

Young Salers suckled bull production: effect of diet on performance, carcass and muscle characteristics and meat quality

E. Serrano, P. Pradel, R. Jailler, H. Dubroeuq, D. Bauchart, J.-F. Hocquette, A. Listrat, J. Agabriel and D. Micol[†]

INRA-Theix, 63122 Saint-Genès-Champanelle, France

(Received 12 May 2006; Accepted 9 March 2007)

The aim of this work was to improve the knowledge on young suckled Salers bull production and to study the effect of forage type and concentrate level on performance, carcass and muscle characteristics as well as on meat quality. Twenty-four Salers male calves of 150 days of age were assigned to six groups: CO (fed exclusively with hay and dam's milk and slaughtered at approximately 6 months of age), and HH (hay – high concentrate), HL (hay – low concentrate), GH (cut grass – high concentrate), GL (cut grass – low concentrate) and CP (control pasture: pasture – high concentrate) groups differing in feeds received until slaughter and slaughtered unweaned at approximately 10 months of age. Carcass weights averaged 210 kg at 10 months of age at slaughter. Average daily weight gain (ADWG) in HH and GH groups tended to be higher ($P = 0.09$) than in HL and GL groups (1354 v. 1248 g/day). ADWG in CP group (1542 g/day) was higher ($P < 0.05$) than in the other groups. Carcass weight in CP group (230 kg) tended to be higher ($P < 0.1$) than in HL (198 kg) and GL (200 kg) groups. Carcass muscle weight was higher ($P < 0.05$) in GH (155 kg) and CP groups (165 kg) than in HL (141 kg) and GL (142 kg) groups. Carcass and offal fatty tissue weights and carcass fatness did not differ between groups. Neither forage type nor concentrate level had significant effect on the area of muscle fibres or on muscle metabolic enzyme activities (namely, lactate dehydrogenase – LDH, phosphofructokinase – PFK, isocitrate dehydrogenase – ICDH, citrate synthase – CS and cytochrome-c oxidase – COX). semitendinosus muscle of CP group presented higher CS enzyme activities (8.10 $\mu\text{mol}/\text{min per g}$) than HH (5.30 $\mu\text{mol}/\text{min per g}$) and GL (4.52 $\mu\text{mol}/\text{min per g}$) groups. Neither total nor insoluble collagen content significantly differed between groups. Lipid content in rectus abdominis muscle was relatively low (average 67.5 mg/g dry matter) and was not affected by diet ($P > 0.05$). The ratio between n-6 and n-3 polyunsaturated fatty acid content was lower ($P = 0.01$) in the low-concentrate-fed than in the high-concentrate-fed group (3.95 v. 5.37, respectively). Sensory analysis noted that longissimus thoracis muscle from CP animals was more tender and juicy than that from HH and GH animals ($P < 0.05$).

Keywords: carcass, concentrates, forage type, meat quality, suckled bulls

Introduction

In the mountain regions of France, most male calves produced from beef herds are sold lean at weaning, i.e. between 8 and 10 months of age (as 'broutards'), to be finished elsewhere. In these areas, since the imposition of Common Agricultural Policy measures, dairy or mixed cow herds have frequently been replaced by suckler herds. In several areas of European Mediterranean countries, beef obtained from young bulls less than 1 year of age represents an important percentage of beef consumption

(Chatellier *et al.*, 2003). Production of 'finished broutards' could thus represent an interesting possibility to enhance the profitability of mountain farms.

Salers is a dual-purpose breed used for beef production in mountainous areas of central France whose medium precocity characteristics and relatively high milking potential (D'Hour *et al.*, 1995 and 1996; Liénard *et al.*, 2002) may be especially adequate for this type of production based on relatively young animals suckled until slaughter.

Many factors influence animal performance, carcass characteristics and meat quality. However, diet and, especially, forage type and concentrate level, are among the most important factors (Listrat *et al.*, 1999; Geay *et al.*,

[†] E-mail: micol@clermont.inra.fr

2002; Nuernberg *et al.*, 2005). The effects of forage type and concentrate level used in different periods of production have previously been studied, but little information is available for young bulls (slaughtered between 10 and 12 months of age) suckled until slaughter. Therefore, the aims of this work were to examine the effect of diet (type of forage and level of concentrate) on performance, carcass and muscle characteristics as well as on meat quality of young suckled Salers bulls.

Material and methods

Animals and experimental design

This study was conducted at the experimental farm of INRA Marcenat (Cantal, France). Twenty-four winter-born (4 January \pm 16.7 days) Salers male calves were used. All animals were reared indoors by the conventional winter calf-rearing procedure of French mountain zones until approximately 150 days of age: they were suckled twice a day by their dams, having free access to medium-quality cocksfoot hay. On turn-out to pasture (24 May) animals were randomly assigned to six groups according to diet and slaughter age: C0 (control) fed exclusively with winter diet and slaughtered at approximately 6 months of age (used as point 0 in carcass composition estimations explained below) and HH, HL, GH, GL and CP groups offered *ad libitum* cocksfoot hay plus concentrate and slaughtered at approximately 10 months of age (HH, hay – high concentrate) or in a quantity equivalent to half of *ad libitum* group (HL, hay – low concentrate); *ad libitum* cut grass plus concentrate (GH, grass – high concentrate) or in a quantity equivalent to half of *ad libitum* group (GL, grass – low concentrate); and *ad libitum* grazed highland grass and *ad libitum* concentrate (CP, control pasture) group.

HH, HL, GH and GL animals were housed in individual pens and feeds were offered once a day and individual intakes were recorded 5 days/week. They were suckled twice a day by their dams throughout the experimental period and the cows' diet consisted of cocksfoot hay for dams of HH and HL animals and grazed grass for dams of GH and GL animals. Grass offered to GH and GL groups was green vegetative herbage (spring growths and summer regrowths) from a natural pasture cut every morning. The CP group remained on pasture (1100 m in altitude) with their mothers; they grazed in a continuous system of high diversity of natural pasture and were offered concentrate *ad libitum* as a group. Table 1 shows species composition (expressed as percentage) of parcel pastured by CP group and parcel used to obtain cut grass for GH and GL groups.

All animals were individually weighed once a week before and after suckling in order to estimate milk ingestion and live weight (Le Neindre, 1973). Calves were weighed in the early morning before feed distribution. CP calves rested in the same pasture but separated from their mothers during the night before weighing. Average daily gain was calculated by linear regression. Concentrate composition

Table 1 Relative presence of species (%) of parcel pastured by group CP and parcel used to obtain cut grass for groups GH and GL[†]

CP group parcel	%	GH and GL groups parcel	%
Dicotyledons			
<i>Plantago lanceolata</i>	8.6	<i>Taraxacum gr. officinale</i>	19.6
<i>Trifolium repens</i>	5.6	<i>Capsella bursa-pastoris</i>	2.8
<i>Achillea millefolium</i>	5.0	<i>Rumex obtusifolius</i>	2.2
<i>Campanula glomerata</i>	3.3	<i>Veronica chamaedrys</i>	1.7
<i>Ranunculus acris</i>	3.1	<i>Stellaria media</i>	1.7
<i>Rhinantus minor</i>	2.8	<i>Veronica arvensis</i>	0.6
<i>Galium verum</i>	2.5	<i>Cerastium fontanum</i>	0.6
<i>Taraxacum gr. officinale</i>	2.2		
<i>Lotus corniculatus</i>	1.9		
<i>Ranunculus bulbosus</i>	1.9		
<i>Polygonum bistorta</i>	1.7		
<i>Stachys officinalis</i>	1.7		
<i>Trifolium pratense</i>	1.5		
<i>Thymus pulegioides</i>	1.4		
<i>Sanguisorba minor</i>	1.1		
<i>Trifolium dubium</i>	1.0		
<i>Rumex acetosa</i>	0.6		
<i>Veronica chamaedrys</i>	0.6		
<i>Cerastium arvense</i>	0.3		
<i>Meum athamanticum</i>	0.3		
<i>Stellaria graminea</i>	0.3		
Monocotyledons			
<i>Agrostis sp.</i>	15.6	<i>Dactylis glomerata</i>	19.0
<i>Festuca nigrescens</i>	10.0	<i>Lolium perenne</i>	15.6
<i>Avenula pubescens</i>	7.0	<i>Agrostis capillaris</i>	13.4
<i>Poa trivialis</i>	3.5	<i>Trisetum flavescens</i>	9.5
<i>Antoxantum odoratum</i>	3.1	<i>Bromus mollis</i>	6.7
<i>Phleum pratense</i>	2.8	<i>Arrhenatherum elatius</i>	3.4
<i>Cynosurus cristatus</i>	2.5	<i>Poa trivialis</i>	1.6
<i>Carex caryophylla</i>	1.9	<i>Poa pratensis</i>	0.6
<i>Avenula pratensis</i>	1.9	<i>Holcus mollis</i>	0.6
<i>Poa pratensis</i>	1.5	<i>Phleum pratense</i>	0.6
<i>Trisetum flavescens</i>	1.1		
<i>Festuca rubra</i>	1.1		
<i>Koeleria pyramidata</i>	0.6		
<i>Luzula campestris</i>	0.3		

