

Meat quality traits and muscle composition of cows differing in lactation performance

Mohamed Hamada^{1,2}, Elke Albrecht¹, Abdel-Rahman El Bagory², Abo-Bakr Edris³, Harald M. Hammon⁴, Gerd Nuernberg⁵ and Steffen Maak¹

¹Research Unit Muscle Biology and Growth, Leibniz Institute for Farm Animal Biology (FBN), Dummerstorf, Germany,

²Department of Food Hygiene & Control, Faculty of Veterinary Medicine, Minufia University, Shibin El Kom, Egypt,

³Department of Food Hygiene & Control, Faculty of Veterinary Medicine, Banha University, Banha, Egypt, ⁴Research Unit Nutritional Physiology »Oskar Kellner«, Leibniz Institute for Farm Animal Biology (FBN), Dummerstorf, Germany,

⁵Research Unit Genetics and Biometry, Leibniz Institute for Farm Animal Biology (FBN), Dummerstorf, Germany

Abstract

Beef and dairy cows differ in the way in which they utilise nutrients and in accretion or mobilisation of body reserves during lactation. Thus far, little is known about the impact of lactation performance on body composition, meat quality, and the related muscle structure of cows with a defined, combined beef and dairy genetic background. In the described experiment, 50 F₂ cows, originating from mating Charolais bulls to German Holstein cows and a following intercross of F₁ individuals, were slaughtered during the second lactation, 30 days after calving. Cows were assigned to 3 groups, each containing representatives of 3 families, according to lactation performance. Standard carcass and meat quality traits were determined. Additionally, samples from *longissimus* muscle were investigated by histology and computer image analysis for muscle fibre profile, intramuscular fat cell size, and marbling traits. Subcutaneous fat cell size was measured to estimate the impact of lactation on body fat reserves. The results suggest no influence of the duration of the first lactation on body composition, meat quality or muscle structure. However, the amount of milk per day influenced body weight, body composition, and marbling traits. Relationships between traits were low, but showed consistently that increasing milk yield was negatively correlated with tissue accretion. Changes of muscle fibre and fat cell profile, indicating protein or fat mobilisation by lactation, could not be detected. In the presented study, lactation had only minor consequences for meat quality.

Keywords: lactation performance, muscle fibre, meat quality, fat cell, marbling

Introduction

Beef and dairy cattle represent divergent metabolic types that disseminate nutrients preferably into either meat or milk and differ in nutrient accretion (Pareek *et al.* 2007, Lahann *et al.* 2010). Charolais as a typical beef breed is known for the distinct nutrient accretion and low milk yield. In contrast, German Holstein is a typical dairy breed known for high milk secretion and low tissue accretion of nutrients. These two breeds were the P₀ founder breeds for the SEGFAM experiment at the Leibniz Institute for Farm Animal Biology (FBN) Dummerstorf, Germany, which is described in detail by Kühn *et al.* (2002). The cows used in

the presented study were part of the F_2 offspring of this experiment. This model enabled us to study effects of variability in lactation performance of cows having identical, combined beef and dairy genetic background on carcass and meat quality traits.

Lactation is a physiological state associated with significant metabolic adaptations and changes in energy balance. This adaptation has been considered as an energy-saving mechanism to facilitate the availability of energy for milk production (Xiao *et al.* 2004). The capacity for milk production is the main metabolic driving force; so differences in milk production are accompanied by differences in body composition (Hammon *et al.* 2010). Daniel (2004) found variable quality and differences in carcass traits in cows of different lactation performance. Khadem *et al.* (1995) reported that it is possible to produce carcasses and meat with desirable quality from lactating heifers, although carcass weights, dressing-out percentages, and possibly level of fatness are likely to be lower than in non-lactating heifers. In the lactating cow and during transition from the pregnant, non-lactating state to the non-pregnant, lactating state, there are increased demands of the foetus and for mammary gland development with initiation of milk synthesis. Furthermore, the decreased dry matter intake just before calving and the rapid increase in milk yield with delayed compensatory feed intake lead to a state of negative energy balance (NEB; Duffield 2000, Gray 2008). As a result of this, and to meet the nutritional demands of milk synthesis, cows need to mobilise body reserves, mainly fat as energy source, until nutrient intake covers the demands (Nebel & McGilliard 1993, Hattan *et al.* 2001, Grummer & Rastani 2003). The study of Waltner *et al.* (1994) showed that fat cell diameter can be sensitive to alterations in lactation rate and stage, being an indicator of fat mobilisation. In high producing dairy cows, muscle degradation and protein catabolism can be involved in restoring energy balance in conjunction with lipolysis and an increase in appetite. Indicators of skeletal muscle breakdown and increased degradation of skeletal muscle protein can be detected during lactation (Chibisa *et al.* 2008, Gray 2008). Muscle fibre size and type composition could therefore also be influenced in lactating cows. Numerous studies have reported relationships among muscle fibre characteristics, lean meat content and meat quality (Lee *et al.* 2010). The presented study was conducted to investigate, whether fat cell and muscle fibre size, muscle fibre type composition and consequently carcass composition and meat quality traits are influenced by lactation performance and differ between cows producing different amounts of milk.

