk of adaptation to experimental treatments and progressive achievement of ad libitum feeding for FR and SL diets, bulls were fattened for a minimum of 228 d and were slaughtered at the same average age of 17 to 18 mo, as usually done for this type of animal. Experimental procedures were conducted in ac-

Table 1. Ingredient, measured chemical composition, and tabulated energy content of the experimental diets¹

Item	Diet ²		
	FR	SL ³	SLR ³
Straw-to-concentrate ratio (DM basis)	12:88	13:87	18:82
Chemical composition, g/kg DM			
OM	806	828	829
NDF	406	249	269
ADF	227	140	154
Starch	70	297	282
Crude protein	145	179	171
Ether extract	25	41	39
GE, MJ/kg DM	18.9	19.7	19.6
NE, ⁴ MJ/kg DM	6.05	7.32	7.04

¹FR: diet composed of 88% concentrate rich in fiber and 12% straw, SL: diet composed of 87% concentrate rich in starch and lipids and 13% straw, SLR: diet composed of 83% concentrate rich in starch and lipids and 17% straw.

²Ingredient composition of the concentrate (g/kg DM): dehydrated alfalfa, 224; wheat bran, 219; cereal middlings, 184; dehydrated beet pulp, 212; rapeseed meal, 35; barley, 25; palm kernel meal, 40; molasses, 30; mineral-vitamin premix, 8; magnesium oxide, 10; dicalcium phosphate, 6; sodium chloride, 6.

³Ingredient composition of the concentrate (g/kg DM): maize, 280; barley, 98; oats, 86; maize bran, 30; extruded mixture (50% linseed, 30% wheat bran, 20% sunflower meal), 120; soybean meal, 20; dehydrated beet pulp, 60; rapeseed meal, 214; molasses, 70; urea, 4; mineral-vitamin premix, 5; calcium carbonate, 10; sodium bicarbonate, 3.

⁴Calculated from feed tables (INRA, 2007).

cordance with French Ministry of Agriculture guidelines on animal welfare and use for experimental purposes (http://www2.vet-lyon.fr/ens/expa/acc_regl.html).

The FR diet concentrate consisted mainly of cereal by-products, dehydrated alfalfa, and dehydrated beet pulp. The SL and SLR diet concentrate consisted of cereals and an extruded mixture containing 500 g/kg linseed (Valorex, Combourtillé, France) to achieve a theoretical level of 12 g of omega-3 FA from linseed per kilogram of DM of concentrate. In all 3 dietary treatments, bulls were offered barley straw ad libitum in a rack in each pen. This ad libitum distribution was expected to result in a greater proportion of straw in the SLR diet because of the feed restriction. Diet ingredients and chemical composition are reported in Table 1. Net energy for gain, estimated from diet composition according to INRA (2007) feed tables, was 6.05, 7.32, and 7.04 MJ/kg DM for the FR, SL, and SLR diets. Concentrates had the same ratio of NE_g to MP expressed in INRA (2007) units, equal to 16 g MP/MJ NE_g. Diets were formulated according to recommendations (INRA, 2007) to meet NE_g and MP requirements needed for maintenance and theoretical BW gain (1,500 g/d for FR and 1,800 g/d for SL). The theoretical BWG for the FR diet corresponds to previously observed gain with the same diet distributed ad libitum to Charolais bulls. It was assumed that the SL diet distributed ad libitum would be consumed at similar DMI as the FR diet, leading to greater expected gains.

Anion-cation balance was 134 and 119 meq/kg DM for FR and SL concentrates, respectively. Bulls fed the SLR diet were offered restricted amounts of concentrate mixture to provide the same average NE and MP per unit metabolic BW ($BW^{0.75}$) as those of FR diet animals for similar theoretical BWG. The amount of concentrate distributed to the SLR group was thus readjusted every 2 wk on the basis of the average NE intake per kilogram of BW of the FR group over the preceding 2 wk. A commercial mineral-vitamin premix was added to the concentrates at a level of 8 and 5 g/kg concentrate DM for FR and SL diets, respectively. Both concentrates were produced as pellets after the ingredients were ground (Jacques Coeur, Joigny, France). Concentrates were distributed once daily at 0800 h using an automatic feeding system (Calan system, Draffhandel Decuyper, Brussels, Belgium). Allowances were adjusted every 2 d to ensure 10% refusals in the ad libitum-fed groups (FR and SL). Fresh water was available at all times in each pen.

Measurements and Samplings during Fattening and at Slaughter

Each bull was equipped with an electronic transponder (Dairy gate, EFEI, Villeroy, France) around its neck that opened its specific feeder, and individual concentrate intake was recorded by measuring offered amounts every day and refusals every 2 d. Straw intake was measured for each pen by weighing each bale. Individual straw intake was calculated from the average intake for the pen, assuming that bedding straw intake was negligible. Each year, 3 feed samples were composed from 8 weekly subsamples taken over 2-mo periods for chemical analyses, that is, a total of 6 samples for each feed. Feeds were ashed at 550°C for 6 h for OM determination: nitrogen was determined by the Kjeldahl procedure (AOAC, 1990); NDF and ADF were determined according to Van Soest et al. (1991); starch was determined by spectrophotometry after enzymatic analysis (Faisant et al., 1995); GE was measured by isoperibolic calorimetry (C200 model, IKA, Staufen, Germany), ether extract (EE) was measured using petroleum extract (AOAC, 1990). Body weight was determined every 14 d and at fixed hours during the whole fattening period.

At the end of fattening, bulls were transported by truck to INRA's experimental slaughterhouse 200 km away (Clermont-Ferrand, France). On arrival at about 1500 h, the bulls were housed in a straw-bedded lairage pen and were offered their usual diet with water at disposal. Feed was removed at 2000 h for an overnight fast. Bulls were slaughtered at the same average age under standard conditions in the same experimental slaughterhouse. Carcasses were processed by removal of the head, tail, feet, and abdominal and thoracic viscera. Hot

carcass, internal fat (i.e., peritoneal, omental, mesenteric, and kidney fat), and splanchnic organ weights were recorded. Carcasses were chilled and stored at 4°C until 24 h postmortem. The sixth rib was excised and dissected to estimate carcass weights of bone, muscle, and fat (in kg) according to the equations proposed by Robelin and Geay (1975) for Charolais bulls.

Preparation of Tissue Samples

Liver samples (~50 g) were taken 35 to 40 min postmortem, cut into small pieces (5 to 10 g), and frozen in liquid nitrogen. Samples from rectus abdominis (RA), longissimus thoracis (LT), and semitendinosus (ST) muscles (120 to 150 g) were taken within 30 min postmortem, cut into small pieces (5 to 10 g), and frozen in liquid nitrogen for measurement of enzyme activities. Samples of the same muscles were taken 24 h postmortem for muscle lipid and FA analysis. All samples were ground in liquid nitrogen in a M20 mill (IKA-Werke, Staufen, Germany) to produce a fine homogeneous powder, then stored at -80°C for lipid and FA analysis.

Metabolic Enzyme Activity

Metabolic enzyme activities characterizing glycolytic (phosphofructokinase [PFK, EC 2.7.1.11] and lactate dehydrogenase [LDH, EC 1.1.1.27]) or oxidative (cytochrome c oxidase [COX, EC 1.9.3.1]) metabolism were determined spectrophotometrically on liver and muscle samples from only FR and SL bulls, as described by Piot et al. (1998) and Jurie et al. (2006). Tissue protein content was determined spectrophotometrically with BSA as the standard according to Bradford (1976). All enzyme activities were measured in duplicate at 25°C and are expressed in micromoles of molecules converted per minute and per gram of wet muscle or per gram of tissue protein.

Muscle Lipid and Fatty Acid Analysis

Muscle DM was assayed gravimetrically after drying at 80°C for 48 h. Total lipids of muscle samples were extracted by grinding 6 g of muscle powder with 2:1 chloroform-methanol (vol/vol) according to Folch et al. (1957) and then were assayed gravimetrically. Long-chain FA (LCFA) of muscle total lipids were extracted and transmethylated at room temperature for 2 × 20 min with sodium methylate (1 M) in methanol followed by boron trifluoride in methanol (14%, vol/vol) according to Glass (1971).