[†]Abbreviations are: CP = control pasture; GH = cut grass – high concentrate; GL = cut grass – low concentrate.

and feed values are given in Tables 2 and 3, respectively. Water and salt blocks were always available to animals.

Slaughter procedure

Animals were slaughtered at the experimental slaughterhouse at INRA, Centre of Clermont Ferrand-Theix (Puy de Dôme, France) in five batches: 1 July for C0 group animals and between 4 October and 8 November for the other groups. In each slaughter batch, the oldest animals in each group were slaughtered first. On the day of slaughter, animals were weighed in the early morning, transported 90 km to the slaughter facility and slaughtered at random within 4 h of removal from experimental farm. Carcasses

Table 2 Concentrate composition

Concentrate ingredients	g/kg of dry matter
Wheat	330
Soya-bean meal	210
Maize feed	200
Wheat bran	100
Dried sugar-beet pulp	90
Sugar-beet molasses	28
Vegetal fats	27
Mineral–vitamin supplement	15

were visually graded according to SEUROP beef carcass grading system for conformation (scale ranging from 18 (S+, very good, superior, conformation) to 1 (P–, very poor conformation)) and fatness (scale ranging from 5 (very high) to 1 (very low)) and placed at room temperature for 2 h, then in a refrigerated room set to 4°C until 24 h *post mortem*. After a 2 h chilling, subjective lean colour was judged by an experienced person using a scale used for veal carcass classification ranging from 1=white to 4=red. pH of *semitendinosus* (ST) and *rectus abdominis* (RA) muscles were measured 24 h *post mortem*. Colorimetric parameters of the CIE L* a* b* uniform colour space (Commission International de l’Eclairage, 1986) were measured on ST and RA muscles using a MINOLTA CM 2002 recording spectrophotometer (illuminant D65, observer angle 10°).

Body composition

The empty body weight, hot carcass weight, and weights of the metacarpus bones and the offal fatty tissues (kidney, heart and digestive tract) were measured. On the following day, the left half carcass of each animal was quartered between the 5th and 6th thoracic vertebrae and the 6th rib was extracted (as described by Robelin and Geay, 1975), weighed and dissected into lean tissue, fat and bone. Two days after slaughter, the right half carcasses of 14 animals (four C0 animals plus two animals of each of the other experimental groups) were dissected and the total weights of lean, bone and fat were recorded according to anatomical distribution.

Regression analysis was used to relate carcass composition traits (muscle, fatty tissues and bone weights) obtained from dissection of right half carcass of 14 animals with the predictors obtained from the dissection of 6th rib, metacarpus bone weight and carcass weight of these animals (Robelin and Geay, 1975). The regression analyses were performed using the GLM procedure of the Statistical Analysis Systems Institute (SAS, 1989) and independent variables were selected by stepwise method. Muscle, fat and bone carcass weights of all experimental animals were estimated using these equations. Total body fat was calculated as the sum of recorded kidney, heart and digestive tract fatty tissues and carcass fat estimated by linear regression.

Table 3 Percentage of DM, chemical composition of feeds and feeding values (for grass, mean (range) of six analyses performed during all experimental period)[†]

	DM (%)	Organic components			Energy		Protein (g)		Bulk BBU/kg DM
		MM (% of DM)	TN (% of DM)	CF (% of DM)	UFL/kg DM	PDIN (g/kg DM)	PDIE (g/kg DM)		
Cocksfoot hay	85.0	7.3	8.9	33.1	0.62	55	69	1.22	
Cut grass	19.8 (18.5–21.6)	8.3 (6.5–10.4)	13.3 (12.0–16.9)	27.4 (23.3–32.4)	0.82 (0.76–0.90)	83 (75–106)	82 (78–94)	1.13 (1.01–1.20)	
Pastured grass	24.7 (24.0–25.0)	7.2 (6.2–8.0)	11.1 (9.6–13.2)	27.4 (25.3–29.0)	0.77 (0.70–0.85)	70 (60–83)	75 (68–84)	1.15 (1.06–1.21)	
Concentrate	88.0	6.2	18.9		1.07	132	111		

[†]Abbreviations are: DM = dry matter; MM = mineral matter; TN = total nitrogen content; CF = crude fibre; UFL = net energy for maintenance and gain expressed in milk feed units (Unités Fourragères Lat); PDIN = proteins truly digestible in the small intestine allowed by the nitrogen content; PDIE = proteins truly digestible in the small intestine allowed by the energy content; BBU = bovine bulk unit.

Muscle characteristics

Two samples of ST and RA muscles of each animal were taken 1 h after slaughter for the determination of muscle fibre size and metabolic enzyme activities. Collagen and lipid contents were determined only in RA muscle samples. The epimysium was carefully dissected and about 300 g of muscle was taken. Part of each sample was frozen in isopentane, chilled in liquid nitrogen for fibre size determination and a further portion was directly frozen in liquid nitrogen and kept at -80°C until analysed for enzyme activities determination. In the case of RA muscle, the rest of the sample was cut in pieces (1 to 2 cm cross section), sealed under vacuum and stored at -20°C until analysed for collagen and lipid content.

Muscle fibre size

Serial sections of 10- μm thick RA and ST muscles were cut on a cryostat at -25°C , perpendicular to the muscle fibres. The cells were stained with azorubine to define their outline and their mean surface areas were measured in two randomly selected areas of serial sections with an image analysis software program (Visilog, INRA, France) (Jurie *et al.*, 1998). An average of 100 fibres were analysed on each serial section.

Metabolic enzyme activities

RA and ST muscle samples were ground and homogenised in 140 mmol/l sucrose and 50 mmol/l triethanolamine buffer (pH 7.5) and centrifuged at $6000 \times g$ for 15 min at 4°C . Enzyme activities were measured in the supernatant. Anaerobic glycolytic metabolism was assessed by lactate dehydrogenase (LDH) and phosphofructokinase (PFK) activities (Beutler, 1971; Brandstetter *et al.*, 1998). Aerobic oxidative metabolism was studied by measuring isocitrate dehydrogenase (ICDH), citrate synthase (CS) and cytochrome-c oxidase (COX) activities (Brandstetter *et al.*, 1998; Piot *et al.*, 1998). Enzyme activities were expressed in $\mu\text{mol}/\text{min}$ per gram of wet muscle.

Collagen

Total hydroxyproline (OH-Prol) content and collagen in the insoluble part were measured as described by Listrat *et al.* (1999 and 2001). Data are presented as means of triplicate measurements and are expressed, for total and insoluble collagen, in μg OH-Prol per mg of dry matter (DM) and also as percentage of OH-Prol in the soluble part per total amount of OH-Prol.

