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# GENETIC AND NUTRITIONAL FACTORS DETERMINING THE PRODUCTION AND QUALITY OF SHEEP MEAT – A REVIEW*

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**Abstract**

**In the last 20 years, the importance of sheep and especially lamb meat as the main product of the sheep industry in European conditions increased noticeably. In the same period, people's interest in food quality grew. This contributed to a significant intensification of research to improve the meat production and quality traits in sheep. The aim of the research performed mainly focuses on the effects of nutrition, the environmental and genetic factors on the value of fattening, slaughter and meat quality characteristics. Much of the research concentrates on determining the fatty acid profile of intramuscular fat, which is important for sensory traits and dietetic value of lamb. Modulation of healthy qualities of lamb is aimed, inter alia, to modify the fatty acid profile, in particular to maintain the proper ratio of polyunsaturated (PUFA) to saturated fatty acids (SFA). It is also desirable to increase the content of omega-3 fatty acids and conjugated linoleic acid (CLA). Furthermore, it has been proven that changes in the expression of genes involved in lipid metabolism are associated with the change in lipid profile in skeletal muscle. The aim of this review was to summarize the information currently available about the influence of genetic and nutritional factors on meat production and quality traits in different sheep breeds.**

**Key words: sheep, gene expression, nutrition, fatty acids, lamb**

In economic terms, sheep are among the most valuable animals known to humankind. Sheep farming is common in many regions worldwide because these animals have adapted to different climatic conditions. Among domestic animals, they are characterized by the most versatile utility, producing wool, meat, milk, hides and manure. At present, meat, i.e. mutton (mature sheep) and lamb (young sheep), is the most important product of sheep. Sheep meat is consumed worldwide and, according

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to the newest FAO data (May 2014), its production is forecast to increase to 13.96 million tonnes (http://www.eblex.org.uk/market-intelligence-news/global-sheep-meat-production-forecast-to-increase/).

In many Central and Eastern European countries including Poland, wool had been the most important sheep product until the end of the 1980s. The 1990s brought a change in the economic significance of sheep products in favor of meat, especially lamb. This fact dramatically affected the size and structure of sheep populations and production systems in those countries. Sheep and lamb meat possesses unique culinary values, such as tenderness, tastiness and high nutritional value, and hence is attractive and enjoys high demand from consumers on many foreign markets. Nevertheless, in Central and Eastern European countries this kind of meat was very often underappreciated and some prejudices persist among people even today. This fact evokes the necessity to improve the public awareness about the sheep meat quality including research work in this field.

For ages, sheep have been a significant component of the environment from both conservational and economic perspectives. Apart from a variety of valuable sheep products in great demand, in many cases sheep are indispensable for the improvement and maintenance of environmental stability (Ciuruś, 1999; Gruszecki, 2012). This is particularly important in mountains, uplands and other difficult-to-farm terrain. It should not be forgotten that sheep husbandry has also played a role in cultural development. Due to the great adaptability of this species, sheep can be raised in almost all climatic conditions, though sheep-keeping systems vary according to climatic zone influencing the health of animals and production efficacy, including meat quality (Knapik, 2005; Knapik and Kieć, 2003). In order to improve production results and meat quality of lamb, crossbreeding schemes are also used. Jandasek et al. (2013) compared meat quality traits between 4 groups of crossbred lambs. The breed of sire had significant effect on protein and intramuscular fat contents as well as on meat texture and juiciness. The main goal of this review article was to summarize the information currently available about the influence of genetic and nutritional factors on meat production and quality traits in different sheep breeds.

**Candidate genes associated with meat production traits and quality characteristics in sheep**

Economically important features of meat, such as meat productive traits, are complex and may depend on many genes or Quantitative Trait Loci (QTL) (Andersson and Georges, 2004). So far, breeding programs have yielded satisfactory results. However, supplementing conventional selection data with information about the molecular basis of a given productive trait can accelerate breeding progress in a short time and increase its cost-efficiency. Genetic marker-assisted selection (MAS) enhances the efficacy of animal selection for traits of interest by being based simultaneously on several alleles. From a longer perspective, the use of MAS may help to eliminate the disadvantageous effects of traditional selection, i.e. reduction of the allelic pool and genetic variability in population (Williams, 2005). However, the appropriate choice of candidate genes (the polymorphisms of which can influence the variability of productive traits) is very difficult.

