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Intrinsic factors affecting sheep meat quality: a review^a

Factores intrínsecos que afectan la calidad de la carne ovina: revisión de literatura

Fatores intrínsecos que interferem na qualidade da carne ovina: revisão de literatura

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Summary

The quality of meat is a multifactorial parameter dependent on the perspective and goals of the link in the production chain. Generally, a variety of factors directly or indirectly affect the quality characteristics of meat and, therefore, the value of meat products. Often, the literature divides the interfering factors into intrinsic and extrinsic. Intrinsic factors are related to animals; therefore, intrinsic factors are less variable. These factors include breed, sex, age, weight, genes, and type of muscle fiber. Some of these factors are not well studied, others have variable influence or are controversial and only a few are known and sometimes controlled. Thus, this study aimed to review some intrinsic factors that influence the quality of lamb meat.

Keywords: cooking losses, meat color, tenderness, water holding capacity.

Resumen

La calidad de la carne es un parámetro multifactorial que depende de la perspectiva y los objetivos del eslabón de la cadena de producción. En general, una amplia variedad de factores afectan directa o indirectamente la calidad de la carne y, en consecuencia, los valores de los productos cárnicos. A menudo, la literatura divide los factores que interfieren intrínseca y extrínsecamente. Los factores intrínsecos están relacionados con los animales, por lo tanto, son menos variable. Estos factores incluyen la raza, el género, la edad, el peso, los genes y

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el tipo de fibra muscular. Algunos de estos factores no están bien estudiados, otros tienen influencia variable o son polémicos, y sólo unos pocos son conocidos y a veces controlados. Por lo tanto, este trabajo pretende revisar algunos factores intrínsecos que influyen en la calidad de la carne de ovino.

Palabras clave: capacidad de retención de agua, color de la carne, perdidas por cocción, terneza.

Resumo

A qualidade da carne é um parâmetro multifatorial, dependente da perspectiva e objetivos do elo da cadeia produtiva. Geralmente, uma grande variedade de fatores afetam direta ou indiretamente as características de qualidade da carne e, consequentemente, os valores dos produtos cárneos. Frequentemente, a literatura divide os fatores interferentes em intrínsecos e extrínsecos. Os fatores intrínsecos são referentes ao animal e, portanto, menos variáveis. Esses fatores incluem raça, sexo, idade, peso, genes e tipo de fibras musculares. Alguns desses fatores não estão bem estudados, outros têm influência variável ou controvertida e somente alguns são conhecidos e, às vezes, controlados. Dessa forma, objetivou-se revisar alguns fatores intrínsecos que influenciam na qualidade da carne ovina.

Palavras chave: capacidade de retenção de água, cor da carne, maciez da carne, perdas por cocção.

Introduction

Currently, the global sheep population is more than 1 billion heads (FAO, 2015). On a global scale, sheep meat production is small, with less than 8.6 million tonnes. The largest producers of sheep meat are China, India, Sudan, Nigeria and Pakistan. The three largest destinations for sheep meat worldwide are China, EU, and US, accounting for about 60% of global exports (FAO, 2015).

Meat is the most important source of animal protein for the human diet (Lawrie, 2005; McAfee *et al.*, 2010). However, the parameters that define its degree of acceptance and quality vary with the point of view and interest of the producer, trade, industry, and consumers.

From an industrial perspective, quality is defined and determined by objective factors relating not only to the quality demanded by the consumer, but also to industrial meat characteristics (Osório *et al.*, 2009). In the context of the supply chain and meat science, the analysis of color, pH, water holding capacity, cooking losses, tenderness, chemical composition, fatty acid composition, among many others, are all important in the concept of integrated quality and the search for more homogeneous products.

Besides being interconnected, quality parameters defined by the final consumer and industry depend on a long list of other intrinsic (inherent to the animal) and extrinsic (inherent to management, environment, etc.) factors. Therefore, meat quality is defined by animal age, sex, and physiological state, and the post-mortem biochemistry of muscle and fat, carcass composition, feed contribution to flavour, protein and fat levels, as well as the effect of genetics on tissues and metabolism, pre and post slaughter handling, and storage, among others (Webb *et al.*, 2005).