Lipids

Total lipids of RA muscle were extracted according to the method of Folch *et al.* (1957), vacuum dried and weighed. They were solubilised into 5 ml chloroform. Fatty acids from total lipids were esterified in boron-trifluoride/methanol as described by Glass (1971). The fatty acid composition was determined by gas-liquid chromatography, using a

chromatograph DELSI DI 200, a flame ionisation detector, a 100-m long CP-Sil 88 (Varian) glass capillary column and H_2 as the gas vector as described by Aourousseau *et al.* (2004).

Sensory assessment

Seventh to 11th ribs were taken 24 h after slaughter from the left side of carcass. Samples were placed in sealed plastic bags under vacuum and kept at 4°C for 8 days for ageing and then frozen at -20°C until analysis. After thawing, ribs were cooked in a double sided grill (280°C) for 2 min and 30 s. Cooked *longissimus thoracis* muscle of each rib was isolated and cut in homogeneous portions and presented to 8 to 10 trained tasters isolated in booths. Each taster scored from 1 to 10 the intensity of the following characteristics: tenderness, juiciness and cardboard, metal, blood, milk, fat and grass flavours. Flavour variables used were selected by tasters in previous training sessions as the most important parameters to characterise young bull meat. Only a comparison of HH, GH and CP groups was conducted.

Statistical analysis

Statistical analyses were performed using the GLM procedure (SAS, 1989). Feed intake, energy utilisation and muscle characteristics data corresponding to HL, HH, GL and GH groups were subjected to analysis of variance to examine the effect of forage type (grass *v.* hay) and concentrate level (high *v.* low) using a two-factor model (2×2). Interaction between the two factors was included in the model when significant. In a second step, the same information corresponding to HL, HH, GL, GH and CP groups was compared using a one-factor ('group') model. Data corresponding to different muscles were analysed independently. Differences between means were separated by DUNCAN test. The results are presented as mean \pm s.e.

For other production results and carcass characteristics, statistical analysis were also performed in two steps: in the first step (for HL, HH, GL and GH groups), model included forage type and concentrate level as independent variables, their interaction and weight at turn-out to pasture as covariate variable; in the second step (HL, HH, GL, GH and CP groups), model only included 'group' as independent variable and weight at turn-out to pasture as covariate. Forage type \times concentrate level interaction was eliminated from the model when not significant ($P > 0.1$). Differences between means were separated by the PDIFF procedure of SAS. The results are presented as least-squared mean \pm s.e.

Variance analysis of sensory results was performed taking the effects of group and taster into consideration.

Results

Intake

Table 4 shows average daily intake of milk, concentrate and forage for all the experimental period (151 ± 14 days,

Table 4 Effect of forage type and concentrate level on voluntary intake and energy utilisation in HL, HH, GL and GH groups[†]

	Group				s.e.	P values	
	HL	HH	GL	GH		Forage type	Concentrate level
Milk intake (kg/day)	5.17	5.16	5.23	5.02	0.580	0.943	0.863
DM concentrate intake (kg/day)	1.73 ^b	3.18 ^a	1.71 ^b	3.26 ^a	0.060	0.626	0.0001
DM forage intake (kg/day)	2.26 ^a	1.41 ^b	2.55 ^a	1.24 ^b	0.298	0.843	0.003
Net energy intake (UFL/day)	4.75 ^c	5.76 ^{ab}	5.40 ^b	5.96 ^a	0.210	0.065	0.003
PDI intake (g/day)	482.5 ^c	595.9 ^{ab}	560.5 ^b	623.3 ^a	21.43	0.029	0.001
Feed efficiency (live-weight gain (kg)/UFL)	0.255	0.234	0.234	0.232	0.008	0.180	0.201

^{a,b,c}Means within a row with different superscripts differ significantly ($P < 0.05$).

[†]Abbreviations are: DM = dry matter; HL = hay – low concentrate; HH = hay – high concentrate; GL = cut grass – low concentrate; GH = cut grass – high concentrate; UFL = net energy for maintenance and gain expressed in milk feed units (Unités Fourragères Lait); PDI = protein truly digestible in the small intestine.

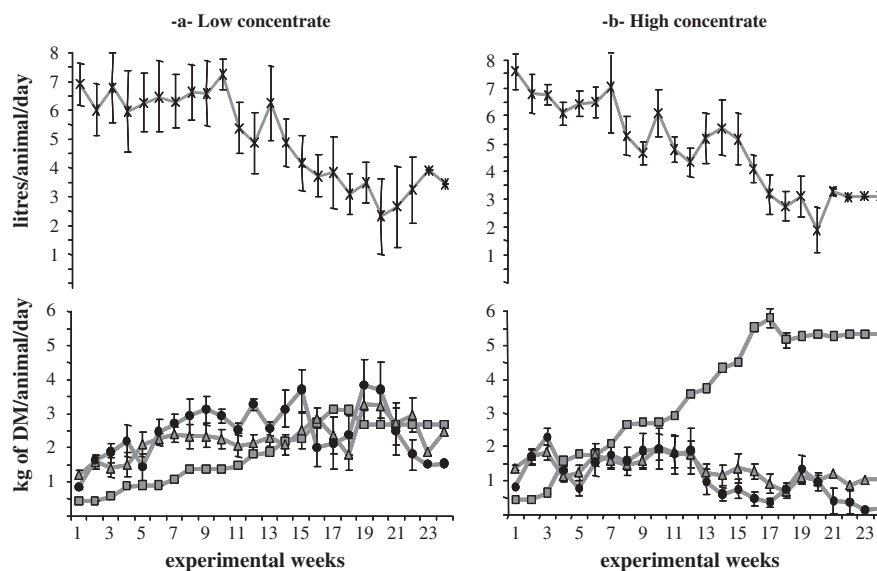


Figure 1 Milk (—X—), concentrate (—■—), hay (—▲—) and grass (—●—) voluntary intakes in (a) low- and (b) high-concentrate groups from turn-out on pasture to slaughter. (DM = dry matter).

between turn-out to pasture and slaughter). Figure 1 represents weekly intake of milk, concentrate, hay and grass in HL and GL groups (Figure 1a – low concentrate) and in HH and GH groups (Figure 1b – high concentrate).

Total milk drunk was not different between HL, HH, GL and GH groups. DM concentrate intake in high-concentrate groups (HH and GH) increased from 0.5 kg/day to approximately 5.5 kg/day (Figure 1b) and was, as expected, almost twice as much of that of HL and GL groups. Average daily forage intake in low-concentrate groups was, approximately 1.8 times that of the high-concentrate groups (Table 4). Forage type had no effect on forage intake considering daily average values for the whole experimental period. But as illustrated in Figure 1b, concentrate substitution effect was higher in grass than in hay groups after the 13th experimental week.

Net energy intake tended to be affected by forage type ($P = 0.06$) and by concentrate intake level ($P = 0.003$). PDI (protein truly digestible in the small intestine) intake was

affected by forage type ($P = 0.03$) and by concentrate intake level ($P = 0.001$). Values in HL group were lower than those in the other groups ($P < 0.05$) reflecting the lower feeding value of hay. Net energy and PDI intake values in GH group were higher than that in GL group ($P < 0.05$), and those of HH group were intermediate between those in GL and GH groups and not significantly different from these ($P > 0.05$).

Average total concentrate intake of CP group was 377 kg, approximately 17% and 23% lower than in HH and GH groups. Mean values for total and daily milk intake tended to be higher ($P = 0.07$ and $P = 0.08$, respectively) in CP group than in the others groups (942 ± 146 kg and 5.86 ± 0.73 kg/day).

Growth, carcass yield and carcass composition

Initial live weight (at turn-out to pasture, 141 ± 9 days of age) was on average 166 ± 9 kg. Age at slaughter was not

different between groups (286, 290, 291, 296 and 293 ± 6 days for groups HL, HH, GL, GH and CP, respectively).