Long-chain fatty acid analysis was performed by gas-liquid chromatography on a Peri 2100-model chromatograph (Perichrom, Saulx-les-Chartreux, France) fitted with a CP-Sil 88 glass capillary column (Varian,

Lake Forest, CA; length: 100 m; i.d.: 0.25 mm) with H₂ as the carrier gas under conditions described by Scislowski et al. (2005). Total LCFA were quantified using C19:0 as the internal standard. Identification and calculation of the response coefficient of each individual LCFA were achieved using a quantitative mix of C4 to C24 FA methyl esters (Supelco, Bellefonte, PA).

Digestibility Trial

At the end of the experiment, the digestibility of the FR and SL diets was measured using 6 dry dairy cows (initial BW 643 ± 52 kg) because our facilities were not equipped for separating urine and feces in bulls. Cows received the 2 diets for two 3-wk periods in a crossover design. Cows were tethered and kept in individual pens with clean, fresh water and mineral blocks available at all times. A 2-wk diet adaptation period was followed by a 6-d fecal collection period. Diet composition was 13% barley straw and 87% of either the FR or SL concentrate. Feeds were the same as those given to bulls during fattening. Cows were fed in restricted amounts to keep expected NE intakes the same between diets. Straw and concentrate were given in 3 equal parts at 0900, 1100, and 1600 h. Fecal contamination by urine was avoided thanks to a urine collector attached to the vulva of the cow. Representative feed samples were taken, and the total feces of each animal was pooled to 1 sample per animal. An aliquot of feed and feces samples was dried at 103°C for DM determination. Another aliquot was dried at 60°C for 72 h and then ground through an 0.8-mm screen before chemical analysis. Crude protein, ash, NDF, ADF, and GE were determined according to the above-mentioned methods. The NE content of diets was calculated from digestible energy according to equations proposed by INRA (2007). It was assumed that the NE value determined in dry cows applied to fattening bulls.

Calculations and Statistical Analysis

Total NE_gI in the 3 dietary treatments was calculated from the results of the digestibility trial and not from the feed table (INRA, 2007) values. The feed efficiency during a given period was estimated by the ratio of BWG to NE_gI during that period. Mean NE_gI, BWG, and feed efficiency were calculated during 4 fattening periods (0 to 56 d, 56 to 126 d, 126 to 196 d, and 0 to 196 d). The 0 to 196 d period started at the end of the adaptation period and finished at the first slaughter, where all the bulls were present. Muscle and fat gain efficiencies were calculated from the whole fattening period as the ratios of carcass muscle or fat mass to NE_g or digestible CP intakes. Eleven bulls were removed from the experiment due to 3 accidental causes and 8 deaths diagnosed as enterotoxemia

Table 2. Feed intake and digestibility of the experimental diets measured in dry cows

Item	Diet ¹		SEM	Diet <i>P</i> -value
	FR	SL		
Feed intake, kg DM/d	9.86	7.81	0.011	<0.001
Digestibility, %				
DM	71.5	75.9	0.88	<0.001
OM	69.7	75.2	0.92	<0.001
NDF	66.0	48.4	1.65	<0.001
ADF	57.7	44.1	1.73	<0.001
CP	60.5	79.5	1.12	<0.001
GE	71.0	77.5	0.93	<0.001

¹FR: diet composed of 88% concentrate rich in fiber and 12% straw, SL: diet composed of 87% concentrate rich in starch and lipids and 13% straw.

(*n* = 4, 2, and 2 for the SL, SLR, and FR diets, respectively). Fattening data analysis ultimately dealt with 129 bulls, and carcass data analysis dealt with 123 bulls.

Analysis of variance was run using the MIXED procedure of SAS (SAS Inst. Inc., Cary, NC). For digestibility data, the model included diet and period and their interaction as fixed effects. For intake, growth, and carcass data, the following statistical analysis was chosen to take into account the unbalanced number of pens allocated to each of the 3 diets. Thus, the effect of the 20 pens was considered as the only fixed effect. These pen effects were appropriately combined to estimate diet effects using the “estimate” option of the MIXED procedure. This same “estimate” option was also used to calculate differences between 2 diets. The “contrast” option was ultimately used to test the significance of the diet effect combining 2 of the 3 contrasts among the above diet estimates. For data measured on muscles (lipid and FA composition and enzymatic data), the model included muscle, diet, and their interaction. Muscle was considered to be repeated on the same animal. For data measured on the liver (enzymatic data), diet was the only fixed effect. For all the data measured on bulls, diet means were compared by orthogonal contrasts: FR vs. SL, FR vs. SLR, and SL vs. SLR. Significant interactions were calculated using Student’s *t* test to identify muscle differences and individual treatment differences. Significance was considered when *P* ≤ 0.05.

RESULTS

Diet Digestibility and Energy Value

The apparent total tract digestibility of the OM was 5.5% units lower (*P* < 0.001) for cows consuming the FR diet than for cows fed the SL diet (Table 2). SL diet digestibility was lower than expected, as discussed further below. For the FR diet, NDF and ADF digestibility was 17.6% units greater (*P* < 0.001) than

Table 3. Feed intake, growth performance, and feed efficiency ratio for bulls offered the experimental diets during 196-d fattening

Item	Diet ¹			SEM ²	Diet <i>P</i> -value	Contrast		
	FR	SL	SLR			FR vs. SL	FR vs. SLR	SL vs. SLR
Number of animals	53	50	26					
Initial BW, kg	339	337	341	5.6	0.824	0.723	0.909	0.541
Final BW, kg	649	666	639	9.6	0.168	0.083	0.483	0.159
Feed intake, kg DM/d								
d 0 to 56	8.08	7.52	5.93	0.173	<0.001	0.002	<0.001	<0.001
d 56 to 126	10.94	9.49	8.68	0.234	<0.001	<0.001	<0.001	<0.001
d 126 to 196	11.79	10.61	9.64	0.234	<0.001	<0.001	<0.001	<0.001
d 0 to 196	10.31	9.24	8.16	0.185	<0.001	<0.001	<0.001	<0.001
NE _g intake, MJ/d ³								
d 0 to 56	53.81	57.01	44.00	1.251	<0.001	0.013	<0.001	<0.001
d 56 to 126	72.81	71.88	63.08	1.706	<0.001	0.590	0.001	<0.001
d 126 to 196	78.47	80.48	70.16	1.663	<0.001	0.234	<0.001	<0.001
d 0 to 196	68.68	70.03	59.46	1.333	<0.001	0.320	<0.001	<0.001
CP intake, kg/d	1.50	1.65	1.39	0.031	<0.001	<0.001	0.023	<0.001
BW gain, g/d								
d 0 to 56	1,470	1,537	1,289	53.7	<0.001	0.220	0.020	<0.001
d 56 to 126	1,784	1,786	1,796	47.8	0.812	0.958	0.866	0.575
d 126 to 196	1,478	1,692	1,290	51.4	<0.001	<0.001	0.012	<0.001
d 0 to 196	1,585	1,682	1,471	33.8	<0.001	0.006	0.020	<0.001
Feed efficiency, g BW gain/MJ NE _g								
d 0 to 56	27.4	26.9	29.3	0.78	0.089	0.535	0.089	0.030
d 56 to 126	24.6	25.1	28.6	0.69	<0.001	0.435	<0.001	<0.001
d 126 to 196	18.8	21.1	18.4	0.63	0.003	<0.001	0.669	0.071
d 0 to 196	23.1	24.1	24.9	0.44	<0.001	0.025	0.006	0.010

¹FR: diet composed of 88% concentrate rich in fiber and 12% straw, SL: diet composed of 87% concentrate rich in starch and lipids and 13% straw, SLR: diet composed of 83% concentrate rich in starch and lipids and 17% straw.

²SEM was calculated with $n = 26$.