Material and methods

Animals

A sample of 50 cows was selected from a F_2 resource population generated from the founder breeds Charolais and German Holstein (Kühn *et al.* 2002). The experimental procedures were carried out according to the animal care guidelines and were approved by the relevant authorities of the State Mecklenburg-Vorpommern, Germany. Heifers were reared in a free-stall barn and were inseminated at 18.1 months of age with semen from German Holstein sires. Heifers calved after 280 ± 0.4 days of pregnancy and were milked after parturition twice daily in a milking parlour. Feeding details are described by Hammon *et al.* (2007, 2010). Fifty F_2 heifers of 3 families were assigned to 3 groups according to their milk yield or lactation

performance during the first lactation. The groups were named high lactating (HL, n=16), low lactating long (LLL, duration of first lactation at least 100 days, n=19), and low lactation short (LLS, duration of first lactation shorter than 100 days, n=15). Cows were inseminated again on average at 33.8 months of age and were slaughtered 30 days after calving during the second lactation. The age at slaughter varied between 1 127 and 1 774 days, being 1 308 days or 43.6 months in average.

Sample collection

Samples of *m. longissimus dorsi* (MLD) and subcutaneous fat were taken immediately after slaughter from the left side of dressed carcass, snap frozen in liquid nitrogen, and stored at -70°C until use. Samples used for determination of meat quality were taken from the 12th rib area of MLD after chilling at 4°C for 24 h. A 2 to 3 cm thick slice of this piece was taken for marbling evaluation. This slice was fixed in at least 1 L of 10% neutral buffered formalin for each 100 g of muscle for at least 3 weeks.

Carcass traits

Body weight was measured after 24 h fasting immediately before slaughter. Hot carcass weight was recorded 45 min after slaughter. Cold carcass weight was measured after chilling at 4°C for 24 h. The chilled carcass was dissected as described in detail by Pfuhl *et al.* (2007). Fat weights were recorded as cold carcass fat (summarized from the different cuts i.e. intramuscular fat, intermuscular fat, and subcutaneous fat), fat in organs, and fat in internal depots. In this study, the different components of fat weights were determined individually as abdominal, omental, and perirenal fat and then summarized to internal fat. Cold carcass protein was summarized from different cuts individually measured with Near Infrared Spectroscopy (Infratec 1255 Food & Feed Analyzer, Foss Analytical A/S, Denmark). All measurements were described by Pfuhl *et al.* (2007).

Meat quality traits

Meat quality data were determined for the MLD using standard procedures. The muscle weight and dimensions were recorded, pH value (pH-Star, Matthäus Company, Klausau, Germany), colour (Minolta CR 200, Minolta Ltd, Ahrensburg, Germany), water binding capacity, and Warner-Bratzler shear force at 24 h and 14 days *post mortem* (Emerson Electric, St. Louis, MO, USA) were measured according to Pfuhl *et al.* (2007). Intramuscular fat content of MLD samples was obtained in triplicates via the Soxhlet extraction method using petroleum ether as solvent and determined gravimetrically after evaporating the extracting solvent (AOAC 2000).

Histology and image analysis

For assessment of marbling traits, fixed MLD slices were stained with Oil Red-O and prepared for computer image analysis as described by Albrecht *et al.* (1996). Stained slice provided a good contrast between fat (red), connective tissue (white), and muscle (pink). Marbling traits were measured with the Cell[^]F image analysis software (OSIS, Münster, Germany) as described by Albrecht *et al.* (2011). For fat cell size determination (either in MLD or in