Average daily weight gain (ADWG) in CP group (1542 g/day) was significantly higher than that in the other four groups ($P < 0.05$). This group also had the highest live weight at slaughter (LWS), empty body weight (EBW) and carcass weight (395, 348 and 230 kg, respectively). However, significant differences were found only with HL group ($P < 0.05$) for EBW. LWS values of CP group tended to be higher than those of HL, HH and GL groups ($P < 0.1$). Carcass weight of CP group tended to be higher than those of HL and GL groups ($P < 0.1$). Dressing percentage in CP group was significantly higher ($P < 0.05$) than in the rest of experimental groups (66.2% and 64.2% for CP v. HL, HH, GL and GH groups, respectively).

ADWG tended to be higher ($P = 0.09$) in high-concentrate groups than in low-concentrate groups (1248 and 1354 g/day for HL and GL v. HH and GH groups, respectively). Forage type did not affect ADWG (Table 5).

Concentrate level affected EBW ($P = 0.05$). Carcass weight tended to be higher ($P = 0.07$) in high-concentrate groups than in low-concentrate groups. After CP animals, GH presented the highest EBW and carcass weight values (334 and 216 kg, respectively) followed by HH (331 and 212 kg), GL (312 and 200 kg) and HL (308 and 198 kg) groups, in this order. Differences tended to be significant ($P < 0.1$) only for EBW between GH and HL groups.

Concentrate level significantly affected carcass muscle weight ($P = 0.04$). GH bulls were heavier than HL and GL bulls (155, 141 and 142 kg, respectively; $P < 0.05$). Carcass fatty tissue was not affected by either of the two experimental factors, forage type – concentrate level. Carcass muscle weight in CP group (average 165 kg) was higher ($P < 0.05$) than HL and GL groups. Offal fatty tissues

weight, carcass fatness and conformation scores did not differ between groups (Table 5).

Muscle characteristics

Colour and pH. Muscle pH (Table 6) was not affected by forage type or concentrate level. All animals obtained the maximal value (4=red) of carcass lean colour score. The CP group had higher b^* values than HL and HH groups ($P < 0.05$).

Histological and enzymatic characteristics. Table 7 presents muscle fibre areas and enzyme activities for RA and ST muscles. Whatever the muscle, neither the type of forage nor the concentrate level affected the cross-sectional areas or metabolic enzyme activities of muscle fibres. CP group exhibited the highest values of muscle fibre area for ST muscle but 'group' factor was not significant. When comparing the five experimental groups, 'group' factor tended to be significant for CS enzyme activity ($P = 0.06$) in ST muscle. The highest values corresponded to CP group but differences were significant ($P < 0.05$) only when comparing CP v. HH and GL groups.

Total and heat-soluble collagen. Neither total collagen content nor insoluble collagen content were affected by forage type or concentrate level factors (Figure 2). Similarly, when comparing the five experimental groups, 'group' factor was not significant. However, quality of collagen estimated by soluble/total collagen ratio was significantly affected by forage type ($P = 0.03$). Collagen solubility was lower in HH group than the other three groups ($P < 0.05$). When comparing the five experimental groups, 'group' factor was significant ($P = 0.01$). The highest collagen

Table 5 Average daily weight gain, weight at slaughter and carcass characteristics in five experimental groups (HL, HH, GL, GH, CP) and effect of forage type and concentrate level†

	Five group comparison						Forage type+concentrate level comparison					
	HL	HH	GL	GH	CP	s.e.	P values		s.e.	P values		Initial weight
							Group	Initial weight		F	C	
Live weight at slaughter (kg)	349.8 ^d	359.5 ^d	354.0 ^d	373.2 ^{cd}	394.7 ^c	9.5	0.028	0.013	8.6	0.321	0.125	0.037
Average daily weight gain (g/day)	1232 ^b	1340 ^b	1264 ^b	1368 ^b	1542 ^a	55	0.011	0.017	56	0.606	0.091	0.076
Empty body weight (kg)	307.9 ^b	331.1 ^{ab}	312.2 ^{ab}	334.0 ^a	347.8 ^a	10.9	0.110	0.056	9.9	0.730	0.048	0.093
Warm carcass weight (kg)	197.8 ^d	211.7 ^{cd}	200.2 ^d	215.6 ^{cd}	230.4 ^c	7.9	0.069	0.065	7.1	0.673	0.068	0.142
Dressing percentage	64.3 ^b	63.9 ^b	64.1 ^b	64.5 ^b	66.2 ^a	0.50	0.036	0.513	0.48	0.672	0.998	0.837
Carcass composition:												
Muscle weight (kg)	140.8 ^b	151.7 ^{ab}	141.6 ^b	154.5 ^a	164.8 ^a	5.9	0.070	0.112	5.1	0.737	0.044	0.278
Fatty tissue weight (kg)	21.7	22.7	23.2	24.0	24.0	1.2	0.145	0.070	1.2	0.248	0.452	0.043
Bone weight (kg)	35.3	37.2	35.3	37.1	39.6	1.2	0.113	0.011	1.2	0.948	0.156	0.036
Offal fatty tissue (kg)	7.39	9.65	9.09	9.50	9.61	1.10	0.588	0.638	0.93	0.473	0.226	0.765
Offal fatty tissue/EBW (%)	2.39	2.91	2.91	2.84	2.75	0.27	0.650	0.241	0.24	0.401	0.457	0.830
Total fatty tissue (kg)	29.2	32.3	32.3	33.4	35.7	2.1	0.324	0.419	1.9	0.299	0.302	0.156
Fatness score	2.23	2.13	2.25	2.13	2.12	0.16	0.954	0.919	0.12	0.960	0.545	0.657
Conformation score	5.57	5.57	5.76	6.85	7.16	0.54	0.160	0.026	0.50	0.217	0.357	0.113

^{a,b}Means within a row with different superscripts differ significantly ($P < 0.05$).

^{c,d}Means within a row with different superscripts tended to differ significantly ($P < 0.1$).

† Abbreviations are: HL = hay – low concentrate; HH = hay – high concentrate; GL = cut grass – low concentrate; GH = cut grass – high concentrate; CP = control pasture; F = forage type; C = concentrate level; EBW = empty body weight.

Table 6 pH and colour parameters values in five experimental groups (HL, HH, GL, GH, CP) and effect of forage type and concentrate level in these variables of rectus abdominis and semitendinosus muscles[†]

	Five group comparison							Forage type+concentrate level comparison			
	HL	HH	GL	GH	CP	s.e.	P value		s.e.	P values	
							Group	F		C	
<i>Rectus abdominis</i> muscle											
pH 24 h	5.78	5.76	5.87	5.74	5.72	0.05	0.400		0.06	0.581	0.254
L*	36.75	35.38	36.08	36.36	31.40	1.62	0.182		1.80	0.933	0.770
a*	8.35	7.01	8.12	7.34	11.0	1.14	0.164		1.22	0.967	0.405
b*	9.87 ^b	8.73 ^b	12.06 ^{ab}	10.55 ^{ab}	14.04 ^a	1.21	0.058		1.31	0.154	0.333
<i>Semitendinosus</i> muscle											
pH 24 h	5.65	5.73	5.70	5.72	5.72	0.04	0.299		0.05	0.661	0.300
L*	37.81	37.81	37.94	35.38	35.27	1.45	0.480		1.56	0.477	0.428
a*	8.73	7.61	8.19	8.37	8.79	0.83	0.854		0.85	0.901	0.588
b*	12.34 ^b	12.58 ^b	13.32 ^{ab}	13.10 ^{ab}	14.80 ^a	0.55	0.053		0.50	0.164	0.983

^{a,b}Means within a row with different superscripts differ significantly ($P < 0.05$).

[†]Abbreviations are: HL = hay – low concentrate; HH = hay – high concentrate; GL = cut grass – low concentrate; GH = cut grass – high concentrate; CP = control pasture; F = forage type; C = concentrate level.