³Net energy for gain measured from digestibility data.

for the SL diet, whereas CP digestibility was 19.0% units lower. Gross energy digestibility was 6.5% units greater for the SL diet than for the FR diet ($P < 0.001$).

From these results, NE_g was calculated as 6.67 and 7.59 MJ/kg DM for the FR and SL diets, respectively. For the SLR diet, NE_g was recalculated as 7.30 MJ/kg DM after taking into account the greater percentage of straw in the diet (18% instead of 13% for SL), and the energy digestibility of barley straw was taken as 40% (INRA, 2007). These figures were used for subsequent calculations of NE intake and feed efficiency.

Intake, Growth Performance, and Feed Efficiency

Effect of Type of Energy in Ad Libitum-Fed Bulls (FR vs. SL). Net energy intake did not differ between diets over the whole fattening period, although it was greater ($P = 0.013$) for SL bull than for FR bulls during the 0 to 56 d period (Table 3). The average BWG of bulls offered the SL diet was 6% greater ($P = 0.006$) than that of bulls fed the FR diet over 196 d of fattening, mostly because of strong gains in the last

70 d of fattening. Feed efficiency was greater with the SL diet than with the FR diet over the whole fattening period ($P = 0.025$). This difference stemmed from a strong difference in the 126- to 196-d period, where feed efficiency was 11.9% greater with the SL diet than with the FR diet ($P < 0.001$).

Effect of Intake Level (SL vs. SLR). Bulls fed the SLR diet consumed a greater proportion of straw than bulls fed SL diet (18% vs. 13%). Bulls fed the SLR diet consumed daily 1.1 kg DM less ($P < 0.001$) than bulls fed the SL diet, and NE_gI was consistently around 15% lower over the whole experimental period ($P < 0.001$) for SLR vs. SL bulls; SLR-fed bulls thus had a 12.5% lower BWG ($P < 0.001$) than SL-fed bulls. The efficiency for growth was greater for the SLR diet than for the SL diet ($P = 0.01$).

Effect of Type of Energy in Feed-Matched Bulls (FR vs. SLR). Net energy intake by SLR-fed bulls was planned to be similar to that of FR-fed bulls. However, because of a lower difference in digestibility between FR and SL and a greater proportion of straw in DMI, NE_gI were not as isoenergetic as planned, with NE_gI

Table 4. Carcass characteristics for bulls offered the experimental diets

Item	Diet ¹			SEM ²	Diet P-value	Contrast		
	FR	SL	SLR			FR vs. SL	FR vs. SLR	SL vs. SLR
Number of animals	50	47	26					
BW at slaughter, kg	709	732	687	9.7	0.002	0.039	0.130	<0.001
Age at slaughter, d	540	537	532	1.7	0.002	0.067	0.006	0.051
Empty BW, kg	625	661	602	9.1	<0.001	<0.001	0.118	<0.001
HCW, kg	426	453	414	6.7	<0.001	<0.001	0.254	<0.001
Cold carcass weight, % BW	57.4	59.0	57.8	0.30	<0.001	<0.001	0.271	0.002
Carcass composition, ³ %								
Muscle	71.3	69.6	71.7	0.34	<0.001	<0.001	0.922	<0.001
Fat	14.8	17.0	14.2	0.36	<0.001	<0.001	0.446	<0.001
Bone	14.2	13.6	14.4	0.12	<0.001	<0.001	0.136	<0.001
Carcass composition ³ , kg								
Muscle	304	315	297	5.0	0.012	0.044	0.254	0.004
Fat	61.7	75.6	57.5	2.00	<0.001	<0.001	0.106	<0.001
Bone	60.4	61.8	59.4	0.85	0.086	0.161	0.335	0.031
Muscle-to-fat ratio	4.84	4.23	5.07	0.136	<0.001	<0.001	0.406	<0.001
Internal fat, kg	18.5	26.0	15.9	1.18	<0.001	<0.001	0.212	<0.001
Organ weight, kg								
Empty digestive tract	34.8	31.9	30.6	8.45	<0.001	<0.001	<0.001	0.089
Reticulorumen	13.5	11.2	10.6	0.33	<0.001	<0.001	<0.001	0.151
Omasum	5.22	3.84	4.06	0.201	<0.001	<0.001	<0.001	0.391
Abomasum	2.16	2.20	1.96	0.064	0.012	0.550	0.044	0.004
Intestines	14.0	14.7	13.9	0.28	0.042	0.029	0.476	0.036
Liver	6.53	6.69	6.35	0.137	0.156	0.292	0.413	0.056
Energetic efficiency, g/MJ								
Muscle/NE _g	17.48	17.82	21.59	0.343	<0.001	0.379	<0.001	<0.001
Fat/NE _g	3.63	4.29	4.32	0.089	<0.001	<0.001	<0.001	0.803
Protein efficiency, g/kg								
Muscle/digestible CP	1,312	940	1,086	20.2	<0.001	<0.001	<0.001	<0.001
Fat/digestible CP	273	226	217	5.1	<0.001	<0.001	<0.001	0.168

¹FR: diet composed of 88% concentrate rich in fiber and 12% straw, SL: diet composed of 87% concentrate rich in starch and lipids and 13% straw, SLR diet composed of 83% concentrate rich in starch and lipids and 17% straw.

²SEM was calculated with $n = 26$.

³Estimated from sixth rib composition obtained by dissection. Fat weight is the sum of internal, subcutaneous and intermuscular fat weights.

ultimately 13% lower ($P < 0.001$) in the SLR treatment vs. the FR treatment over the whole fattening period (Table 3). Average BWG from 0 to 196 d of fattening was 7% lower ($P = 0.02$) with the SLR diet vs. the FR diet. Overall, feed efficiency from 0 to 196 d was 7.6% greater for the SLR diet than for the FR diet ($P = 0.006$).

Slaughter Performance, Carcass Traits, and Efficiency of Muscle and Fat Gain

Effect of Type of Energy in Ad Libitum-Fed Bulls (FR vs. SL). Consistent with the greater average NE_g and CP intakes, SL bulls had 3% greater BW ($P = 0.039$) and 6% greater HCW ($P < 0.001$) at slaughter than FR bulls (Table 4). The ratio of cold carcass weight to on-farm BW was also greater for SL bulls ($P < 0.001$). Carcass composition showed proportionally more fat and less muscle ($P < 0.001$) for SL bulls than for FR bulls. Muscle-to-bone ratios were similar, with a value of 5.

Consequently, muscle mass was 11 kg greater (315 vs. 304 ± 4.28 kg; $P < 0.05$) and carcass fat mass was 14 kg greater (75.6 vs. 61.7 ± 1.74 kg; $P < 0.001$) in SL bulls than in FR bulls, and fat mass in the fifth quarter was also 7.5 kg greater (SEM = 1.18; $P < 0.001$). The lower forestomach weights (reticulorumen and omasum) in the bulls fed the SL diet ($P < 0.001$) were consistent with their lower DMI. Conversely, intestinal weight was greater in the SL bulls ($P = 0.029$), probably because of their greater intestinal digestion compared with that of FR bulls. Liver weight was unaffected.

The efficiency of NE_g use for muscle gain was not affected, whereas the efficiency of NE_g use for fat gain was 18% greater for the SL diet than for the FR diet ($P < 0.001$). The efficiency of digestible CP transfer into muscle and fat was reduced ($P < 0.001$) in the bulls fed SL diet. Had digestibility not been accounted for, differences in N efficiency would have been greatly reduced.

Effect of Intake Level (SL vs. SLR). Compared with SL bulls, SLR bulls had 6% lower BW at slaughter ($P < 0.001$), 8.6% lower HCW ($P < 0.001$) but with a greater carcass muscle-to-fat ratio (5.07 vs. 4.23 \pm 0.11; $P < 0.001$), and a similar muscle-to-bone ratio of 5. Consequently, both carcass muscle and fat mass were lower in SLR vs. SL bulls ($P < 0.001$), as was the amount of fat in the fifth quarter (Table 4). Forestomach weight was not significantly affected by the difference in DMI, but abomasal and intestinal weights were significantly lower in SLR vs. SL bulls ($P = 0.004$ and $P = 0.036$, respectively), and liver weight tended to be lower ($P < 0.06$). Although muscle gain was lower in SLR bulls, efficiencies of NE_g and digestible CP use for muscle gain were significantly increased ($P < 0.001$). Efficiency of NE_g use for fat gain was not different between the 2 diets. Efficiency of digestible CP use for muscle gain was greater for the SLR diet ($P < 0.001$).