subcutaneous fat), frozen samples were cryosectioned (10 or 20 μm thick, for muscle and adipose tissue, respectively) using a Leica CM3050 S (Leica, Bensheim, Germany) cryostat microtome. Sections were stained with haematoxylin & eosin (H/E; MLD) or eosin only (subcutaneous fat) according to Böck (1989). Fat cell size was measured using the interactive measurement module of an image analysis system equipped with a Nikon Microphot SA microscope (Nikon Instruments Europe B.V., Kingston, UK), a CCD-12 high resolution colour camera (OSIS, Münster, Germany), and Cell \wedge F image analysis software (OSIS, Münster, Germany). Fat cell size was determined as average diameter of about 300 adipocytes for each animal. For muscle fibre typing, serial sections of muscle tissue were reacted for actomyosin Ca^{2+} adenosine triphosphatase stability after alkaline pre-incubation (pH 10.4) as described by Wegner *et al.* (2000). This histochemical reaction allowed a clear discrimination between three fibre types, one slow-twitch fibre, type I (white fibres) and two fast-twitch fibre types, types IIA (light blue) and IIB (dark blue) as described by Wegner *et al.* (2000). Muscle fibre size and types were measured with an image analysis system equipped with a Jenaval microscope (Carl Zeiss, Jena, Germany), an Altra20 CCD camera (OSIS, Münster, Germany), and a special muscle fibre measurement module (MAS, Freiburg, Germany) of the Cell \wedge D software (OSIS, Münster, Germany). A minimum of 300 muscle fibres per animal in randomly selected muscle fibre primary bundles, usually 4 to 6 fields of one section, were measured and classified. Data of fibre size (from H/E stained section), fibre type (from ATPase stained section), and number of nuclei lying inside a muscle fibre (from H/E stained section) were combined as described by Albrecht *et al.* (2011).

Statistical analysis

Statistical analysis was performed using the SAS statistical software 9.2 (SAS Institute Inc., Cary, NC, USA). Data were analysed by ANOVA using a mixed model containing a covariate age at slaughter or parturition (first or second parturition for lactation data) and fixed factors group, family, and group \times family interaction. At first, all data were analysed for 3 groups of cows, according to the different duration of the first lactation (Table 1). However none of the analysed traits (Table 2-4) showed a significant difference between both low lactation groups (LLL and LLS). To simplify the analyses, both low lactation groups were considered together as one LL group. Therefore all comparisons are provided between cows with high (HL) or low (LL) amount of milk per day.

Table 1
Milk yield in Charolais \times Holstein F_2 crossbred cows

Trait	Group of cows			Adj. <i>P</i> -value
	HL (n=16)	LLL (n=19)	LLS (n=15)	
Duration of lactation (d)				
1st lactation	283.9 \pm 5.9 ^a	111.9 \pm 5.6 ^b	47.6 \pm 6.5 ^c	<0.001
Milk per day, kg/d				
1st lactation	9.68 \pm 0.28 ^a	1.20 \pm 0.27 ^b	0.86 \pm 0.31 ^b	<0.001
2nd lactation	17.95 \pm 1.70 ^a	9.80 \pm 1.35 ^b	8.35 \pm 1.73 ^b	<0.002

The data presented are LSMEAN \pm SE for fixed effect group, adjusted for the same age at parturition.

Since the F_2 heifers were generated over several years within the SEGFAM experiment, the influence of the slaughter years on all considered traits was checked. The slaughter year as fixed factor was significant for water binding capacity, particular marbling traits, and percentage of muscle fibre types and was included in the model for analysis of variance for these traits.

Pearson correlation coefficients were calculated to determine the relationships between milk yield and carcass traits, meat quality, or muscle structure using the CORR procedure of SAS. Additionally, multiple linear regressions were calculated using the REG procedure of SAS. Milk per day of first and second lactation and duration of first lactation were included as independent variables to test, whether the combination of lactation data can enhance the explanation of variations in the investigated carcass and muscle traits.

Results

Milk yield

Cows in our study had a generally low milk yield (Table 1). Nevertheless, milk yield and lactation duration varied sufficiently to generate three groups of different lactation performance, namely HL, LLL, and LLS. Each group was composed of 15 to 19 cows with representatives of 3 families. The analysis of variance revealed no influence of age at parturition and no influence of family and group \times family interaction on duration of the first lactation or amount of milk per day in the second lactation. However, the amount of milk per day in the first lactation was influenced by age at parturition ($P < 0.01$). Therefore, age at parturition was introduced as covariate in the model. The duration of the first lactation period (Table 1) differed among the three groups ($P < 0.01$) being HL > LLL > LLS. The amount of milk per day (Table 1), however, was similar in both low lactating groups and higher in HL ($P < 0.01$) in both lactation periods.

Carcass characteristics

Analysis of variance revealed no difference between LLL and LLS group of cows for none of the investigated traits. Therefore these groups were considered together as LL group to investigate the influence of amount of milk per day on carcass traits. The cows were not at the same age at slaughter, because they were slaughtered 30 days after second parturition. To account for these age differences, age at slaughter was introduced as a covariate in the analysis of variance for all traits.