In the case of lamb, an increase in consumption accompanied by a demand for increased quality has been observed. This situation forces the supply chain to better understand the factors affecting meat quality; we need to consider the number of factors that affect the quality of lamb meat. The main intrinsic factors interfering with the quality of lamb meat are breed, sex, age, genetic characteristics and type of muscle fibres. The aim of this work is to describe how these intrinsic factors cause changes in the quality of sheep meat.

Intrinsic factors affecting sheep meat

Breed

Breed has a large effect on carcass morphology. It is a complex factor and difficult to assess when only its effects on the amount of fat or meat quality are considered. The problem lies at the basis of comparison, as results vary according to the chosen criterion: same carcass weight, same age, same degree of maturity, etc. (Hopkins *et al.*, 2011). Furthermore, racial comparison is complicated due to differences in the adopted selection programs between countries (Sañudo *et al.*, 2008).

It is true that there is genetic variation of meat quality between populations, especially between improved breeds and native breeds. Lambe *et al.* (2008; 2009) showed variation (p<0.05) in final pH and tenderness between the Texel and Scottish Black Face breeds. Changes in tenderness between these genotypes can be partly explained by the difference in the number of muscle fibers (Bünger *et al.*, 2009). Breed also influences other parameters such as the chemical composition (Table 1).

Breed may also influence other nitrogen fractions of meat, besides true protein. Esenbuga *et al.* (2009) observed that Awassi sheep show lower values (p<0.05) of non-protein nitrogen ($2.44 \pm 0.07\%$ versus 2.91 ± 0.09%) and smaller amounts (p<0.05) of nitrogen soluble in water (5.18 ± 0.13 vs. $6.30\% \pm$ 0.16%) when compared to Morkaraman sheep.

Regarding chemical composition at the same carcass weight, animals of breeds with smaller frame

size will be older and have more fat than those with larger frame size (Osório *et al.*, 2008). Breeds such as Dorper and their crosses have greater amount of intramuscular fat at the same age than breeds not specialized for meat production such as Rambouillet breed (Arvizu *et al.*, 2011). Barkawi *et al.* (2009) examined two Egyptian fat-tailed sheep breeds observing that Ossimi breed showed higher (p<0.05) fat content (4.2%) than Rahmani breed (3.3%). The authors noted that Rahmani breed had higher frame size and later maturity with higher levels of circulating insulin growth factor (IGF-I) at different ages.

Typically, selected breeds for meat production have greater number of muscle fibers and smaller amount of intramuscular fat per unit area of muscle (Bünger *et al.*, 2009; Hopkins *et al.*, 2011). Furthermore, Vacca *et al.* (2008) inferred that differences between genotypes alter the activity of lipogenic enzymes in sheep muscle, such as Δ -desaturase, and can influence the amount and composition of deposited fatty acid.

Cholesterol levels are often associated with heart disease and red meat is the primary source of this lipid. Faria *et al.* (2012) showed differences (p<0.05)

Oxford down

Breed

Suffolk

Table 1. Physical-chemical characteristics of Quadriceps femoris from three sheep breeds (mean ± SEM*).

Zwartbles

Dry matter (g/Kg)	22.0 ^{<i>a</i>} ± 0.20	$23.0^{b} \pm 0.26$	$22.8^{b} \pm 0.27$
Ash (g/Kg)	$1.1^{b} \pm 0.01$	1.1 ^a ± 0.01	1.1 ^a ± 0.01
Protein (g/Kg)	19.0ª ± 0.13	18.1 ^a ± 0.18	18.1 ^a ± 0.17
Collagen (g/Kg)	2.3 ^{<i>a</i>} ± 0.32	2.5 ^{ab} ± 0.30	$2.9^{b} \pm 0.31$
Myoglobin (g/Kg)	2.3 ^{<i>a</i>} ± 0.08	2.3 ^{ab} ± 0.36	$2.5^{b} \pm 0.36$
Intramuscular fat (g/Kg)	1.7 ^a ± 0.27	$3.1^{b} \pm 0.36$	$2.8^{b} \pm 0.37$
рН	5.7 ^a ± 0.01	5.7 ^a ± 0.02	5.7 ^a ± 0.02
Water holding capacity (%)	18.8ª ± 0.75	17.9 ^a ± 1.01	17.0 ^a ± 1.03
Lightness index (L*)	48.4 ^a ± 0.72	47.2 ^a ± 0.97	50.1 ^a ± 0.99
Redness index (a*)	8.5 ^a ± 0.40	8.6 ^a ± 0.54	9.2 ^a ± 0.56
Yellowness index (b*)	12.5 ^a ± 0.27	12.1 ^a ± 0.36	13.4 ^a ± 0.34

a.b Means followed by different superscript letters in the same row indicate significant difference (p<0.05) based on Duncan's test.