Table 7 Fibre area and LDH, PFK, ICDH, CS and COX enzyme activities in five experimental groups (HL, HH, GL, GH, CP) and effect of forage type and concentrate level[†]

	Five group comparison							Forage type+concentrate level comparison				
	HL	HH	GL	GH	CP	s.e.	P values		s.e.	P values		
							Group	F		C	F × C	
<i>Rectus abdominis</i> muscle												
Fibre area (μm^2)	2168	2541	2149	2203	2240	233	0.753		252	0.493	0.413	
LDH ($\mu\text{mol}/\text{min per g}$)	841.2	883.7	811.2	908.1	866.6	50.8	0.708		52.4	0.966	0.212	
PFK ($\mu\text{mol}/\text{min per g}$)	123.9	105.6	115.2	124.1	96.6	9.5	0.228		8.8	0.555	0.571	
ICDH ($\mu\text{mol}/\text{min per g}$)	1.32	1.52	1.41	1.24	1.54	0.13	0.450		0.12	0.482	0.930	
CS ($\mu\text{mol}/\text{min per g}$)	4.40	6.04	5.92	4.96	5.86	0.56	0.206		0.51	0.673	0.521	0.027
COX ($\mu\text{mol cytochrome c}/\text{min per g}$)	14.38	15.73	13.54	11.70	17.57	2.24	0.447		2.0	0.246	0.904	
<i>Semitendinosus</i> muscle												
Fibre area (μm^2)	2569	2333	2147	2615	3163	253	0.108		277	0.805	0.683	
LDH ($\mu\text{mol}/\text{min per g}$)	895.4	843.0	900.2	913.2	867.7	60.2	0.923		62.0	0.557	0.757	
PFK ($\mu\text{mol}/\text{min per g}$)	137.8	129.7	126.5	126.2	117.1	9.4	0.653		9.9	0.472	0.701	
ICDH ($\mu\text{mol}/\text{min per g}$)	1.90	2.33	1.51	1.76	1.91	0.60	0.910		0.65	0.476	0.609	
CS ($\mu\text{mol}/\text{min per g}$)	6.40 ^{ab}	5.30 ^b	4.52 ^b	6.67 ^{ab}	8.10 ^a	0.81	0.064		0.90	0.784	0.568	0.096
COX ($\mu\text{mol cytochrome c}/\text{min per g}$)	11.76	16.23	12.70	16.23	14.60	2.24	0.529		2.47	0.853	0.132	

^{a,b}Means within a row with different superscripts significantly differ ($P < 0.05$).

[†]Abbreviations are: LDH = lactate dehydrogenase; PFK = phosphofructokinase; ICDH = isocitrate dehydrogenase; CS = citrate synthase; COX = cytochrome-c oxidase HL = hay – low concentrate; HH = hay – high concentrate; GL = cut grass – low concentrate; GH = cut grass – high concentrate; CP = control pasture; F = forage type; C = concentrate level; LDH = lactate dehydrogenase; PFK = phosphofructokinase; ICDH = isocitrate dehydrogenase.

solubility was found in CP group, in which it was significantly higher ($P = 0.05$) than in HL and HH groups.

Lipid content. Table 8 presents total lipid content and fatty acid composition of RA muscle. The lipid content of RA muscle was relatively low (on average 68.7 mg/g DM) and

was not affected by feeding treatments ($P > 0.05$). Percentages of monounsaturated fatty acids were lower in hay-fed than in grass-fed animals ($P = 0.05$). Percentages of polyunsaturated fatty acids (PUFA) were higher in hay-fed animals but differences were not significant. The ratio between *n-6/n-3* PUFA was lower ($P = 0.01$) in low-concentrate-fed groups than in high-concentrate-fed groups.

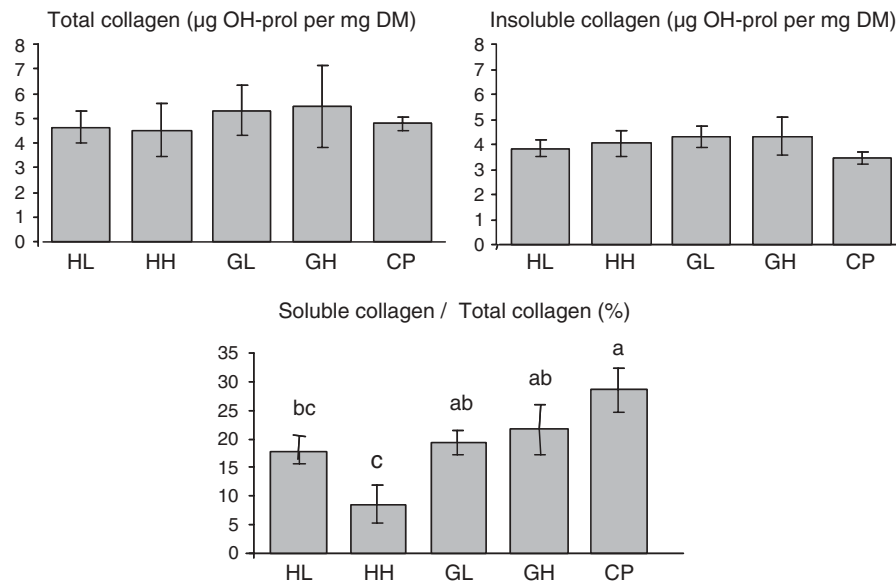


Figure 2 Total and insoluble collagen content, and collagen solubility of *rectus abdominis* muscle in five experimental groups (a–c = means with different letters significantly differ at $P < 0.05$; OH-prol = hydroxy proline; DM = dry matter; HL = hay – low concentrate; HH = hay – high concentrate; GL = cut grass – low concentrate; GH = cut grass – high concentrate; CP = control pasture).

Table 8 Effect of forage type and concentrate level in five experimental groups (HL, HH, GL, GH, CP) on lipid content and FA composition of *rectus abdominis* muscle[†]

	Five group comparison					Forage type + concentrate level comparison					
	HL	HH	GL	GH	CP	s.e.	P values		s.e.	P values	
							Group	F		C	
Total lipids (mg/g dry matter)	74.6	63.5	70.0	66.5	63.0	7.2	0.768		7.9	0.918	0.376
In % of total FA											
∑Saturated FA [‡]	47.7	48.3	46.6	49.4	49.1	2.3	0.909		2.5	0.990	0.489
∑Monounsaturated FA [‡]	31.9	28.9	33.5	32.9	31.2	1.2	0.112		1.3	0.051	0.191
∑PUFA [‡]	14.2	16.2	13.1	12.3	13.6	1.5	0.488		1.5	0.141	0.732
(n-6) PUFA [‡] /(n-3) PUFA [§]	4.25 ^b	5.05 ^{ab}	3.64 ^b	5.69 ^a	4.40 ^{ab}	0.45	0.045		0.47	0.975	0.011
(n-6) + (n-3) PUFA/linear saturated FA	0.32	0.36	0.29	0.26	0.29	0.04	0.624		0.05	0.205	0.938

^{a,b}Means within a row with different superscripts differ significantly ($P < 0.05$).

[†]Abbreviations are: F = forage type; C = concentrate level; HL = hay – low concentrate; HH = hay – high concentrate; GL = cut grass – low concentrate; GH = cut grass – high concentrate; CP = control pasture; FA = fatty acid; PUFA = polyunsaturated fatty acid.

[‡]Saturated FA = sum of total linear and total branched chain saturated FA. Monounsaturated FA = sum of total 16:1 *cis* and *trans* isomers, total 18:1 *cis* and *trans* isomers, C20:1 *cis*, C22:1 *cis* and C24:1 *cis* fatty acids. PUFA = sum of (n-6) PUFA and (n-3) PUFA.

[§](n-6) PUFA = sum of C18:2 n-6, C18:3 n-6, C20:2 n-6, C20:3 n-6, C20:4 n-6, C22:2 n-6, C22:4 n-6 fatty acids.

^{||}(n-3) PUFA = sum of C18:3 n-3, C20:3 n-3, C18:4 n-3, C20:5 n-3, C22:5 n-3 and C22:6 n-3 fatty acids.

^{||}Linear saturated FA = sum of C10:0, C11:0, C12:0, C13:0, C14:0, C15:0, C16:0, C17:0, C18:0, C20:0, C21:0, C22:0, C23:0 and C24:0 fatty acids.