Cows of the LL group were heavier ($P < 0.05$) and achieved higher carcass yields ($P < 0.01$) than HL cows (Table 2). They tended to store more internal fat ($P = 0.06$). The perirenal fat depot was heavier in LL cows ($P = 0.02$), also relative to body weight (data not shown). However, the omental fat weight was not different between groups. Carcasses of LL cows contained also more protein ($P < 0.01$) and tended to contain more fat ($P = 0.08$) than carcasses of HL cows. These differences disappeared when cold carcass protein and cold carcass fat were considered relative to cold carcass weight ($P > 0.5$).

Table 2
Carcass characteristics of Charolais × Holstein F₂ crossbred cows

Trait	Group of cows		Adj. <i>P</i> -value
	HL	LL	
Body weight, kg	715.6±20.3	774.1±13.2	0.032
Carcass yield, %	52.5±0.8	55.3±0.5	0.007
Cold carcass weight, kg	368.3±11.0	422.0±7.2	0.001
Internal fat, kg	41.3±3.4	49.8±2.2	0.061
Perirenal fat, kg	15.8±1.6	20.6±1.0	0.020
Omental fat, kg	16.6±1.1	18.6±0.8	0.155
Cold carcass fat, kg	78.1±6.1	92.3±4.0	0.084
Cold carcass protein, kg	49.5±1.8	55.9±1.2	0.008

The data presented are LSMEAN±SE for fixed effect group, adjusted for the same age at slaughter.

Meat quality

Meat quality traits (Table 3) were determined in MLD. The muscle weight was greater in LL cows ($P<0.02$), accompanied by a slightly larger cross sectional area ($P=0.051$). Intramuscular fat content, colour, and shear force after 14 days were not different between groups ($P>0.4$). The shear force value 24 h after slaughter tended to be higher in HL cows ($P=0.097$). The pH value 24 h after slaughter was also higher in MLD of HL cows ($P=0.011$).

Table 3
Meat quality of MLD of Charolais × Holstein F₂ crossbred cows

Trait	Group of cows		Adj. <i>P</i> -value
	HL	LL	
Weight, kg	7.31±0.31	8.33±0.20	0.016
Cross sectional area, cm ²	77.9±3.7	87.7±2.5	0.051
Intramuscular fat content, %	5.21±0.72	5.60±0.47	0.678
Colour ¹ , L*	30.4±0.6	30.3±0.4	0.809
Water binding capacity, %	24.61±1.16	25.99±0.90	0.350
Shear force 24 h, kg	18.85±0.71	17.28±0.47	0.097
Shear force 14 d, kg	12.83±0.76	12.06±0.50	0.439
pH ₂₄	5.59±0.02	5.52±0.01	0.011

The data presented are LSMEAN±SE for fixed effect group, adjusted for the same age at slaughter. ¹referring to L*a*b* CIE Lab system

In accordance with the intramuscular fat content, there was no difference in marbling fleck area percentage ($P=0.45$, Table 4). However, the largest marbling flecks were larger ($P=0.01$) in MLD of LL cows. Number, size, and distribution of marbling flecks were influenced by group × family interaction ($P<0.05$). However after Tukey adjustment, significant differences were only indicated between groups within family C for size and distribution of marbling flecks and between family B and family C within HL group for marbling fleck distribution.

Table 4
Marbling traits of MLD of Charolais × Holstein F₂ crossbred cows

Trait	Group of cows					
	HL		Family C		LL	
	Family A	Family B	Family C	Family A	Family B	Family C
Marbling fleck area, %	7.30±1.19	6.25±1.13	6.20±1.34	8.06±0.97	7.60±0.70	6.31±0.91
Number marbling flecks	1 015±135	649±128	1 035±151	890±110	970±79	661±103
Marbling fleck size, mm ²	0.68±0.11	0.83±0.10	0.43 ^b ±0.12	0.88±0.09	0.86±0.06	0.90 ^a ±0.08
Largest marbling fleck, mm ²	76.9±26.3	54.0±25.0	42.1±29.6	125.8±21.6	98.4±15.4	81.4±20.2
Marbling fleck elongation	2.34±0.05	2.35±0.05	2.23±0.06	2.35±0.04	2.32±0.03	2.26±0.04
Marbling fleck distribution	1.46 ^{ab} ±0.12	1.81 ^a ±0.12	1.20 ^b ±0.14	1.72±0.10	1.64±0.07	1.76 ^a ±0.09

The data presented are LSMEAN±SE for fixed effect group × family, adjusted for the same age at slaughter. ^{a,b}Means with different superscripts are significantly different ($P < 0.05$) between families. ^{a,b}Means with different superscripts are significantly different ($P < 0.05$) between groups.

Fat cell size and muscle structure

The fat cell size was not different between the groups ($P > 0.3$), showing an average diameter of 58 µm and 86 µm for intramuscular and subcutaneous fat cells, respectively. Analysis of variance revealed neither effect of group, and therefore milk yield, nor of family, nor of group × family interaction on fat cell size.