*Standard error of the mean.

Characteristic

Adapted from Komprda et al. (2012).

in the order of 5.72 mg/g cholesterol lower for Texel x Polwarth lamb meat compared to Texel x Corriedale.

The marbling degree can influence various sensory impressions of sheep meat, especially its juiciness. In a study evaluating breeds with different aptitudes, Cloete *et al.* (2012) observed that the lower amount of intramuscular fat in meat from Merino sheep was associated with lower scores for sensory characteristics of initial juiciness and lasting succulence (after-taste succulence) when compared to sheep of double quality genotypes or cut. In an extensive review, Hopkins *et al.* (2011) had already noted lower juiciness in the Merino genotype.

There are few studies comparing breed and *post-mortem* pH evolution. Hoffman *et al.* (2003) observed that sheep crosses between meat breeds and wool breeds differed (p<0.05) in pH 48 hours *post-mortem*, with values of 5.71 and 5.79 for Merino x Dormer and Merino x Suffolk crosses, respectively. Merino breed has a high final pH, which can be derived from the predominant muscle fiber in the breed. Due to selection for production under grazing conditions, oxidative fibers (1 and 2A) may be prevalent in the muscle of these animals. These fibers are characterized by low levels of glycogen, which is closely related to high final pH values in the muscle (Pösö and Puolanne, 2005).

Associated with juiciness, meat tenderness is another attribute influenced by genotype (Martínez-Cerezo *et al.*, 2005). The differences in the degree of muscularity, age and physiological action of the calpain–calpastatin enzyme complex are mainly responsible for the variation in tenderness of lamb meat (Thompson *et al.*, 2006).

Teixeira *et al.* (2005) showed objective differences (p<0.01) in meat tenderness between Bragançano (7.8 Kg/cm²) and Mirandesa (6.8 Kg/cm²) sheep breeds. According to the authors, the sensory panel also identified differences (p<0.05) in hardness, assigning scores of 4.1 to Bragançano and just 2.8 for Mirandesa. In the latest study, Ekiz *et al.* (2009) evaluated the quality of sheep meat of five genotypes (Turkish Merino, Ramlic, Kivircik, Chios and Imroz) and observed difference (p<0.01) in shear force (kgf) between genotypes.

Physical aspects such as color, water holding capacity and cooking losses are dependent to a greater or lesser extent on the final pH of meat (Table 2). The literature describes variations in color scores, juiciness and water holding capacity between breeds (Hernández-Cruz *et al.*, 2009; Costa *et al.*, 2011).

Osório *et al.* (2008) argued that the most noticeable changes are related with physical aspects of meat, mainly the color because it has a direct impact on appearance and consumer acceptability. Meat color is influenced by the muscle myoglobin content and the electrical state of muscle proteins (Ramos and Gomide, 2007; Khliji *et al.*, 2010). Breed influences the amount of myoglobin present in muscle, as Juárez *et al.* (2009) showed for the Grazalema Merino breed: 3.09 mg/g myoglobin in lactation and 4.01 mg/g myoglobin in the growing phase, while Lebrijana Churra breed showed values of 1.61 mg/g and 2.79 mg/g for the same productive stages, respectively.

Genetics can also influence fatty acids composition of muscle. According to Muchenje *et al.* (2009), differences among breeds reflect underlying differences in gene expression or activity of enzymes involved in fatty acid synthesis, desaturation or chain elongation, and thus deserve more attention.

Demirel *et al.* (2006), Madruga *et al.* (2006), and Marino *et al.* (2008) observed differences in the levels of mono and polyunsaturated fatty acids for different sheep breeds and attributed it to different deposition rates of intramuscular triacylglycerols in adipocytes associated with a dilutive effect of membrane phospholipids.