Effect of Energy Source (FR vs. SLR). Despite differences in NE_g I and BWG, FR and SLR bulls did not differ in any body composition traits except fat depots, which tended to be lower for the SLR diet (57.5 vs. 61.7 kg for the SLR and FR bulls; SEM = 1.74; $P < 0.10$), and forestomach (reticulorumen, omasum) and abomasum weight, which were greater ($P < 0.044$) for the fiber-rich FR diet than for the SLR diet. Compared with FR bulls, SLR bulls showed more efficient NE_g use for muscle and fat gain but less efficient digestible CP use for muscle and fat gain ($P < 0.001$).

Metabolic Enzyme Activity

Despite differences in feed efficiency between the FR and SL groups just before slaughter (d 126 to 196), the enzymatic activity of the liver (which is one of the most metabolically active organs) did not differ between the 2 groups (Table 5) on the basis of COX activity (representative of mitochondrial activity) and LDH and PFK activities (representative of glycolytic metabolism), whatever the unit of expression of the results (per g of wet muscle or per g of tissue protein).

In muscle, LDH activity was slightly greater for the SL diet compared for the FR diet in both ST (+2%) and LT (+5%; $P < 0.047$) muscles when results were expressed per gram of wet tissue, indicating a greater glycolytic metabolism in muscles of animals fed the SL diet (Table 6). However, when results were expressed per gram of muscle protein, the differences lost significance because of a slightly greater protein content, especially in ST muscle (+3.4%; $P = 0.071$) for the SL diet. For all the other measured enzyme activities, we did not find any significant differences between the diets. However, metabolic activity showed differences between the 2 studied muscles, with LT being more

Table 5. LDH, PFK, and COX enzyme activities in liver for bulls offered the FR ($n = 22$) and SL ($n = 21$) diets¹

Item	Diet ²		SEM	Diet <i>P</i> -value
	FR	SL		
Activity, $\mu\text{mol}\cdot\text{min}^{-1}\cdot\text{g liver}^{-1}$				
LDH	57.5	62.7	2.4	0.138
PFK	3.12	2.96	0.13	0.405
COX	48.9	48.1	2.26	0.806
Activity, $\mu\text{mol}\cdot\text{min}^{-1}\cdot\text{g protein}^{-1}$				
LDH	313	334	15.0	0.324
PFK	17.0	15.8	0.78	0.297
COX	265	258	13.4	0.704
Protein, g/kg liver	185	189	3.4	0.503
COX/LDH, %	86.9	77.3	4.60	0.150

¹Lactate dehydrogenase (LDH), phosphofructokinase (PFK), and cytochrome c oxidase (COX).

²FR: diet composed of 88% concentrate rich in fiber and 12% straw, SL: diet composed of 87% concentrate rich in starch and lipids and 13% straw.

oxidative (because of a greater COX/LDH ratio) than ST for the FR diet, as expected. Note that this difference was negated in the SL diet, as indicated by a significant muscle \times diet interaction for some variables (especially the COX/LDH ratio).

Lipids and Fatty Acids in Muscles

Total lipids and total FA (g/100 g fresh tissue) and individual FA and FA class (mg/100 g fresh tissue) contents of LT, RA and ST muscles are given in Table 7. Total lipid contents differed with muscle type and body localization, being 1.6 to 2.0 and 1.4 to 1.6 times greater in LT and RA muscles, respectively, than in ST muscle ($P < 0.001$). Similar variations with muscle type were noted for total FA content, which was 1.9 to 2.3 and 1.7 to 1.9 times greater in LT and RA muscles than in ST muscle, respectively ($P < 0.001$). Total lipid and FA contents were significantly influenced by diets, being greater with the SL diet than with the FR and SLR diets ($P < 0.001$) which had similar lipid and FA contents. A significant ($P < 0.001$) muscle \times diet interaction was found for total lipids but not for total FA (Table 7).

Total SFA muscle content varied with muscle type and diet in patterns similar to those of total lipids and FA (Table 7). Saturated FA were mainly palmitic acid (16:0, $\approx 22\%$ of total FA) and stearic acid (18:0, $\approx 16\%$). Total and individual SFA did not differ between the FR and SLR diets but were greater for SL than for the other 2 diets ($P < 0.001$), with significant muscle \times diet interactions ($P = 0.002$ to 0.003 according to FA). The ratio of 16:0 to 18:0 was mainly influenced by muscle type, being 10.3, 17.9, and 17.2 lower in LT muscle

Table 6. LDH, PFK, and COX enzyme activities in longissimus thoracis (LT) and semitendinosus (ST) and muscles (M) for bulls offered the FR ($n = 22$) and SL ($n = 21$) diets (D)¹

Item	Diet and muscle ²				SEM	P-value		
	FR		SL			M	D	M × D
	LT	ST	LT	ST				
Activity, $\mu\text{mol} \cdot \text{min}^{-1} \cdot \text{g muscle}^{-1}$								
LDH	1,019	1,014	1,070	1,035	12.7	0.267	0.047	0.413
PFK	127	108	135	122	5.0	0.029	0.115	0.663
COX	12.4 ^a	9.8 ^b	11.5 ^{a,b}	11.3 ^{a,b}	0.38	0.015	0.663	0.032
Activity, $\mu\text{mol} \cdot \text{min}^{-1} \cdot \text{g protein}^{-1}$								
LDH	4,719	4,980	4,911	4,933	65.9	0.138	0.442	0.207
PFK	588	529	621	584	24.6	0.172	0.212	0.750
COX	57.7	48.4	52.8	53.4	1.84	0.103	0.978	0.063
Protein, g/kg muscle	216	204	218	211	1.8	<0.001	0.071	0.334
COX/LDH, %	1.23 ^a	0.97 ^b	1.08 ^{a,b}	1.09 ^{a,b}	0.038	0.030	0.814	0.016

^{a,b}Within a row, means without a common superscript differ ($P < 0.05$).

¹Lactate dehydrogenase (LDH), phosphofructokinase (PFK), and cytochrome c oxidase (COX).

²FR: diet composed of 88% concentrate rich in fiber and 12% straw, SL: diet composed of 87% concentrate rich in starch and lipids and 13% straw.

than in RA and ST muscles from bulls given the FR, SL, and SLR diets, respectively ($P < 0.001$).

Total MUFA, composed of *cis* and *trans* isomers, represented 32% to 42% of total FA according to the type of muscle and diet considered (Table 7); MUFA deposition was 1.9 to 2.1 and 2.0 to 2.4 times greater in RA and LT muscles than in ST muscle, respectively ($P < 0.001$), whatever the dietary conditions. *Cis*-MUFA, which represented 88% to 93% of total MUFA, were dominated by oleic acid (18:1 *n*-9 *cis*, 77% to 82%) irrespective of diet and muscle type. As for SFA, muscle deposition of total SFA was significantly ($P < 0.001$) influenced by dietary energy level, being 1.9 to 2.2, 1.5 to 1.8, and 1.7 to 1.8 times greater for the SL diet than for the 2 other diets for LT, RA, and ST muscles, respectively ($P < 0.001$). Similar diet effects were found for muscle *trans*-MUFA contents. However, *trans*-MUFA contents were 1.7, 1.6, and 1.5 times greater in RA, LT, and ST muscles of bulls given the SLR diet than in those of bulls given the FR diet ($P = 0.010$). All 18-carbon MUFA isomers were greater in RA and LT than in ST, and most of them were diet dependent (Table 8). The main *cis* isomers, oleic acid (*cis*-9 18:1), and *cis* vaccenic acid (*cis*-11 18:1) were greater in SL samples than in SLR samples ($P < 0.001$). The coelution of *trans*-11 (*trans* vaccenic acid) and *trans*-10 18:1, which is the major peak of *trans*-MUFA, is greater for the SL diet than for the SLR diet ($P = 0.038$) and greater for the SL and SLR diets than for the FR diet ($P < 0.01$).