Muscle structure and fibre type composition data are presented in Table 5. Analysis of variance indicated an influence of family on muscle fibre size and number of nuclei per muscle fibre but no influence on fibre type composition.

Table 5
Muscle fibre size and type profile in Charolais × Holstein F₂ crossbred cows

Trait	Group of cows		Adj. <i>P</i> -value
	HL	LL	
Cross section area, µm ²			
Total muscle fibres	4 248±240	3 801±152	0.158
Fast twitch	5 077±325	4 843±206	0.582
Intermediate	4 762±312	4 004±198	0.068
Slow twitch	2 437±150	2 174±95	0.183
Area percentage, %			
Fast twitch	44.8±3.6	48.7±2.3	0.415
Intermediate	39.3±3.3	34.6±2.1	0.275
Slow twitch	15.9±1.2	16.7±0.8	0.607
Number nuclei/muscle fibre			
Total muscle fibres	1.47±0.06	1.26±0.04	0.013
Fast twitch	1.66±0.08	1.45±0.05	0.039
Intermediate	1.56±0.08	1.28±0.05	0.012
Slow twitch	1.11±0.06	0.97±0.04	0.090

The data presented are LSMEAN±SE for fixed effect group, adjusted for the same age at slaughter.

Between HL and LL cows, there was neither significant difference in muscle fibre size ($P > 0.15$), except a tendency for larger intermediate fibres ($P = 0.068$) in HL cows, nor in muscle fibre type composition ($P > 0.27$). On the other hand, the number of nuclei per muscle fibre was significantly increased ($P < 0.04$) in total, fast, and intermediate muscle fibres of HL cows. The number of nuclei in slow fibres tended to be higher in HL cows ($P = 0.09$).

Considering the families, family A had smaller fast fibres ($P=0.049$) and tended to have smaller intermediate fibres ($P=0.054$) than family C. The number of nuclei per fast fibre was smaller in family A than in families B and C ($P=0.017$ and $P=0.004$, respectively) and the number of nuclei per intermediate fibre was smaller in family A than in family C ($P=0.016$).

Lactation effect on muscle, carcass and meat quality

Pearson correlation coefficients were calculated to estimate the influence of lactation performance on carcass, meat quality, and muscle structure. Relationships were generally low or not significant, but showed consistently that increasing milk yield was negatively correlated with tissue accretion (Table 6). Shear force and pH_{24} were positively correlated with increasing milk yield. However, there were no relationships detected between milk yield and marbling traits or muscle structure traits, except with number of nuclei per muscle fibre (Table 6).

Multiple linear regressions were calculated to test whether the combination of all three lactation traits (duration of lactation 1, milk per day lactation 1 and 2) provides a better explanation of trait variations. The closest relationship was detected to carcass yield ($R^2=0.35$) and pH_{24} ($R^2=0.31$).

Table 6

Pearson correlation coefficients between milk yield and carcass, meat quality, and muscle traits

Trait	Milk per day lactation 1	Duration of lactation 1	Milk per day lactation 2
Hot carcass weight	-0.40**	-0.38**	-0.32*
Cold carcass weight	-0.41**	-0.40**	-0.31*
Carcass yield	-0.46***	-0.40**	-0.58***
Perirenal fat	-0.32*	-0.28*	-0.26
Cold carcass protein	-0.34*	-0.32*	-0.35*
MLD weight	-0.38**	-0.33*	-0.44**
pH_{24}	0.49***	0.51***	0.51***
Shear force MLD	0.29*	0.35*	0.29*
Number nuclei/muscle fibre	0.44**	0.44**	0.32*

*** $P<0.001$, ** $P<0.01$, * $P<0.05$

Discussion

Milk production was generally low in the first lactation period. Possibly, animals might have been not physically mature and they required nutrients for their own continued growth (Taylor *et al.* 2006, Wathes *et al.* 2007). In our study, F_2 heifers were still growing, increasing their body weight during first lactation (data not shown). It could be assumed that F_2 heifers were in a positive energy balance from the beginning of lactation just as assumed for other F_2 heifers of the same experiment (Hammon *et al.* 2007). Low milk yield in both lactation periods is consistent with the low milk production in Charolais cows, but was too low when compared with the high production of the German Holstein cows (Pareek *et al.* 2007). Milk yield increased with progress of age in consistence with Bajwa *et al.* (2004) who reported increase in milk yield with increase in parity. Nevertheless, milk yield varied sufficiently to

create groups to investigate the influence of different lactation performance on carcass composition, meat quality and muscle structure.