Mean n-6/n-3 ratio in CP group (4.40) was intermediate between the highest values corresponding to HH and GH groups and the lowest values corresponding to HL and GL groups. Differences were significant ($P < 0.05$) only when GH v. HL and GL groups were compared.

$P = 0.003$, respectively). CP group presented significantly lower tenderness and juiciness values ($P < 0.05$) than HH and GH groups.

Discussion

The production system adapted resulted in the production of relatively lean carcasses averaging 210 kg. High-concentrate-fed groups presented slightly higher ADWG than low-concentrate-fed groups (approximately 100 g).

Muscle sensory traits. Table 9 presents the results for the taste panel scores in *longissimus thoracis* corresponding for groups CP, HH and GH. 'Group' factor was significant only for tenderness and juiciness variables ($P = 0.01$ and

Table 9 Meat sensory traits in longissimus thoracis muscle of HH, GH and CP groups[†]

	Group			s.e.	P values	
	HH	GH	CP		Group	Taster
Tenderness	5.17 ^a	5.42 ^a	4.14 ^b	0.96	0.01	0.004
Juiciness	4.60 ^a	4.79 ^a	3.63 ^b	0.75	0.003	< 0.0001
Flavours						
Cardboard	1.55	1.43	1.77	0.49	0.33	< 0.0001
Metal	1.48	1.43	1.48	0.67	0.98	< 0.0001
Blood	1.59	1.11	1.16	0.67	0.25	< 0.0001
Milk	0.87	1.07	1.01	0.41	0.57	< 0.0001
Fat	0.88	1.00	0.96	0.65	0.92	< 0.0001
Grass	0.87	0.93	1.06	0.49	0.72	< 0.0001

^{a,b}Means within a row with different superscripts differ significantly ($P < 0.05$).

[†]Abbreviations are: HH = hay – high concentrate; GH = cut grass – high concentrate; CP = control pasture.

High-concentrate feeding increased carcass weight by 15 kg compared with low-concentrate feeding. Differences in ADWG between high-concentrate and low-concentrate groups were expressed by differences in carcass weight associated with higher muscle weight but without differences in fatness. Carcass fatness is affected by several factors like sex, age, genotype and growth rate (Micol *et al.*, 1993). Usually, higher growth rates are associated with higher carcass fatness, but many experiments that found this effect were performed with bulls slaughtered at higher ages than in the present work (Steen and Kilpatrick, 1995; Listrat *et al.*, 1999; Sami *et al.*, 2004) or with animals differing in sex (heifers or steers) and age (French *et al.*, 2001). Sinclair *et al.* (1998) indeed observed significant differences in carcass weight but not in carcass fatness in young Charolais bulls slaughtered between 10 and 19 months, with daily gains differing on average by 600 g/day (1.41 v. 1.98 kg/day). In the same experiment, these authors obtained carcasses with the same weight but differing in fatness with bulls of a higher precocity genotype (Aberdeen Angus) differing by 300 g/day in growth rate (daily gains of 1.22 v. 1.55 kg/day).

Diet did not affect muscle pH, which agrees with the observations from numerous studies (French *et al.*, 2000 and 2001; Sami *et al.*, 2004) and suggests that all diets supplied sufficient energy to allow a normal pH evolution. Muir *et al.* (1998) indicated that grass-fed animals often presented higher pH values than grain-fed animals as a result of interaction of diet and their higher susceptibility to pre-slaughter stress because they are less used to handling. In our study, animals were slaughtered within 4 h after removal from experimental installations and all groups were used to handling, which may have minimised the impact of stress on the depletion of glycogen deposits.

Muscle colour is an important criterion by which many consumers evaluate meat quality and acceptability. The results concerning subjective classification of muscle colour showed that an important characteristic of the meat pro-

duced is that it was very red compared with traditional veal meat. Diet (forage type and concentrate level) had no effect on L* and a* colour parameters. In the two muscles that were considered, b* values were higher in grass-fed animals but differences were significant only when comparing pasture-fed v. hay-fed animals. Animals raised on pasture presented the lowest L* values compared with the other four groups of animals but differences were not significant. Meat from cattle raised on pasture is indeed known to be darker than meat from animals raised on concentrates (Priolo *et al.*, 2001). But French *et al.* (2000 and 2001) did not observe any difference in colour parameters in steers finished (85 days) on diets constituting combinations of different forages (grass silage, grass or hay) and different concentrate levels allowing the same or different growth rates and slaughtered at the same age. Varela *et al.* (2004) also failed to find differences in meat colour between steers finished (3 months) exclusively on pasture or with corn silage and concentrate, slaughtered at the same age and live weight. On the contrary, Nuernberg *et al.* (2005) reported lower L* values (a* and b* values were not measured) in bulls finished on grass-based v. concentrate-based diets. These authors hypothesised that these differences could be associated with higher physical activity of grass-fed animals compared with indoor kept concentrate-fed bulls. It is, however, necessary to point out that in this work the experimental period (between 11 and 19 months) was longer and started when animals were younger than in the experiments cited before and pasture-finished animals were slaughtered at higher age than concentrate-fed ones (18 v. 24 months). In agreement with our observations, Monserrat *et al.* (2001) also noted higher b* values in pasture-fed than in concentrate-hay-fed young bull meat.

Neither forage type nor concentrate level affected muscle fibre area. These results are in accordance with those of Listrat *et al.* (1999) who did not find any difference in muscle fibre area between Salers bulls fed on isoenergetic and isoproteic diets based on grass silage or hay and concentrate. Cassar-Malek *et al.* (2004a), Maltin *et al.* (2001) and Sami *et al.* (2004) also failed to find differences in muscle fibre surface between animals finished on high- or low-energy diets and presenting moderate differences in growth rates (between 200 and 400 g/day). In contrast with these observations, Jurie *et al.* (1999) showed that restricted growth rate was associated with lower fibre surface, but differences in growth rate observed in this latter experiment (approximately 640 g/day) were greater than differences observed in our study and in experiments cited before. It is interesting to note that in the ST muscle, the highest values of fibre size corresponded to pasture animals, although differences were not significant. In agreement with this observation, Jurie *et al.* (1998) observed an increase in ST muscle fibre size in animals housed in loose housing compared with those housed in tying-type housing.

Several works have reported the effect of diet on muscle energy metabolism. The results obtained in several studies suggested an association between grass or grass silage

feeding and an increase in oxidative activities of muscles (Jurie *et al.*, 1999; Listrat *et al.*, 1999). In the present work, diet did not affect enzyme activities. This result agrees with observations of Maltin *et al.* (1998) who did not find differences in these parameters in young bulls fed on grass-silage-based or barley-based diets. However, we found higher CS enzyme activities in pasture-fed animals. This observation agrees with the results of Jurie *et al.* (2004) and Cassar-Malek *et al.* (2004b) who observed that in the development of muscle metabolic characteristics mobility is a much more important factor than diet. In agreement with our results, Jurie *et al.* (1998) observed that effects of physical activity on enzyme activities depended on type of muscle studied, or more precisely, the involvement of this muscle in movement (e.g. ST) or posture (e.g. RA).

Quantity and solubility of collagen may be influenced by several factors, including growth rate, nature of diet, physical activity and muscle analysed (Bailey and Light, 1989). We did not observe significant differences between groups in total and insoluble collagen contents of RA muscle but soluble/insoluble collagen content ratio was higher in the three grass-fed groups. Contradictions exist in the literature about effects of growth rate and diet nature on collagen pattern. Sami *et al.* (2004), comparing four diets based on different proportions of maize silage and concentrate formulated to allow different growth rates, did not find differences in collagen content but higher collagen solubility in animals with higher daily weight gain. Maltin *et al.* (1998) observed higher collagen content in *longissimus lumborum* muscle of animals finished on grass-silage-based diet having low growth rate than in animals finished on barley-based diet having high growth rate (approximate weight gain differences of 400 g/day) and no effect on collagen solubility. Listrat *et al.* (1999), comparing two groups of Salers bulls fed on diets based on grass silage or hay, did not observe differences in ST muscle collagen content. In this experiment, hay-fed animals presented lower growth rates and higher collagen solubility than grass-silage-fed animals (−122 g/day).