Total PUFA, composed of *n*-6 PUFA, *n*-3 PUFA, and conjugated linoleic acids (CLA, mainly rumenic acid, *cis*-9, *trans*-11 18:2) varied according to muscle ($P < 0.001$) and diet ($P < 0.001$) and accounted for 12% to 16%, 12% to 14% and 19% to 24% of total FA for RA, LT, and ST, respectively, with ST having the lowest total FA content

(Table 7). The *n*-6 PUFA were mainly composed of 18:2 *n*-6 (linoleic acid) and 20:4 *n*-6 (arachidonic acid). In all muscles considered, linoleic acid represented 10.9% and 9.6% of total FA in muscles from bulls fed at the lowest energy intakes (FR and SLR diets) but only 6.6% of total FA in the SL diet. Quantitatively, linoleic acid content was 16% to 20% greater in RA and LT muscles than in ST muscle, irrespective of diet ($P < 0.001$), whereas arachidonic acid content was greater in ST than in RA and LT. The *n*-3 PUFA were mainly composed of 18:3 *n*-3 (linolenic acid) as well as 20- and 22-carbon *n*-3 PUFA, mainly represented by 20:5 *n*-3 (eicosapentaenoic acid, EPA; 2.3 to 7.8 mg/100 g) and especially 22:5 *n*-3 (docosapentaenoic acid, DPA; 6.9 to 12.3 mg/100 g) but poor in 22:6 *n*-3 (docosahexaenoic acid, DHA; <1.3 mg/100 g; Table 7). Muscle linolenic acid, EPA, DPA, and DHA content was, in all 3 muscles, highly and mainly influenced by linseed supplementation, being greater for the SL and SLR diets (rich in linolenic acid) than for the FR diet ($P < 0.001$). Eicosapentaenoic acid and DPA content was mainly influenced by muscle type, being 47% to 70% and 16% to 23% greater in ST than in RA and LT, respectively ($P < 0.001$), irrespective of diet. In other respects, CLA content was 1.5 to 1.8 and 2.7 to 3.2 times greater in SL bulls than in FR and SLR bulls, respectively ($P < 0.001$), for all muscles.

The *n*-6:*n*-3 PUFA ratio and 18:2 *n*-6 to 18:3 *n*-3 ratio differed among muscles and were greater for bulls given the FR diet than for bulls fed the SL and SLR diets ($P < 0.001$). In other respects, PUFA:SFA ratio was 1.7 to 2.0 times greater in ST muscle than in RA and LT muscles ($P < 0.001$), irrespective of diet.

Table 7. Total lipids and total fatty acids (FA) and individual FA and FA classes in rectus abdominis (RA), longissimus thoracis (LT), and semitendinosus (ST) muscles (M) from bulls fed experimental diets

Item	Diet and muscle ¹												P-value			Contrast	
	FR			SL			SLR			SEM	M × D	M	D	FR vs. SL	FR vs. SLR	SL vs. SLR	
	RA	LT	ST	RA	LT	ST	RA	LT	ST								ST
Total lipids, g/100 g fresh tissue	1.85 ^{b,c,d}	1.94 ^{b,c}	1.23 ^{e,f}	2.44 ^b	3.04 ^a	1.50 ^{e,de}	1.76 ^{e,e}	1.92 ^{b,c}	1.23 ^{d,f}	0.130	<0.001	<0.001	<0.001	<0.001	0.814	<0.001	
Total FA, g/100 g fresh tissue	1.22 ^{b,c,e}	1.32 ^{b,c}	0.70 ^{d,f}	1.78 ^b	2.30 ^a	1.01 ^{c,de}	1.27 ^{b,c,d}	1.33 ^{b,c}	0.69 ^{e,f}	0.147	<0.001	NS ²	<0.001	<0.001	0.907	<0.001	
Fatty acids, ³ mg/100 g fresh tissue																	
16:0	308 ^{b,c,d}	332 ^{b,c}	155 ^{d,e}	431 ^b	547 ^a	216 ^{d,e}	280 ^{b,c,d}	292 ^{b,c,d}	135 ^e	34.0	<0.001	<0.001	0.003	0.002	0.468	<0.001	
18:0	199 ^{b,c}	261 ^b	106 ^{d,e}	240 ^b	393 ^a	133 ^{c,d,e}	193 ^{b,c,d}	233 ^b	97 ^e	22.5	<0.001	<0.005	0.002	0.012	0.556	0.002	
<i>cis</i> -18:1 <i>n</i> -9	322 ^{c,e}	337 ^{c,e}	170 ^{d,f}	582 ^b	739 ^a	305 ^{c,d,e}	358 ^{c,d}	374 ^{c,d}	172 ^{e,f}	47.0	<0.001	<0.001	<0.001	<0.001	0.659	<0.001	
18:2 <i>n</i> -6	120 ^a	115 ^{a,b}	99 ^{c,d}	119 ^a	126 ^a	98 ^{b,c,d}	111 ^{a,b,c}	101 ^{b,c}	86 ^d	4.07	<0.001	0.004	0.022	0.492	0.012	0.002	
18:3 <i>n</i> -3	10.7 ^{e,f}	11.7 ^{e,f}	8.6 ^f	24.7 ^b	31.9 ^a	19.6 ^{c,d}	20.4 ^{b,c}	21.1 ^{b,c}	15.9 ^{d,e}	1.20	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	
CLA	3.9 ^{c,d}	3.8 ^{c,d}	1.8 ^d	10.5 ^{a,b}	12.2 ^a	5.8 ^{c,d}	6.9 ^{b,c}	6.8 ^{b,c}	3.3 ^d	0.92	<0.001	<0.001	0.002	<0.001	0.033	<0.001	
20:4 <i>n</i> -6	24.4 ^b	20.1 ^{c,d}	27.9 ^a	20.7 ^{c,d}	18.8 ^d	25.2 ^{a,b}	23.0 ^{b,c}	19.7 ^d	24.9 ^{a,b}	1.20	<0.001	<0.001	0.083	<0.001	0.015	0.157	
20:5 <i>n</i> -3	2.35 ^e	2.28 ^e	3.95 ^d	4.32 ^{c,d}	4.55 ^{b,c,d}	7.01 ^a	5.23 ^{b,c}	5.39 ^b	7.80 ^a	0.24	<0.001	<0.001	0.042	<0.001	<0.001	0.002	
22:5 <i>n</i> -3	8.1 ^{c,d}	6.9 ^d	9.8 ^b	10.4 ^b	9.8 ^{b,c}	12.3 ^a	11.1 ^{a,b}	10.0 ^b	12.3 ^a	0.38	<0.001	<0.001	0.750	<0.001	<0.001	0.369	
22:6 <i>n</i> -3	0.04 ^c	0.09 ^c	0.16 ^c	0.18 ^c	0.13 ^c	0.80 ^b	0.91 ^b	0.76 ^b	1.27 ^a	0.11	<0.001	<0.001	0.003	0.026	<0.001	<0.001	
Σ SFA	586 ^{b,c}	680 ^b	297 ^{d,e}	764 ^b	1064 ^a	396 ^{c,d,e}	544 ^{b,c,d}	599 ^{b,c}	264 ^e	62.8	<0.001	<0.001	0.003	0.004	0.468	<0.001	
Σ <i>cis</i> -MUFA	397 ^{b,c}	409 ^{b,c}	215 ^e	719 ^b	1026 ^a	382 ^c	451 ^{b,c}	461 ^{b,c}	223 ^c	71.6	<0.001	<0.001	<0.001	<0.001	0.621	<0.001	
Σ <i>trans</i> -MUFA	38 ^{c,d,e}	45 ^{b,c,d}	17 ^e	68 ^b	102 ^a	35 ^{c,d,e}	63 ^{b,c}	72 ^b	26 ^{d,e}	66.0	<0.001	<0.001	<0.001	<0.001	0.010	0.051	
Σ MUFA	435 ^{c,d}	454 ^{c,d}	232 ^e	788 ^b	994 ^a	417 ^{c,d,e}	514 ^c	533 ^{b,c}	249 ^{d,e}	61.9	<0.001	<0.001	<0.001	<0.001	0.431	<0.001	
Σ PUFA <i>n</i> -6	162 ^{a,b,d}	154 ^{a,b,c,d}	143 ^{c,e}	167 ^{a,b,c}	178 ^a	144 ^{d,e}	160 ^{a,b,c,d}	144 ^{b,c,d,e}	127 ^e	5.88	<0.001	<0.018	0.013	0.152	0.154	0.005	
Σ PUFA <i>n</i> -3	21.4 ^c	21.3 ^c	22.9 ^c	40.3 ^b	46.8 ^a	40.6 ^b	38.3 ^b	38.4 ^b	38.0 ^b	1.50	0.065	<0.001	0.009	<0.001	<0.001	0.008	
Σ PUFA	189 ^{b,c,d}	180 ^{c,d}	168 ^d	219 ^{a,b}	237 ^a	191 ^{c,d}	206 ^{a,b,c}	190 ^{b,c,d}	168 ^d	7.83	<0.001	<0.001	0.008	<0.001	0.289	0.002	
<i>n</i> -6: <i>n</i> -3	7.7 ^a	7.3 ^b	6.3 ^c	4.2 ^{d,f}	3.8 ^{e,gh}	3.6 ^{gh}	4.2 ^{d,e}	3.8 ^{fg}	3.3 ^h	0.124	<0.001	<0.001	<0.001	<0.001	<0.001	0.516	
18:2:18:3	11.5 ^a	10.0 ^b	11.6 ^a	5.0 ^{cd}	4.2 ^e	5.1 ^{cd}	5.5 ^c	4.8 ^{d,e}	5.4 ^{c,d}	0.205	<0.001	<0.001	0.006	<0.001	<0.001	0.043	
16:0:18:0	1.5 ^{a,b,d}	1.3 ^{e,g}	1.4 ^{c,f}	1.7 ^a	1.4 ^{d,e,f}	1.6 ^{b,c}	1.5 ^{b,c,d,e}	1.2 ^{fg}	1.4 ^{b,c,d,e}	0.053	<0.001	0.012	0.014	0.018	0.698	0.006	
PUFA:SFA	0.36 ^b	0.30 ^b	0.65 ^a	0.35 ^b	0.30 ^b	0.58 ^a	0.41 ^b	0.38 ^b	0.68 ^a	0.011	<0.001	0.152	0.395	0.535	0.203	0.059	