Sex

Proximate composition of meat is affected by sex, especially fat content (Peña *et al.*, 2005; Gerrard and Grant, 2006; Pérez *et al.*, 2007). Meat from females is often richer in lipids. Santos *et al.* (2007) observed that native animals from Spain had higher (p<0.05) lipids levels in the meat of female (2.3%) compared with male lambs (1.9%) of the same age. Rodríguez *et al.* (2008) also found differences (p<0.05) in the fat content of meat from males and females (1.6 vs. 2.9%, respectively) in Assaf sheep, attributing these differences (p<0.05) to the amount of carcass fat,

Variable	Genotype ¹					p-value	
-	CA	ACA	RA	ARA	Α	-	
рН	5.59 ± 0.1	5.75 ± 0.1	5.63 ± 0.1	5.89 ± 0.1	5.58 ± 0.1	0.14	
Cooking losses (%)	27.6 ± 1.5	29.3 ± 1.5	27.7 ± 1.5	28.2 ± 1.5	29.8 ± 1.5	0.81	
Water holding capacity (%)	21.5 ± 1.2	20.8 ± 1.2	21.6 ± 1.2	21.7 ± 1.2	21.4 ± 1.2	0.99	
Shear force (Kg/cm ²)	2.28 ± 0.2	1.49 ± 0.2	1.87 ± 0.2	1.91 ± 0.2	2.03 ± 0.2	0.17	
Color							
Lightness index (L*)	36.6 ± 1.1 ^c	40.4 ± 1.1^{b}	38.2 ± 1.1 ^{bc}	41.0 ± 1.1 ^{ab}	43.61 ± 1.1 ^a	0.001	
Redness index (a*)	5.39 ± 0.4	5.57 ± 0.4	5.39 ± 0.4	5.31 ± 0.4	5.40 ± 0.4	0.37	
Yellowness index (b*)	10.9 ± 1.4	11.7 ± 1.4	10.5 ± 1.4	12.9 ± 1.4	12.60 ± 1.4	0.68	
Chroma	12.5 ± 1.1	13.2 ± 1.1	12.5 ± 1.1	14.4 ± 1.1	14.4 ± 1.1	0.55	
H-Angle	60.6 ± 4.6	62.3 ± 4.6	57.9 ± 4.6	63.4 ± 4.6	61.0 ± 4.6	0.94	

Table 2. Meat quality parameters of longissimus muscle as affected by lamb genotypes (mean ± SEM*).

a.b.c Different superscript letters in the same row indicate significant differences based on the stablished p-value.

¹Genotypes: CA = F_1 Charollais-Awassi; ACA = B_1 Awassi-Charollais-Awassi; RA = F_1 Romanov-Awassi; ARA = B_1 Awassi-Romanov-Awassi; A = Awassi. *Standard error of the mean.

Adapted from Abdullah et al. (2011).

being higher in females (10.9%) than in males (8.6%). When intact and castrated males are compared, meat from castrated animals has higher (p<0.01) fat content (Haddad *et al.*, 2006; Warren *et al.*, 2008).

Physical parameters of meat quality are influenced by sex. Johnson *et al.* (2005) evaluated muscle and meat deposition of Texel male and female lambs, observing increased (p<0.01) deposition of muscle and less fat in males for variables adjusted to the same carcass weight. In the same study, meat quality reflected differences (p<0.01) for gender in tenderness (74.5 N for females and 82.4 N for males) and final pH (5.60 for females and 5.74 for males).

Decreasing pH is influenced by many factors, among which glycogen, ATP, and creatine phosphate reserves are the most determinant. McGeehin *et al.* (2001) observed that pH drop is faster (p<0.05) in females than in males, with constant differences of 0.18 pH units. It can be inferred that glycogen content in females is higher due to less sexual activity. Another possible hypothesis is that the higher reactivity of males is promoted by testosterone and depletes muscle glycogen faster via catecholamines. Adrenaline recruits glucose to the bloodstream and stimulates muscle glycolysis (Pösö and Puolanne, 2005).

Okeudo and Moss (2008) evaluated the influence of sex (intact males, castrated males, vasectomized males, and females) on meat quality of sheep (Table 3).

The differences in cooking losses and shear force between males and females can be partly explained by higher intramuscular fat content of females (Okeudo and Moss, 2008). In reviewing aspects of meat quality, Koohmaraie and Geesink (2006) claimed that fat has lower water content than muscle; therefore, muscles richer in adipose tissue have reduced water loss. Moreover, authors point out that a greater amount of adipocytes implies that the amount of muscle fibers per area is reduced, thereby favouring smaller shear force values.