Intramuscular fat content can be modified by several factors like age, genotype and growth rate. In general, intramuscular fat content increases with age and with growth rate and is higher in mixed breeds than in beef breeds (Nürnberg *et al.*, 1998). In the present experiment, intramuscular fat content was not affected by production strategies and values obtained (between 15.1 and 17.7 mg/g wet matter muscle and between 63.0 and 74.6 mg/g dry muscle) were very low compared with those obtained in other works for *longissimus thoracis* muscle, in general a muscle less fatty than RA muscle analysed in the present work. These results could be explained by the moderate growth rates obtained and by the young age at slaughter. For example, Serra *et al.* (2004) reported mean values of intramuscular fat content of 24 mg/g wet muscle in Bruna dels Pirineus bulls slaughtered at 30 months. Varela *et al.* (2004) did not observe differences in intramuscular fat content between 33 months Rubia Gallega steers finished

on pasture or on maize-silage-based and concentrate-based diets. These authors also obtained, for *longissimus thoracis* muscle, mean values of 27 mg of total fat/g wet muscle. Maltin *et al.* (1998) observed an important effect of age on intramuscular fat content but did not find differences between animals with growth rates differing between 300 and 600 g/day. They reported intramuscular fat content of 171.1 mg/g DM in Aberdeen Angus and Charolais bulls slaughtered at 11.5 months of age.

United Kingdom Department of Health recommends a polyunsaturated:saturated (P/S) ratio ~ 0.45 in the whole diet of man, and increasing intake of *n*-3 relative to *n*-6 PUFA and achieving a *n*-6/*n*-3 fatty acids ratio below 4.0 (Enser *et al.*, 1998). Ruminant meats are known to have low polyunsaturated/saturated fatty acid ratio because of rumen biohydrogenation of dietary unsaturated fat (Geay *et al.*, 2002). In the present experiment, production strategies did not affect P/S ratio. Hornick *et al.* (1996) showed that inclusion of milk in fattening diet of bulls increased saturated fatty acid content of intramuscular fat and decreased monounsaturated and polyunsaturated fatty acid contents. In our experiment, all animals remained unweaned until slaughter and, as in the experience of Hornick *et al.* (1997), closure of oesophageal groove remained active. P/S ratios in the present work were similar to those obtained by Varela *et al.* (2004) in Rubia Gallega steers, weaned at 9 months of age, maintained on pasture until 30 months of age and then finished for 3 months on concentrate or pasture systems (approximately 0.25 and 0.33, respectively). However, P/S ratios were higher than those reported by Nuernberg *et al.* (2005) in Holstein and Simmental bulls slaughtered between 17 and 25 months of age and assigned to concentrate-based or grass-based production systems from weaning, at 6 months, to slaughter (0.17 and 0.21 for Holstein bulls and 0.20 and 0.32 for Simmental bulls). These results may, in part, be explained by the fact that when intramuscular fat content is low, as occurred in the present work, the relative importance of membrane phospholipids, rich in unsaturated fatty acids, is higher (Bas and Sauvant, 2001).

The *n*-6/*n*-3 PUFA ratio in muscle fatty acids of ruminants is often too high relative to the recommendation noted above for man (Enser *et al.*, 1998). Generally, muscles of grass-fed ruminants have lower *n*-6 PUFA and higher *n*-3 PUFA than concentrate-fed ruminants although adding sources of linoleic acid to concentrate (such as linseed) improves the equilibrium between these fatty acids in meat (Enser *et al.*, 1998; Geay *et al.*, 2002). In the present work, in agreement with the observations of Enser *et al.* (1998), Arousseau *et al.* (2004) and Nuernberg *et al.* (2005) the more favourable values of *n*-6/*n*-3 PUFA ratio corresponded to meat from animals fed on low concentrate and higher forage.

Higher growth rates have been associated with the production of more tender meat (French *et al.*, 2001; Nuernberg *et al.*, 2005). In the present work, pasture-fed animals obtained significantly lower tenderness and

juiciness scores than other groups, although they presented higher growth rates. Sami *et al.* (2004) and Sinclair *et al.* (2001) have not observed differences in tenderness of meat from 15 months bulls or steers, respectively, differing in growth rate. Listrat *et al.* (1999) obtained more tender meat in hay-fed Salers bulls than in grass-silage-fed animals having higher growth rates. Factors other than growth rate, such as diet composition (Listrat *et al.*, 1999) or physical activity (Jurie *et al.*, 1998), can affect the metabolic and histological characteristics of the muscle and, as a result, the meat tenderness. The results referring to metabolic and histological characteristics of the muscle indicated that pasture animals could have more oxidative muscles and could be constituted of fibres with larger surface than other groups. Several authors have associated these characteristics with tougher meat (Jurie *et al.*, 1998; Renand *et al.*, 2001) but not with a lower juiciness, more associated with other characteristics such as fat content (Geay *et al.*, 2002). Differences in juiciness could be explained considering correlation between tenderness and juiciness scores ($r = 0.46$; $P < 0.0001$), and that the pasture group presented the lowest mean value of fat content although values were not statistically different. Considering the importance of ageing process in quality of bovine meat coming from pasture systems (French *et al.*, 2000; Renand *et al.*, 2001), these results question whether the 8 days ageing period used was sufficient or not.

Conclusion

The results obtained suggest that the diets used have only a small effect on performance, offal fatty tissue weight, carcass and muscle characteristics and on meat eating quality traits. Meat produced was characterised by a very low fat content and a relatively high unsaturated fatty acid content, which could be favourable in a context of increased demand for leaner beef and consumer resistance to beef with a high fat content.

Acknowledgements

The authors wish, in particular, to thank I. Constant and C. Cirie for their help and support. The authors also thank Gloria López, INRA-Marcenat staff, M.C. Bayle, C2M and NEM staffs and the team of the experimental slaughterhouse in Theix.

References

Aurousseau B, Bauchart D, Calichon E, Micol D and Priolo A 2004. Effect of grass or concentrate feeding systems and rate of growth on triglyceride and phospholipid and their fatty acids in the *M. longissimus thoracis* of lambs. *Meat Science* 66, 531–541.

Bailey AJ and Light ND 1989. *Connective tissue in meat and meat products*. Elsevier Applied Science, London and New York.

Bas P and Sauvant D 2001. Variations de la composition des dépôts lipidiques chez les bovins. *INRA Productions Animales* 14, 311–322.

Beutler E 1971. Phosphofructokinase. In *Red cell metabolism. A manual of biochemical methods* (ed. E Beutler), pp. 42–44. Grune and Straton Inc., New York, USA.

Brandstetter AM, Picard B and Geay Y 1998. Muscle fibre characteristics in four muscles of growing male cattle. I. Postnatal differentiation. *Livestock Production Science* 53, 15–23.

Cassar-Malek I, Hocquette JF, Jurie C, Listrat A, Jailler R, Bauchart D, Briand D and Picard B 2004a. Muscle-specific metabolic, histochemical and biochemical responses to a nutritionally induced discontinuous growth path. *Animal Science* 79, 49–59.

Cassar-Malek I, Jurie C, Bernard C, Barnola I, Gentes G, Guivier N, Dozias D, Micol D and Hocquette JF 2004b. La conduite des bœufs au pâturage modifie les caractéristiques métaboliques des muscles et l'expression de certains gènes musculaires. *Rencontres autour des Recherches sur les Ruminants* 11, 124.

Chatellier V, Guyomard H and Le Bris K 2003. La production et les échanges de viande bovine dans le monde et dans l'Union européenne. *INRA Productions Animales* 16, 365–380.

Commission International de l'Eclairage 1986. *Colorimetry*, 2nd edition. CIE publication no. 15.2. Commission International de l'Eclairage, Vienna, Austria.

D'Hour P, Petit M, Pradel P and Garel JP 1995. Evolution du poids de la production laitière au pâturage de vaches allaitantes Salers et Limousines dans deux milieux. *Rencontres autour des Recherches sur les Ruminants* 2, 105–108.