^{a-h}Within a row, means without a common superscript differ ($P < 0.05$).

¹FR: diet composed of 88% concentrate rich in fiber and 12% straw, SL: diet composed of 87% concentrate rich in starch and lipids and 13% straw, SLR: diet composed of 83% concentrate rich in starch and lipids and 17% straw.

²NS = not significant.

³Σ SFA = sum of even- and odd-chain SFA from 12 to 24 C; 12:0 + 13:0 + 14:0 + 15:0 + 16:0 + 17:0 + 18:0 + 20:0 + 21:0 + 22:0 + 23:0 + 24:0; Σ *cis*-MUFA = *cis*-14:1 *n*-5 + *cis*-15:1 *n*-6 + *cis*-16:1 *n*-7 + *cis*-17:1 *n*-8 + Σ *cis*-18:1 + *cis*-20:1 *n*-11; Σ *trans*-MUFA = Σ *trans*-16:1 + Σ *trans*-18:1; Σ MUFA = Σ *cis*-MUFA + Σ *trans*-MUFA; Σ PUFA *n*-6 = *trans*,*cis*-18:2 *n*-6 + *cis*,*cis*-18:2 *n*-6 + *cis*,*cis*-18:2 *n*-6 + 18:3 *n*-6 + 20:2 *n*-6 + 20:3 *n*-6 + 20:4 *n*-6 + 22:2 *n*-6; Σ PUFA *n*-3 = 18:3 *n*-3 + 20:3 *n*-3 + 20:4 *n*-3 + 20:5 *n*-3 + 22:3 *n*-3 + 22:4 *n*-3 + 22:5 *n*-3 + 22:6 *n*-3; Σ PUFA = Σ PUFA *n*-6 + Σ PUFA *n*-3 + Σ CLA + Σ conjugated PUFA.

Table 8. Contents in *cis* and *trans* C18:1 isomers of rectus abdominis (RA), longissimus thoracis (LT), and semitendinosus (ST) muscles (M) of bulls offered experimental diets (D)¹

Fatty acid	FR						SLR						P-value						Contrast	
	RA		LT		ST		RA		LT		ST		SEM	M	D	M × D	FR vs. SL	FR vs. SLR	SL vs. SLR	
	RA	LT	ST	RA	LT	ST	RA	LT	ST											
cis 18:1 isomers, mg/100 g fresh tissue																				
<i>cis</i> -9	322 ^{b,c}	337 ^{b,c}	170 ^c	582 ^b	852 ^a	305 ^c	358 ^{b,c}	374 ^{b,c}	172 ^c	59.9	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.701
<i>cis</i> -11	18.8 ^{c,d}	19.6 ^{c,d}	12.2 ^{c,d}	35.3 ^b	46.9 ^a	21.8 ^{c,d}	24.4 ^{b,c}	24.4 ^{b,c}	14.2 ^d	2.88	<0.001	<0.001	0.001	<0.001	0.001	<0.001	<0.001	<0.001	<0.001	0.192
<i>cis</i> -12	4.57 ^{b,c,d}	4.95 ^{b,c,d}	2.56 ^d	7.50 ^b	11.27 ^a	4.59 ^{c,d}	6.84 ^{b,c}	6.53 ^{b,c}	3.70 ^d	0.77	<0.001	<0.001	0.002	<0.001	0.002	<0.001	<0.001	<0.001	<0.001	0.042
<i>cis</i> -13	1.53 ^c	1.53 ^c	0.89 ^c	4.45 ^{a,b}	6.24 ^a	2.58 ^{b,c}	2.53 ^{b,c}	2.43 ^{b,c}	1.29 ^c	0.53	<0.001	<0.001	0.006	<0.001	0.006	<0.001	<0.001	<0.001	<0.001	0.179
<i>cis</i> -14	3.83 ^{b,c}	4.26 ^{b,c}	1.84 ^c	7.06 ^b	11.57 ^a	3.49 ^c	5.51 ^{b,c}	5.09 ^{b,c}	2.23 ^c	0.87	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.268
<i>cis</i> -15	0.51 ^{b,c}	0.94 ^{a,b,c}	0.32 ^{b,c}	1.58 ^{a,b,c}	2.94 ^a	0.42 ^{b,c}	1.52 ^{a,b,c}	2.16 ^{a,b}	0.64 ^c	0.45	<0.001	0.101	0.077	<0.001	0.044	<0.001	<0.001	<0.001	<0.001	0.010
<i>trans</i> 18:1 isomers, mg/100 g fresh tissue																				
<i>trans</i> -6	1.00 ^a	1.37 ^a	0.36 ^a	0.36 ^a	1.08 ^a	0.25 ^a	0.46 ^a	0.54 ^a	0.42 ^a	0.26	0.011	0.113	0.388	0.120	0.388	<0.001	<0.001	<0.001	<0.001	0.047
<i>trans</i> -9	4.00 ^{b,c,d}	4.09 ^{b,c,d}	1.93 ^d	5.57 ^{b,c}	9.24 ^a	3.55 ^{b,c,d}	4.77 ^{b,c,d}	5.27 ^b	2.41 ^{c,d}	0.73	<0.001	0.002	0.019	<0.001	0.019	<0.001	<0.001	<0.001	<0.001	0.276
<i>trans</i> -10-11 ²	20.8 ^{c,d}	25.6 ^{b,c,d}	9.2 ^d	49.1 ^{b,c}	88.5 ^a	24.2 ^{b,c,d}	45.6 ^{b,c}	52.6 ^b	18.2 ^d	6.95	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.006
<i>trans</i> -12	3.61 ^{b,c,d}	4.41 ^{b,c,d}	1.76 ^d	5.55 ^{b,c}	9.83 ^a	2.28 ^d	5.16 ^{b,c,d}	6.18 ^b	2.27 ^{c,d}	0.78	<0.001	0.004	0.010	<0.001	0.010	<0.001	<0.001	<0.001	<0.001	<0.001

a-d Within a row, means without a common superscript differ ($P < 0.05$).