Carcass data revealed a much higher body weight in LL than HL cows in consistence with higher accretion of muscle protein and body fat reserves. Other body condition traits were less affected by lactation performance in F₂ crossbred cows, suggesting that cows were still growing and not in a mature state with increased fat gain. Furthermore HL and LL cows might have been in a state of positive energy balance and therefore did not mobilise fat for lactation due to the relatively low level of milk production in both groups when compared to dairy cows. This captures the concept of homeorhetic control of metabolism of both fat and protein in lactating animal, depending on stage of lactation, rate of milk production, and genetic differences (McNamara 2000).

Crossbred heifers for meat production are internationally known, but references to meat and eating quality aspects are rare (Hoving-Bolink *et al.* 1999). In the presented study, we investigated the effect of lactation performance on meat quality of MLD as a representative muscle of the carcass. The reduced MLD weight in HL cows suggests less protein accretion in muscles with higher milk yield. Because of the overall low milk yield, it is unlikely that the difference is caused by protein degradation to meet the needs for lactation according to McNamara (2000), who reported that high lactating cows in early lactation can lose significant amounts of body protein. It is more likely in consistence with the view that heifers which calved for the first time are not mature and continue to accrete body protein during their lactating life (Coffey *et al.* 2006). In our study, cows were slaughtered during the second lactation and could have continued to accrete body protein in a different extent.

Ultimate pH was increased with higher milk yield, but still within a range of normal meat quality. In high lactating cows a lower ultimate pH could be expected because of increased glycolysis and lactate output by skeletal muscle, as well as by adipocytes, to facilitate the efficient partitioning of nutrients to the mammary gland for milk production (Xiao *et al.* 2004). On the other hand, it is quite obvious that other MLD quality traits were not affected by lactation performance.

Visual appearance of IMF (marbling) is the primary criterion for grading of beef carcass quality even at low intramuscular fat content, and plays an important role in purchasing decisions by consumers because it is often linked with beef palatability due to the positive influence on taste, juiciness, and tenderness of meat (Chambaz *et al.* 2003, Platter *et al.* 2005, Albrecht *et al.* 2006). It is not just the intramuscular fat content which is important for meat quality, but the fat distribution in the muscle tissue as well (Albrecht *et al.* 1996). Number and size of marbling flecks, marbling fleck area percentage and marbling fleck distribution were similar in HL and LL cows. The increased size of largest marbling fleck and an altered shape in LL cows, indicated by the higher value for elongation of marbling flecks, suggest an effect of milk yield on marbling.

Because body lipid mass in sub-adult and adult ruminants is primarily a function of adipose hypertrophy, the relationship of fat cell size to body lipid mass is quite strong in lactating cattle (McNamara 2000). The expected difference in fat cell size between HL and LL cows in our study, however, could not be detected.

Muscle fibre type profile is an indicator for muscle metabolism (Wegner *et al.* 2000). In the presented study, the muscle fibre type profile did not indicate a relationship to milk yield. Nevertheless, muscle would contribute to whole body adaptation by production of

biosynthetic intermediates and reduced fatty acid uptake (Xiao *et al.* 2004). Furthermore, Izumiya *et al.* (2008) observed the role of fast/glycolytic fibres in regulating whole-body metabolism through their ability to alter the metabolic properties of remote tissues, in addition to well-established role of oxidative fibres in regulating whole-body metabolism. On the other hand, increasing the proportion of fast/glycolytic fibres has been reported to improve meat tenderness through improved *post mortem* maturation in cattle, but there were no universal relationship between myofibre characteristics and meat quality traits among species because both traits are influenced by multiple factors (Lefaucheur 2010).

Number of nuclei per muscle fibre was significantly increased in HL cows in total muscle fibres, fast/glycolytic and oxido/glycolytic fibres. This might be explained by adaptation of skeletal muscle fibres to changes in function, which was not only to modulate the pattern and/or amount of gene expression among existing myonuclei, but also altered the total number of myonuclei (Allen *et al.* 1996). On the other hand, analysis of variance indicated a clear influence of family on muscle fibre size, indicating that genetic causes rather than lactation performance were responsible for variations in muscle fibre size. Therefore, the F₂ families can be considered as different metabolic types which are characterized by divergent nutrient dissemination with a combined dairy and beef genetic background (Hammon *et al.* 2007). Lactation directly affected some important carcass, meat quality, and muscle traits. Carcass weight, carcass yield, and muscle weight were negatively correlated with lactation performance, while shear force was positively correlated. This may explain a substantial proportion of variation in sensory assessment of beef tenderness and may be partly responsible for the view that meat of lactating cows is low quality meat. Number of nuclei in muscle fibres is positively related with milk yield as an adaptation of skeletal muscle fibres to changes in function (Allen *et al.* 1996). Negative correlations of perirenal fat weight or carcass protein with the amount of milk per day suggest fewer capabilities for nutrient accretion with increasing milk production. Higher rates of fat mobilisation from internal depots can be excluded because of the overall low milk production. However, in low merit cows lipogenesis occurs at higher rates while lipolysis occurs at slower rates but in a continued manner, even in positive energy balance to maintain milk-fat output (McNamara 2000).