Frequent differences in meat tenderness are found for most species between intact and castrated males. Lage *et al.* (2009) observed higher shear strength and smaller values for the myofibrillar fragmentation

Sex	pHi [#]	pHf [#]	Sarcomere length (µm)	Cooking losses (%)	Shear force (Kg)
Castrated males	6.45	5.67	1.72	21.67 ^b	6.04 ^{ab}
Intact males	6.51	5.73	1.75	20.43 ^b	6.65 ^b
Vasectomized males	6.54	5.69	1.73	20.42 ^b	7.03 ^b
Females	6.52	5.69	1.77	17.64 ^a	5.35ª
Standard error	0.065	0.037	0.036	1.369	0.617
Significance	NS	NS	NS	*	*

Table 3. Effect of sex on sheep meat quality.

^{a,b}Means followed by different superscript letters in the same column indicate significant difference (p<0.05).

[#]pHi = initial pH; pHf = final pH.

NS = not significant, * (p<0.05).

Adapted from Okeudo and Moss (2008).

index in *Longissimus dorsi* of castrated compared to non-castrated animals. The authors also observed no difference in m-calpain and μ -calpain activity 24 hours *post-mortem* in relation to sex. Calpastatin was 81% higher in intact animals compared with castrated males. Besides high calpastatin activity, another explanation for the low meat tenderness of non-castrated animals would be their higher zinc concentration, which is a potent inhibitor of calpain (Koohmaraie and Geesink, 2006). Furthermore, Gökdal *et al.* (2010) found higher (p<0.05) collagen content in meat from intact males (4.03 ± 0.44 mg/g) compared to immunologically castrated males (2.52 ± 0.28 mg/g).

Sex differences for fatty acid content are documented in the literature. Tejeda *et al.* (2008) showed differences (p<0.01) in fatty acid composition of *Longissimus lumborum* of Merino males and females. They associated it to higher levels of polyunsaturated fatty acids in intact males. Intramuscular fat is more saturated than membrane phospholipids for example, and females have higher deposition of intramuscular fat. Therefore, it is common in the literature to refer to female sheep meat as being more saturated.

In addition to fatty acid composition, castration affects cholesterol levels of meat from males. According to Madruga *et al.* (2001), castration increased (p<0.05) cholesterol in meat from castrated goats (62.5 mg/g) compared to that of intact animals (58.0 mg/g). It can be inferred that cholesterol mobilization by intact animals is higher because

steroid hormones are derived from this lipid, which contributes to less deposition of this metabolite into the meat. The sensory panel rated by Navajas *et al.* (2008) and Tejeda *et al.* (2008) classified the meat of intact males with higher scores for "bad taste".

Age and body weight

These factors are analyzed together because if no manipulation of food occurs or the animal does not suffer severe food restriction, a greater weight in the same genetic background implies greater age. The slaughter weight affects consumer acceptability in many countries (Martínez-Cerezo *et al.*, 2005; Font i Furnols *et al.*, 2006; Muela *et al.*, 2010) and therefore deserves special attention in the study of meat quality.

The growth curve of sheep is sigmoid, with a period of accelerated lean tissue deposition that coincides with puberty and a stabilization period of protein deposition and increased fat deposition known as maturity. The increase in protein deposition is mediated by growth hormones (GH), which increase muscle fibers hypertrophy and reduce fat hormones deposition. The increase in fat deposition amounts to the extent that sex hormones increase their concentration in the bloodstream (Gerrard and Grant, 2006).

Differences in sheep meat quality at different ages necessarily correspond to changes in the amount of carcass fat and its relationship to physical and chemical aspects of meat (Table 4). Barkawi *et al.*

Item	Slaughter weight			Standard error	Significance
	20 Kg	30 Kg	40 Kg	_	
pН	5.92	5.90	5.88	0.03	NS
Cooking losses (%)	44.0	44.0	42.3	1.1	NS
Water retention (%)	26.1ª	24.6 ^a	20.9 ^b	0.9	***
Shear force (N)	35.9 ^b	35.9 ^b	41.8ª	1.5	**
Color					
Lightness index (L*)	40.49 ^a	38.09 ^b	36.33 ^c	0.5	***
Redness index (a*)	3.77 ^b	5.03ª	5.34 ^a	0.3	***
Yellowness index (b*)	14.56	13.88	14.17	0.4	NS
Chroma	15.14	14.63	15.22	0.4	NS
H-Angle	75.1ª	69.6 ^b	68.5 ^b	1.4	**
Chemical composition (%)					
Moisture	77.1ª	75.8 ^b	75.4 ^b	0.4	*
Protein	19.4	19.6	19.9	0.3	NS
Fat	2.30 ^b	3.30ª	3.10ª	0.3	*
Ash	1.07	1.05	1.09	0.02	NS

Table 4. Parameters of Semimembranosus muscle meat quality of Awassi sheep slaughtered at different weights.

a.b.cMeans followed by different superscript letters in the same row indicate significant difference based on the established p-value.