¹FR: diet composed of 88% concentrate rich in fiber and 12% straw, SL: diet composed of 87% concentrate rich in starch and lipids and 13% straw, SLR: diet composed of 83% concentrate rich in starch and lipids and 17% straw.

²Coeluted isomers.

DISCUSSION

Alternative strategies to feeding high-cereal diets to fattening bulls have to focus not only on achieving high levels of growth but also on using alternative feeds that do not compete with human food, improve feed efficiency, and ensure nutritionally good-quality meat (Hocquette et al., 2007; Doreau et al., 2013). Three strategies were tested here on the basis of 1) using high-concentrate diets to maximize intake, 2) replacing part of the cereals with a fat source to ensure energy density and to limit the risks of acidosis, and 3) using highly digestible fiber sources. The effects of energy source were separated from those of intake level. Starch-based diets are known to increase carcass fat at similar metabolizable energy intake (Brennan et al., 1987), but the effect may also depend on the rate of gain (Coleman et al., 1995). Few experiments have studied the impact of energy source in finishing cattle at controlled intakes (Brennan et al., 1987; Bartoň et al., 2007; Costa et al., 2013). The effect of the source and amount of energy has most often been studied in growing cattle, often during winter growing programs, showing little carryover effects on body composition and fat depots over fattening (e.g., Sharman et al., 2013). To our knowledge, there is no published experiment comparing fiber-rich and starch-plus-lipid-rich concentrate diets fed to bulls continuously over the growing and fattening phases and dissociating the effects of energy source from those of intake level.

Nutritional Value of Diets and Ad Libitum Intakes

Dry cows were used instead of bulls for digestibility measurements. A bias in results cannot be excluded because of differences in age and sex and because cows were fed in restricted amounts. However, the difference may have a low extent, as shown by Dulphy et al. (1990): OM digestibility was 1% to 3% units greater in cows than in bulls receiving the same diets. In any case, NE calculations from effective digestibility measurements are likely more accurate than calculations arising from feed tables.

According to the INRA (2007) feeding system, we expected to record approximately a 17% difference in NE content between FR and SL diets. However, the digestibility trial showed more limited differences, leading to a SL diet energy value that was 12% lower than expected. This may be due to limited fiber digestion with high-starch diets because of disturbances to the ruminal microbial ecosystem, that is, fewer cellulolytic bacteria and fewer protozoa (Dehority and Orpin, 1997), but it is not likely to be due to fat addition, which was too low to impair ruminal fiber digestion (Doreau et al., 2009).

The digestibility of the SLR diet was further reduced because of a greater proportion of straw in the diet (18% vs. 13%), but the greater straw intake contributed to limiting the difference in $NE_g I$ between the SLR and FR diets. Consequently, when dietary NE_g was calculated from the results of the digestibility trial, $NE_g I$ was lower in SLR bulls than in FR bulls, so the objective of the design was not reached. A time course adaptation of the ruminal microbial ecosystem may be assumed for bulls fed the SL and SLR diets, which may lead to a greater energy value for these diets after a few months of fattening, but that process was impossible to quantify here.

Ad libitum intake was the first evaluation criterion of the diets. Despite the fact that SL diet intake may have been limited by possible digestive discomfort resulting from high-cereal diets (Mialon et al., 2008) and by a more friable consistency, ad libitum intakes were high. Conversely, bulls fed the FR diet did not consume enough feed to achieve their growth potential. This result is especially surprising because the bulls were used to consuming the FR concentrate before weaning from as early as 8 wk of age, and the role of learning on food preferences is well known (Provenza, 1995). The FR diet probably resulted in a greater ruminal bulk, as suggested by a greater reticulorumen weight, but a physical limitation of intake at the ruminal level is unlikely as the diet was offered as pellets with high digestibility. We can posit that SL concentrate is more palatable than FR concentrate, independent of postingestive consequences (Favreau-Peigné et al., 2013). In a feedlot trial comparing high-fiber and high-starch concentrates in 45% forage diets, Mueller et al. (2011) observed a greater DMI for high-fiber diets but similar ME intake between diets and thus a metabolic regulation of intake.

Taken together, the intake differences in NE_g and digestible CP were lower than expected between FR bulls and SL or SLR bulls. Actual $NE_g I$ did not differ between the FR and SL diets but was lower in the SLR diet than in the FR (by 13%) and SL (by 15%) diets. These treatment differences will thus be discussed together.

Growth, Slaughter Characteristics, and Efficiency

The intake level at a given diet composition (SL vs. SLR) affected growth rates and body and carcass composition, as expected (Hoch and Agabriel, 2004). Body and carcass weights were decreased at restricted intakes, with leaner carcasses and lower visceral weights (abomasum + intestine + liver). This result is consistent with the results of Sami et al. (2004) for Simmental bulls that were finished on corn silage-concentrate diets and slaughtered at 18 to 19 mo and with knowledge of intake level effects on visceral mass

(Ortigue and Doreau, 1995). The covariance adjustment for differences in fasted BW (data not shown) indicated that differences in visceral mass were due to changes in BW. However, differences in body composition were not due to changes in weight gain but to an increased fat-to-protein gain ratio in the SL diet. The greater dressing percentage with the SL diet is not due to differences in splanchnic organ weight, which tends to be greater for SL diets. Feed efficiency (BWG/NE_g) was significantly improved at restricted intakes, along with the efficiency of digestible N depot as muscle, whereas the efficiency of NE_g use for fat depot was not significantly modified, which is in line with Geay et al. (1987). On these bases, performance comparisons of the FR bulls vs. the SL and SLR bulls should be able to dissociate the impact of the intake level from the impact of the intake composition.

First, the increased fatness of SL (vs. FR) bulls may have stemmed from cumulating factors over the long feeding period (approximately 300 d). The numerically greater energy intake for the SL diet than for the FR diet resulted in a greater weight gain, which was more marked after 126 d of fattening, with a difference of 14.5%. Bulls fed the SL diet may have needed a fairly long period of adaptation to express changes in fat deposition. Break points are known to exist before fat, particularly in intramuscular fat depots, increases (Carter et al., 2002). Charolais bulls might need to have already achieved most of their growth to efficiently use this starch- and lipids-rich diet and increase their intramuscular fat contents, as was seen in SL muscles.

Strict effects of diet composition could be identified. The most striking differences, interpreted as being due to diet composition, were noted for the proportion of muscle in the carcass and the greater efficiency of digestible N use for muscle depot. Muscle-to-fat ratio was greater for FR vs. SL bulls (4.9 vs. 4.2) at similar muscle-to-bone ratio. This diet composition effect was confirmed after covariance adjusting tissue gain for differences in empty BW (data not shown). Starch supply likely enhances fat gain. At similar metabolizable energy intake, Mueller et al. (2011) did not find any differences in daily gain between fiber and starch diets. Still, isoenergetic and isonitrogenous high-starch vs. fiber-rich rations that also resulted in similar daily gains and muscle depot induced fatter carcasses with starchy diets in young bulls after 8 mo of fattening (Costa et al., 2013). Increased lipogenesis with starch diets was associated with greater ruminal propionic fermentations and possibly greater starch bypass and greater insulinemia (Majdoub et al., 2003). However, Schoonmaker et al. (2004) also showed that energy source affected hyperplasia, whereas the amount of energy affected hypertrophy of fat tissues, implying that

the type of energy affects adiposity when applied in the growing phase. In the present trial, $NE_g I$ were similar in the 56- to 196-d period for SL and FR bulls, but the energy source of these diets differed. Increased fatness with the SL diet could thus result from a combination of different energy sources fed from the growing post-weaning phase onward and nonsignificant differences in $NE_g I$ in the last 70 d of fattening.