In conclusion, milk yield was generally low but significantly different between the groups. These differences were accompanied by differences in body weight and carcass composition, but had only minor effects on meat quality. Muscle fibre size and composition of MLD as well as fat cell profile were not influenced by lactation performance. No indication for fat or protein mobilisation from muscle or subcutaneous fat was found, probably because cows were not in a negative energy balance. The results suggest that cows of both groups utilized nutritional energy for lactation and tissue accretion to a different extent. Cows of the LL group gained more weight and stored more fat than HL cows and reached higher carcass yields.

Acknowledgement

We thank the staff at the Research Farm of our institute for handling the cows and the staff of the experimental slaughterhouse at Leibniz Institute for Farm Animal Biology (FBN), Dummerstorf, Germany. The authors express their gratitude to Karola Marquardt for excellent technical assistance.

References

- Albrecht E, Wegner J, Ender K (1996) A new technique for objective evaluation of marbling in beef. *Fleischwirtsch* 76, 1145-1148
- Albrecht E, Teuscher F, Ender K, Wegner J (2006) Growth- and breed-related changes of marbling characteristics in cattle. *J Anim Sci* 84, 1067-1075
- Albrecht E, Gotoh T, Ebara F, Xu JX, Viergutz T, Nürnberg G, Maak S, Wegner J (2011) Cellular conditions for intramuscular fat deposition in Japanese Black and Holstein steers. *Meat Sci* 89, 13-20
- Allen DL, Yasui W, Tanaka T, Ohira Y, Nagaoka S, Sekiguchi C, Hinds WE, Roy RR, Edgerton V (1996) Myonuclear number and myosin heavy chain expression in rat soleus single muscle fibres after spaceflight. *J Appl Physiol* 81, 145-151
- Association of Analytical Chemists (AOAC) (2000) *Official Methods of Analysis*. 17th ed. Washington, DC, USA
- Bajwa IR, Khan MS, Khan MA, Gondal KZ (2004) Environmental factors affecting milk yield and lactation length in Sahiwal cattle. *Pak Vet J* 24, 23-27
- Böck P (1989) *Romeis-Mikroskopische Technik*. 17th ed., Urban & Schwarzenberg, Munich/Vienna/Baltimore, Germany/Austria/USA
- Chambaz A, Scheeder MRL, Kreuzer M, Dufey PA (2003) Meat quality of Angus, Simmental, Charolais and Limousin steers compared at the same intramuscular fat content. *Meat Sci* 63, 491-500
- Chibisa GE, Gozho GN, Van Kessel AG, Olkowski AA, Mutsvangwa T (2008) Effects of Peripartum Propylene Glycol Supplementation on Nitrogen Metabolism, Body Composition, and Gene Expression for the Major Protein Degradation Pathways in Skeletal Muscle in Dairy Cows. *J Dairy Sci* 91, 3512-3527
- Coffey MP, Hickey J, Brotherstone S (2006) Genetic aspects of growth of Holstein-Friesian dairy cows from birth to maturity. *J Dairy Sci* 89, 322-329
- Daniel JD (2004) *Understanding and Improving B Cattle Carcass Quality*. Division of agriculture and natural resources. In: University of California, Agriculture and Natural Resources (ed.) ANR Publication 8130, California, USA, 1-23
- Duffield TF (2000) Metabolic disorders in ruminant. Subclinical ketosis in lactating dairy cattle. *Vet Clin N Am* 16, 231-253
- Gray TS (2008) *The breakdown of skeletal muscle in dairy cows during peak lactation*. MS Thesis. Waikato University, New Zealand
- Grummer RR, Rastani RR (2003) Review: When should lactating dairy cows reach positive energy balance? *Professional Animal Scientist* 19, 197-203
- Hammon HM, Bellmann O, Voigt J, Schneider F, Kühn C (2007) Glucose-dependent insulin response and milk production in heifers within a segregating resource family population. *J Dairy Sci* 90, 3247-3254
- Hammon HM, Metges CC, Schulz A, Junghans P, Steinhoff J, Schneider F, Pfuhl R, Bruckmaier RM, Weikard R, Kühn C (2010) Differences in milk production, glucose metabolism, and carcass composition of 2 Charolais × Holstein F₂ families derived from reciprocal paternal and maternal grandsire crosses. *J Dairy Sci* 93, 3007-3018
- Hattan AJ, Beever DE, Cammell JD, Sutton JD (2001) *Energy Metabolism in Animals*. In: Chwalibog A, Jakobsen K (eds.) *Energy metabolism in high yielding dairy cows during early lactation*. Wageningen Press, Wageningen, The Netherlands, 325-328
- Hoving-Bolink AH, Hanekamp WJA, Walstra P (1999) Effects of diet on carcass, meat and eating quality of once-bred Piemontese × Friesian heifers. *Livest Prod Sci* 57, 267-272
- Izumiya Y, Hopkins T, Morris C, Sato K, Zeng L, Viereck J, Hamilton JA, Ouchi N, LeBrasseur NK, Walsh K (2008) Fast/Glycolytic muscle fibre growth reduces fat mass and improves metabolic parameters in obese mice. *Cell Metab* 7, 159-172
- Khadem AA, Purchas RW, Morris ST, McCutcheon SN, Parker WJ (1995) Carcass and meat quality characteristics of pasture-fed unbred and once-bred Hereford × Friesian heifers. *N Z J Agric Res* 38, 187-196