Adapted from Abdullah and Qudsieh (2009).

(2009) evaluated the chemical composition of meat from native lambs at two ages (270 and 360 days) and observed a reduction (p<0.01) of moisture (75.8 to 75.1%) and an increase (p<0.01) in fat (3.3 to 4.2%) with increasing slaughter age.

Regarding color, the increased weight and age at slaughter tend to increase the amount of pigments, red content (a^{*}) and reduced luminosity (L^{*}). Juárez *et al.* (2009) observed an increase (p<0.01) in myoglobin (3.09 to 4.01 mg/g), low (p<0.01) luminosity (45.10 to 40.19 L^{*}) and increased (p<0.01) redness (7.35 to 9.79 a^{*}) with increasing (p<0.01) slaughter weight of Grazalema Merino sheep breed. In another study, Teixeira *et al.* (2005) identified a reduction (p<0.05) in L^{*} of 40.0 \pm 0.55 to 39.0 \pm 0.54 when slaughter weight increased from 9-14 to 19-24 Kg.

Silva Sobrinho *et al.* (2005) evaluated meat quality from lambs of different exotic genotypes slaughtered at two ages. They found that Warnen-

Bratzler measurement was higher in meat from animals slaughtered at 300 days compared to 150 days at slaughter, indicating that larger shear forces were required to cut the samples from older animals. Tejeda *et al.* (2008) studied the texture composition of sheep meat at different slaughter weights (24 or 29 Kg) observing higher meat fibrosity at 29 Kg body weight. This parameter was related to increased thermal and mechanical stability of collagen (Purslow, 2005).

Regarding juiciness, meat from young animals should be moister at the first bite and have a drier aftertaste, while heavier and older animals have a tendency toward greater juiciness due to fat content. Corroborating this assertion, Juárez *et al.* (2009) reported higher end juiciness with increasing age at slaughter.

Russo *et al.* (2003) evaluated the quality of beef carcasses, observing higher water holding capacity (0.33 for light, 0.36 medium and 0.39 for heavy carcasses); however, the increase in slaughter weight

NS = not significant; * = p<0.05; ** = p<0.01; *** = p<0.001.

also increased cooking losses. It can be inferred that sheep meat takes longer to reach the degree of doneness (70 °C in the center of beef) as age increases, resulting in higher losses. Nevertheless, Pinheiro *et al.* (2009) observed contrary results, reporting higher cooking losses in lambs (46.44%) compared to adult sheep (39.33%).

The influence of weight and slaughter age on fatty acid composition in sheep meat is quite controversial. Some results indicate no influence of slaughter weight on the fatty acid composition of meat (Díaz *et al.*, 2003). However, Wood *et al.* (2008) reviewed the influence of age on fatty acids concentrations in adipose tissue of ruminants and reported an increase in the proportion of monounsaturated fatty acids. According to the authors, the proportion of saturated fatty acids falls while linolenic acid levels remain constant. This study also showed that the proportion of conjugated linolenic acid (CLA) in the fat increased with the age of the animal.

Warren *et al.* (2008) analyzed fatty acids content, triglycerides levels, and phospholipids in Aberdeen Angus cattle at three different ages (14, 19, and 24 months). The authors observed the extent to which fattening progresses increase muscle triglycerides; however, phospholipids remain reasonably constant. The phospholipids to total lipids ratio fell by 30% at 14 months and 12% at 24 months, and these decreases were accompanied by an increase in the proportion of monounsaturated fatty acids and a decrease of ω -6 polyunsaturated in the total lipids. This seems to be similar in sheep, as Marino *et al.* (2008) observed increasing saturated lipids and decreasing unsaturated lipids in intramuscular (*Longissimus dorsi*) fat of sheep native to Italy.

Genes

The study of gene influence on meat quality is recent and its implications are still poorly understood (Thompson *et al.*, 2006). In sheep, the main set of genes (loci of quantitative traits) affecting carcass characteristics and meat are: Callipyge, Carwell or rib eye muscling (REM), Double muscling (Cockett *et al.*, 2005).