Lipid supplementation may influence daily gain, but the literature data do not converge (review by Clinquart et al., 1995). When lipid supplementation using linseed does not result in changes in DMI but increases energy intake, daily gain is either increased (Maddock et al., 2006) or unchanged (Bartoň et al., 2007). The greater fat content in SL bulls than in FR bulls may be due to lipid supply in addition to starch. The positive effect of dietary lipids on fat percentage in carcasses is frequently observed (Clinquart et al., 1995) but not systematically reproduced (Corazzin et al., 2012). In addition, linseed may have improved feed efficiency, as shown by Maddock et al. (2006), and protein deposition efficiency, thereby increasing the amount of energy to be deposited as fat. Indeed, in growing steers, omega-3 LCFA, which are present in linseed-containing diets, were shown to potentiate the effect of insulin on protein metabolism via the mammalian target of rapamycin (**mTOR**) signaling pathway and to reduce amino acid oxidation (Gingras et al., 2007).

Interestingly, the efficiency of utilization of digestible N for muscle depot was greater for the FR diet than for the SL and SLR diets, despite a greater visceral mass. This effect could be strictly attributed to differences in diet composition and/or digestibility. This pattern is opposite that of the efficiency of CP transfer into milk, which is increased by high-starch diets (Cantalapiedra-Hijar et al., 2014).

Metabolic Indicators

On a metabolic basis, a better use of nutrients can be achieved either by changes in weights of tissue or organs or by changes in the specific metabolic activity of each tissue or organ (see reviews by Ortigues and Visseiche [1995] and Hocquette et al. [2007]). Genetic selection on residual feed intake (an indicator of feed efficiency) has been shown to regulate the activities of enzymes involved in FA and glucose metabolisms in the liver and in muscle tissue (Le Naou et al., 2012; Faure et al., 2013). Here, where gross feed efficiency (BWG/NE_g) and partial efficiency of NE_g use for fat depot differed between FR and SL treatments, we hypothesized differences in muscle and liver energy metabolism activity between the SL and FR bulls. In fact, we observed no difference in specific metabolic activity

in the liver and a difference in LDH activity expressed per gram of tissue in only muscles. These limited differences may be explained by several reasons: a difference in the efficiency of muscle or fat gain (<20% between SL and FR diets) that was not sufficient to alter metabolic activity, changes in other metabolic pathways (such as protein metabolism) not assessed here, and the implication of other biological mechanisms. However, note that the first enzyme to be regulated is LDH, as reported in pigs (Le Naou et al., 2012). Lactate dehydrogenase plays a pivotal role in the cross talk between skeletal muscle (conversion of glucose into lactate) and liver (neosynthesis of glucose from lactate), and thus an increased Cori cycle has been associated with lower feed efficiency (Le Naou et al., 2012). Another potential mechanism that probably regulates feed efficiency is the lower weight of the empty digestive tract for the SL diet than for the FR diet, which results from a lower fiber intake (Fitzsimons et al., 2014).

Effect of Energy Source on Muscle Fatty Acid Composition

Improving the nutritional quality of beef is a key challenge for the beef industry. Despite extensive hydrogenation of dietary FA in the rumen, nutritional quality can still be enhanced, especially by a greater deposition of *n*-3 PUFA in muscles to give a greater *n*-3/*n*-6 ratio in meat (see reviews by Wood et al. [2008] and Doreau et al. [2011]). Here, we report the first evidence of significant effects of muscle type and diet factors on beef total lipids and FA composition in finished cattle in which nutritional conditions varied by the level and chemical nature of dietary energy. Indeed, data reported in the literature on variations of beef lipid and FA characteristics with nutritional factors have mainly concerned the effects of basal diet, especially between grass-fed and concentrate-fed diets differing in *n*-6/*n*-3 ratio (Dannenberger et al., 2004; Aldai et al., 2011) and dietary lipid supplements (Raes et al., 2004; Bauchart et al., 2005; Herdmann et al., 2010).

The greater total lipid and FA contents in LT and RA muscles than in ST muscle irrespective of dietary energy characteristics confirmed previous data comparing the nutritional qualities of 9 types of muscles from finishing Charolais cattle (Bauchart et al., 2008). The very significant stimulatory effect of the high dietary energy level on muscle lipid deposition, noted in all studied muscles, has never previously been reported in the bovine species. In contrast, there was a lack of effect of the chemical nature of ingredients (fiber of the FR diet and linseed oil of the SLR diet made isoenergetic to a lower-energy diet) on muscle lipid deposition (noted in all studied muscles), as previ-

ously reported in cattle given lipid-supplemented diets (Bartoň et al., 2007; Herdmann et al., 2010).

The greater deposition of lipids and of FA observed in muscles of bulls given the SL diet, which was greater in energy, would be explained by a stimulation of lipogenic pathways in intra- and intermuscular adipocytes. The hypothesis of this kind of lipogenic effect was confirmed by the greater contents, in muscle cells, of saturated and monounsaturated FA known to be synthesized preferentially by such adipose cells. On the other hand, the greater deposition of linolenic acid at the expense of linoleic acid in muscles of bulls given linolenic acid-rich linseed clearly confirms the capacity of muscle cells to incorporate this dietary *n*-3 PUFA in their lipids, as reported earlier (Noci et al., 2007), thus improving the health value of beef lipids for human consumers.

The intensity of conversion of dietary linolenic acid into *n*-3 long-chain PUFA by reactions of elongation and desaturation in hepatic cells and their subsequent tissue deposition is evaluated by determining EPA, DPA, and DHA contents in muscle cells. Our results clearly showed that EPA, DPA, and DHA were efficiently produced and deposited in muscle tissues, especially in lean (ST) muscle, in finishing bulls given linseed-supplemented diets (SL and SLR diets), thus confirming previous data in meat cattle given different sources of linolenic acid (see Dannenberger et al. [2004], Maddock et al. [2006], and Herdmann et al. [2010] for EPA, DPA, and DHA; see Bartoň et al. [2007] for only EPA and DPA). However, DHA content remained low, showing the low extent of the last desaturation step, which may be due to the low activity of Δ 4-desaturase and to competition between DHA and other LCFA for incorporation in phospholipids (Raes et al., 2004). Additionally, we demonstrate, for the first time, that such metabolic conversion of linolenic acid into LC *n*-3 PUFA is not dietary energy dependent because the greatest muscle deposition of DHA was still observed in bulls fed the energy-restricted SLR diet.

Compared to the FR diet, the SL diet increased the amount of total and all individual *cis* and *trans* isomers (except *trans*-6 18:1 to *trans*-8 18:1) in all muscles. However, isomer proportions changed: among *trans* isomers, the coelution of *trans*-10 18:1 and *trans*-11 18:1 increased, whereas *trans*-12 to *trans*-16 isomers decreased (data not shown). This result is probably due to linolenic acid supply, which has been shown to increase *trans*-12 18:1 to *trans*-16 18:1 isomers at the expense of *trans*-9 18:1 and *trans*-10 18:1 isomers in bulls fed grass (Dannenberger et al., 2004) and in culled cows fed linseed (Habeanu et al., 2014) compared with animals fed cereal diets. In our trial, *trans*-9 18:1 did not change, perhaps because of the opposing effects of cereals and linseed.

Conclusion

One of the novelties of this study was to separate the effects of the source and level of energy intake on fattening performance and carcass responses in bull production. This study compared 2 concentrates differing by the source of energy, based on a mixture of starch and linseed or on fibrous byproducts, and also by the level of energy. Results show that it is possible to modulate performance and meat quality by changing the source of energy in ad libitum-fed diets. Feed efficiency was significantly improved at restricted energy intakes. High dietary energy level increased muscle FA deposition. As expected, the muscle omega-3 FA content was increased by including feeds rich in omega-3 FA, especially in lean (ST) muscle, independent of the dietary energy level.

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