- Kühn C, Bellmann O, Voigt J, Wegner J, Guiard V, Ender K (2002) An experimental approach for studying the genetic and physiological background of nutrient transformation in cattle with respect to nutrient secretion and accretion type. *Arch Tierz* 45, 317-330
- Lahann P, Voigt J, Kühn C, Pfuhl R, Metges CC, Junghans P, Schönhusen U, Hammon HM (2010) Energy expenditure, urea kinetics, and body weight gain within a segregating resource family population. *J Dairy Sci* 93, 5118-5128
- Lee SH, Joo ST, Ryu YC (2010) Skeletal muscle fibre type and myofibrillar proteins in relation to meat quality. *Meat Sci* 86, 166-170
- Lefaucheur L (2010) A second look into fibre typing – Relation to meat quality. *Meat Sci* 84, 257-270
- McNamara JP (2000) Integrating genotype and nutrition on utilization of body reserves during lactation of dairy cattle. In: Cronjé PB (ed.) *Ruminant Physiology: Digestion, Metabolism, Growth and Reproduction*. CABI Publishing, Wallingford/New York, UK/USA, 353-369
- Nebel RL, McGilliard ML (1993) Interactions of High Milk Yield and Reproductive Performance in Dairy Cows. *J Dairy Sci* 76, 3257-3268
- Pareek N, Voigt J, Bellmann O, Schneider F, Hammon HM (2007) Energy and nitrogen metabolism and insulin response to glucose challenge in lactating German Holstein and Charolais heifers. *Livest Sci* 112, 115-122
- Pfuhl R, Bellmann O, Kühn C, Teuscher F, Ender K, Wegner J (2007) Beef versus dairy cattle: a comparison of feed conversion, carcass composition, and meat quality. *Arch Tierz* 50, 59-70
- Platter WJ, Tatum JD, Belk KE, Koontz SR, Chapman PL, Smith GC (2005) Effects of marbling and shear force on consumers' willingness to pay for beef strip loin steaks. *J Anim Sci* 83, 890-899
- Taylor VJ, Beever DE, Bryant MJ, Wathes DC (2006) Pre-pubertal measurement of the somatotrophic axis as predictors of milk production in Holstein-Friesian dairy cows. *Domest Anim Endocrinol* 31, 1-18
- Waltner SS, McNamara JP, Hillers JK, Brown DL (1994) Validation of indirect in lactating cows measures of body fat in Lactating cows. *J Dairy Sci* 77, 2570-2579
- Wathes DC, Cheng Z, Bourne N, Taylor VJ, Coffey MP, Brotherstone S (2007) Differences between primiparous and multiparous dairy cows in the inter-relationships between metabolic traits, milk yield and body condition score in the periparturient period. *Domest Anim Endocrinol* 33, 203-225
- Wegner J, Albrecht E, Fiedler I, Teuscher F, Papstein HJ, Ender K (2000) Growth- and breed-related changes of muscle fibre characteristics in cattle. *J Anim Sci* 78, 1485-1496
- Xiao XQ, Grove L, Smith MS (2004) Metabolic adaptations in skeletal muscle during lactation: complementary deoxyribonucleic acid microarray and real-time polymerase chain reaction analysis of gene expression. *Endocrinology* 145, 5344-5354

Received, accepted 7 June 2011, 31 August 2011.

Corresponding author:

Elke Albrecht

email: elke.albrecht@fbn-dummerstorf.de

Research Unit Muscle Biology and Growth, Leibniz Institute for Farm Animal Biology (FBN), Wilhelm-Stahl-Allee 2, 18196 Dummerstorf, Germany