Recently, the existence of a gene that causes muscle hypertrophy in sheep was identified. Preliminary evidence suggests an autosomal dominant gene may be responsible for this effect in muscle and carcass composition. Compared with normal lambs, "Callipyge" lambs have 32.30% superior muscularity, with no change in birth weight. An advantage of the "Callipyge" phenotype is that unlike double muscling in cattle, the condition in sheep does not occur until a few weeks after birth. So dystocia at birth is not a problem for carrier animals (Sosnicki and Newman, 2010; Masri et al., 2011a). Despite the advantages in weight and carcass yield, the meat is considered extremely tough and somewhat bland due to low marbling (Goodson et al., 2001). Meat toughness can be attributed to high levels of calpastatin, which inhibit the calpain system - enzymes responsible for proteolysis of muscle post-mortem (Koohmaraie and Geesink, 2006; Kemp et al., 2010). "Callipyge" sheep meat presents significant decrease of myofibrillar fragmentation, indicative of a decrease in protein degradation (Hopkins et al., 2011). Kuber et al. (2003) observed that calpastatin activity in "Callipyge" phenotype was 58% higher than the normal genotype, while Abdulkhalig et al. (2007) reported 2.9 shear force (kgF) for "Callipyge" sheep and 5.4 for the normal genotype.

Besides the increased hypertrophy of "Callipyge" sheep, changes in muscle fiber type occur. This mutation increases the amount of glycolytic fibers, which reduce oxidative metabolism. Thus, it can be inferred that the muscles of "Callipyge" are more sensitive to a sudden drop in pH (Warner *et al.*, 2010). Changes in pH may be responsible for higher cooking losses (31% for mutant and 29.6% for normal genotype; Abdulkhaliq *et al.*, 2007).

Another mutation in sheep genome influencing carcass and meat quality was documented in Poll Dorset sheep in Australia. The "Carwell" phenotype has 8-10% rib eye area increments at similar carcass weights (Warner *et al.*, 2010). Significant effects on muscularity, an increase in protein deposition and up to 35% meat toughness increase have been documented in "Carwell" sheep (Warner *et al.*, 2010). However, Hopkins *et al.* (2007) reported no

increase (p>0.05) in sheer force of *Longissimus* or *semimembranosus*, or any other effects on pH or meat color. It can be inferred from the current literature that the effects of the "Carwell" phenotype are far less impacting on meat quality than those documented by the "Callipyge" phenotype (Hopkins *et al.*, 2011).

According to McFarlane *et al.* (2005), myostatin controls muscle fiber proliferation through transcription of gene groups responsible for myoblasts and fibroblasts differentiation and their subsequent aggregation in the myotube. A mutation in the myostatin (GDF8) gene resulting in inhibited transcription has been shown to increase muscularity in Texel sheep and other breeds (Clop *et al.*, 2006). Other studies have reported that myostatin mutations influence muscle and fat (Kijas *et al.*, 2007; Lambe *et al.*, 2011).

The g + 6723GNA mutation increased the percentage of glycolytic fibers, but did not affect shear force. However, a reduction of intramuscular fat and sensory scores on overall meat quality, including juiciness, was observed (Kijas *et al.*, 2007; Hopkins *et al.*, 2011). Masri *et al.* (2011b) observed that myostatin mutations in Texel and Poll Dorset breeds reduce *Longissimus* intramuscular fat. The authors recommend paying attention to meat quality, especially juiciness, of mutant animals.

In another study evaluating meat quality of mutant myostatin Texel sheep observed that *Longissimus* and *Semimembranosus* shear force was not affected by the mutation (Johnson *et al.*, 2005; Lambe *et al.*, 2011). According to Warner *et al.* (2010), myostatin mutations in sheep do not seem to have any influence on shearing force, despite a reduction in the perception of juiciness by consumers, perhaps due to a reduction in the amount of intramuscular fat.

Besides amount of fat, fatty acid composition of mutant beef and sheep deserves attention. Raes *et al.* (2003) showed that the double-muscling genotype in cattle has lower proportion of monounsaturated and higher of polyunsaturated fatty acids compared with the non-mutant genotype. The authors attributed this to a low concentration of total lipids in muscle and a higher proportion of phospholipids in the total lipids, increased by the mutation. Thus, studies on the impact

of double-muscling on fatty acid composition in beef and sheep are required.