D'Hour P, Petit M and Garel JP 1996. Effet de la conduite alimentaire sur le développement et l'âge à la puberté de génisses Limousines et Salers. *Rencontres autour des Recherches sur les Ruminants* 3, 233–236.

Enser M, Hallett KG, Hewett B, Fursey GAJ, Wood JD and Harrington G 1998. Fatty acid content and composition of UK beef and lamb muscle in relation to production system and implications for human nutrition. *Meat Science* 49, 329–341.

Folch J, Lees M and Stanley GHS 1957. A simple method for the isolation and purification of total lipids from animal tissue. *Journal of Biological Chemistry* 226, 497–509.

French P, O'Riordan EG, Monahan FJ, Caffrey PJ, Vidal M, Mooney MT, Troy DJ and Moloney AP 2000. Meat quality of steers finished on autumn grass, grass silage, or concentrate-based diets. *Meat Science* 56, 173–180.

French P, O'Riordan EG, Monahan FJ, Caffrey PJ, Mooney MT, Troy DJ and Moloney AP 2001. The eating quality of meat of steers fed grass and/or concentrates. *Meat Science* 57, 379–386.

Geay Y, Bauchart D, Hocquette JF and Culioli J 2002. Valeur diététique et qualités sensorielles des viandes de ruminants. Incidence de l'alimentation des animaux. *INRA Productions Animales* 15, 37–52.

Glass RL 1971. Alcoholysis, saponification and the preparation of fatty acid methyl esters. *Lipids* 6, 919–925.

Hornick JL, Clinquart A, Van Eenaeme C, Diez M and Istasse L 1996. Influence of whole milk in diet of growing fattening Belgian Blue bulls on animal performances and on fatty acid composition in subcutaneous, intermuscular and intramuscular fats. *Livestock Production Science* 48, 51–58.

Jurie C, Picard B and Geay Y 1998. Influences of the method of housing bulls on their body composition and muscle fibre types. *Meat Science* 50, 457–469.

Jurie C, Listrat A, Giraud X, Picard B, Geay Y and Hocquette JF 1999. Influence du niveau de croissance et de la nature de l'alimentation sur les caractéristiques musculaires de bœufs Charolais de 20 mois. *Rencontres autour des Recherches sur les Ruminants* 9, 259.

Jurie C, Ortigues-Marty I, Micol D, Cassar-Malek I, Dozias D, Picard B and Hocquette JF 2004. Effets respectifs de la nature de l'alimentation et de la mobilité sur le potentiel métabolique des muscles de bœufs charolais. *Viandes et Produits Carnés (special issue)*, 71–72.

Le Neindre P 1973. Observations sur l'estimation de la production laitière des vaches allaitantes par la pesée du veau avant et après la tétée. *Annales de Zootechnie* 22, 413–422.

Liénard G, Lherm M, Pizaine MC, Le Maréchal JY, Boussange B, Barlet D, Esteve P and Bouchy R 2002. Productivité de trois races bovines françaises, Limousine, Charolaise et Salers. *INRA Productions Animales* 15, 293–312.

Listrat A, Rakadjijiski N, Jurie C, Picard B, Touraille C and Geay Y 1999. Effect of the type of diet on muscle characteristics and meat palatability of growing Salers bulls. *Meat Science* 53, 115–124.

Listrat A, Picard B, Jailler R, Collignon H, Peccatte J-R, Micol D, Geay Y and Dozias D 2001. Grass valorisation and muscular characteristics of blonde d'Aquitaine steers. *Animal Research* 50, 105–118.

Maltin CA, Sinclair KD, Warris PD, Grant CM, Porter AD, Delday MI and Warkup CC 1998. The effects of age at slaughter, genotype and finishing system on the

- biochemical properties, muscle fibre type characteristics and eating quality of bull beef from suckled calves. *Animal Science* 66, 341–348.
- Maltin CA, Lobley GE, Grant CM, Miller MA, Kyle DJ, Horgan GW, Matthews KR and Sinclair KD 2001. Factors influencing beef eating quality. 2. Effects of nutritional regimen and genotype on muscle fibre characteristics. *Animal Science* 72, 279–287.
- Micol D, Robelin J and Geay Y 1993. Composition corporelle et caractéristiques biologiques des muscles chez les bovins en croissance et à l'engrais. *INRA Productions Animales* 6, 61–69.
- Montserrat L, Sánchez L, Varela A, Carballo JA and Oliete B 2001. Producción de terneros de raza Rubia Gallega sacrificados sin destetar: efecto de la extensificación del manejo sobre el color de la carne y la grasa. *ITEA 22* (volumen extra), 559–561.
- Muir PD, Deaker JM and Brown MD 1998. Effects of forage and grain-based feeding systems on beef quality: a review. *New Zealand Journal of Agricultural Research* 41, 623–635.
- Nuernberg K, Dannernberger D, Nuernberg G, Ender K, Voigt J, Scollan ND, Wood JD, Nute GR and Richardson RI 2005. Effect of a grass-based and a concentrate feeding system on meat quality characteristics and fatty acid composition of *longissimus* muscle in different cattle breeds. *Livestock Production Science* 94, 137–147.
- Nürnberg K, Wegner J and Ender K 1998. Factors influencing fat composition in muscle and adipose tissue of farm animals. *Livestock Production Science* 56, 145–156.
- Piot C, Veerkamp JH, Bauchart D and Hocquette JF 1998. Contribution of mitochondria and peroxisomes to palmitate oxidation in rat and bovine tissues. *Comparative Biochemistry and Physiology. Part B: Biochemistry and Molecular Biology* 121, 185–194.
- Priolo A, Micol D and Agabriel J 2001. Effects of grass feeding systems on ruminant meat colour and flavour. A review. *Animal Research* 50, 185–200.
- Renand G, Picard B, Touraille C, Berge P and Lepetit J 2001. Relationships between muscle characteristics and meat quality traits of young Charolais bulls. *Meat Science* 59, 49–60.
- Robelin J and Geay Y 1975. Estimation de la composition de la carcasse des taurillons a partir de la composition de la 6^{ème} cote. *Bulletin Technique CRZV de Theix, INRA* 22, 41–44.
- Sami AS, Augustini C and Schwarz FJ 2004. Effects of feeding intensity and time on feed on performance, carcass characteristics and meat quality of Simmental bulls. *Meat Science* 67, 195–201.
- Statistical Analysis Systems Institute 1989. *SAS/STAT® user's guide, version 6, 4th edition*. SAS Institute Inc., Cary, NC, USA.
- Serra X, Gil M, Gispert M, Guerrero L, Oliver MA, Sañudo C, Campo MM, Panea B, Olleta JL, Quintanilla R and Piedrafita J 2004. Characterisation of young bulls of the *Bruna dels Pirineus* cattle breed (selected from old Brown Swiss) in relation to carcass, meat quality and biochemical traits. *Meat Science* 66, 425–436.
- Sinclair KD, Cuthbertson A, Rutter A and Franklin MF 1998. The effects of age at slaughter, genotype and finishing system on the organoleptic properties and texture of bull beef from suckled calves. *Animal Science* 66, 329–340.
- Sinclair KD, Lobley GE, Horgan GW, Kyle DJ, Porter AD, Matthews KR, Warkup CC and Maltin CA 2001. Factors influencing beef eating quality 1. Effects of nutritional regimen and genotype on organoleptic properties and instrumental texture. *Animal Science* 72, 269–277.
- Steen RWJ and Kilpatrick DJ 1995. Effects of plane of nutrition and slaughter weight on the carcass composition of serially slaughtered bulls, steers and heifers of three breed crosses. *Livestock Production Science* 43, 205–213.
- Varela A, Oliete B, Moreno T, Portela C, Monserrat L, Carballo JA and Sánchez L 2004. Effect of pasture finishing on the meat characteristics and intramuscular fatty acid profile of steers of the Rubia Gallega breed. *Meat Science* 67, 515–522.