Muscle fibers

Differences in muscle fibers correspond to variations in the type of myosin chain (light or heavy) responsible for myofibril contraction. This polymorphism affects the enzymatic composition of the fiber, its buffering capacity and its biology (Gerrard and Grant, 2006; Bünger *et al.*, 2009). Despite several nomenclatures in meat science, three types of muscle fibers with different characteristics are described (Table 5).

The number and type of muscle fibers of the species affect meat color. In sheep, the proportion of red, intermediate and white fibers is approximately 15, 31 and 54%, respectively (Gerrard and Grant, 2006). For the same species, Gallo *et al.* (2009) reported frequencies of 9.77, 35.01, and 55.21% for red, intermediate and white fibers, respectively. The proportions of these fibers vary between muscles and alter physical-chemical characteristics such as color (Tschirhart-Hoelscher *et al.*, 2006).

In sheep, higher final pH value corresponds to slow-contracting muscles while lower final pH is related to the more rapidly-contracting muscles (Thompson *et al.*, 2006; Tschirhart-Hoelscher *et al.*, 2006). Ryu *et al.* (2006) reported a negative correlation between the amount of white fibers and the final pH of the muscle.

In addition to pH, fiber type and their interaction with calpastatin activity affect muscle softness (Table 6). However, the effect of fiber type is still controversial regarding softness (Lee *et al.*, 2010).

The water content in muscle greatly varies with increasing speed of muscle contraction. Muscles rich in white fibers are larger and have more water compared to proteins (Tschirhart-Hoelscher *et al.*, 2006). According to Lee *et al.* (2010), the water/protein relation affects the ability to retain water, which decreases by increasing this ratio. Thus, less water holding capacity and higher cooking losses are expected in rapidly contracting muscles.

Characteristic	Red	Intermediate	White
Red Intensity	++++	+++	+
Myoglobin content	++++	+++	+
Fiber diameter	+	+	++++
Contraction speed	+	+++	++++
Resistance to fatigue	++++	+++	+
Contractile action	Tonic	Tonic	Phase
Buffering capacity	+	+++	++++
Number of mitochondria	++++	+++	+
Size of mitochondria	++++	+++	+
Capillary density	++++	+++	+
Oxidative metabolism	++++	++++	+
Glycolytic metabolism	+	+	++++
Lipid content	++++	+++	+
Glycogen content	+	+	++++

Table 5. Characteristics of animal muscle fibers.

+ = Low; +++ = Median; ++++ = High.

Adapted from Gerrard and Grant (2006) and Lefaucheur (2010).

Table 6. Content of slow chain myosin (MHC-S) and fast chain myosin (MHC-f), fiber type distribution (Type I and II), shear force, and calpastatin activity in skeletal muscle of sheep.

	LD	TFL	ST	SS	ΤZ	SE	Р
MHC-s	1.30	0.42	1.52	4.06	4.62	0.725	<0.001
MHC-f	2.01	2.02	1.79	0.79	1.30	0.370	<0.05
% type I pH 4.6	8.90	8.10	16.8	30.7	54.5	4.23	<0.001
% type II pH 4.6	91.1	91.9	83.2	69.3	45.5	4.23	<0.001
% type I pH 10.4	7.50	5.70	13.3	35.8	45.3	3.49	<0.001
% type II pH 10.4	92.5	94.3	86.7	64.2	54.7	3.49	<0.001
Shear force	4.16	5.35	5.88	5.11	-	0.51	<0.05
Calpastatin activity	1.16	1.37	0.44	0.44	0.46	0.064	<0.001

LD = Longissimus dorsi; TFL = Tensor fasciae latae; ST = Semitendinosus; SS = Supraspinatus; TZ = Trapezius.

SE = Standard error of the mean.

Adapted from Sazili et al. (2005).

Perspectives

Many factors influence sheep quality, and knowledge of their relevance requires more study accompanied by constant research on consumer and industry demands. Intrinsic factors such as breed, sex, age and weight at slaughter, genes, muscle fiber plasticity and meat quality referring to these factors must be considered in management practices. Due to the influence of intrinsic factors on meat characteristics, quality standards must be known by lamb producers in order to define the type of animal required to meet these demands.

Conflicts of interest

The authors declare they have no conflicts of interest with regard to the work presented in this report.

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