In sheep, the best-known and the most thoroughly studied QTLs are associated with muscular hypertrophy. The best-described callipyge phenotype is linked with postnatal hypertrophy of muscle tissue with simultaneous reduction of carcass fatness (Cockett et al., 1996; Cockett et al., 2005). The callipyge (CLPG) mutation presents phenotypically only in heterozygous offspring which inherit the CLPG mutation from their fathers. This is a unique mode of inheritance, called 'polar over dominance' (Cockett et al., 1996). The callipyge phenotype develops in 3-week-old lambs and causes a rapid increase in their muscle mass by 30%, especially in the hindquarter (Jackson et al., 1997). It was estimated that CLPG-mutation-bearing lambs were characterized by better parameters of musculature in such cuts as leg, loin, ribs and shoulder by 11.8%, 4.7%, 2.5% and 2.3%, respectively, compared with the callipyge-free animals (Busboom et al., 1999). Moreover, the CLPG sheep showed much better results in terms of a higher rate of feed efficiency and lower daily feed intake (Jackson et al., 1997). On the other hand, the CLPG mutation was observed to have a negative impact on meat quality, especially on its hardness. The change in muscle structure, in particular in fiber structure and diameter, probably altered the sensitivity of the muscular tissue to the enzymatic activity of calpain/calpastatin. As a result of this process, meat tenderness greatly decreased, which could have limited its use in production (Koohmaraie et al., 1995; Shackelford et al., 1997).

The rib-eye muscling locus (REM) known as 'Carwell' has been located near the microsatellite sequence OAR18 and the CLPG locus, but its precise position is not well known. What is more, the functional Carwell mutation has not yet been identified. The Carwell locus is associated with muscular hypertrophy, but its effect is limited to the *longissimus dorsi* muscle, with no impact on carcass fatness (Nicoll et al., 1998). Studies by McEwan et al. (2000) demonstrated that the Carwell phenotype was associated with an increase in the loin eye area of 11% and in the weight of the *longissimus dorsi* muscle of about 7%. In contrast to the callipyge phenotype, the Carwell mutation has no influence on meat quality, particularly meat hardness and intramuscular fat content.

The *MSTN* gene encoding myostatin (known also as the growth differentiation factor 8-GDF) belongs to a protein family (TGFβ) which plays an important role in muscle tissue development. In Blue Belgian and Piedmontese cattle, the *MSTN* gene was associated with double muscling of carcasses (McPherron et al., 1997). In Texel sheep characterized by double muscling, Clop et al. (2006) identified a mutation in the 3'UTR region (G6723A) which created a new binding site for mRNA molecules, thus causing muscular hypertrophy. Studies by Kijas et al. (2007) confirmed the significant impact of this mutation on meat and fat content in lamb carcasses. These authors demonstrated the relationship between four microsatellite markers in the *MSTN* gene and muscle and fat content. In addition, Gan et al. (2008) identified several mutations in different regions of the myostatin gene. These authors observed a significant correlation between the chosen haplotypes and average daily gains, and thus indirectly with myostatin function and double muscling. Moreover, Bagatoli et al. (2013) confirmed significant association between expression level of *MSTN* and calpastatin (*CAST*) genes and lamb meat quality. The authors showed that high transcript abundance of both genes were associated with lower values of lamb meat tenderness, and that tenderness is related to the stage of muscular growth.

In sheep, various genes have been listed as candidates responsible for meat quality in lambs. One of them, the calpastatin (*CAST*) gene, encodes the endogenous inhibitor of calpains, which in muscle cells catalyze cytoskeleton proteolysis. The calpain/calpastatin system is involved in many proteolytic processes which can influence muscle development or *postmortem* muscle changes, i.e. meat aging. Interestingly, the calpastatin gene cooperates with the callipyge gene to influence muscle content; namely, the CLPG genotype influences the content of calpastatin protein (Freking et al., 1999). Palmer et al. (1998, 1999) identified and analyzed several polymorphic loci in the *CAST* gene in sheep and indicated their association with daily body weight gain, age-corrected carcass weight and shear force of the *longissimus dorsi* muscle. However, studies by different authors produced contradictory results; accordingly, further intensive investigations of the *CAST* gene in sheep are recommended in the future (Nassiry et al., 2006; Suleman et al., 2012).

The *FABP4* gene (fatty acid binding protein 4, A-FABP) codes for cytoplasmic proteins which bind and transport long-chain fatty acids. In Duroc pigs, several microsatellite markers within the *FABP4* gene were associated with differences in IMF without a concomitant influence on backfat thickness or water-holding capacity (Gerbens et al., 1998). In sheep, *FABP4* gene polymorphism influences IMF level, shear force, and marbling of the *longissimus dorsi* muscle. Allele A of this gene has a positive effect on lamb tenderness (Xu et al., 2011); thus, the obtained results indicate that the *FABP4* gene can be used as a marker of meat quality in lamb.

Leptin (*LEP*), the main protein hormone produced by the fatty tissue, plays a key role in the regulation of energy intake. By influencing feed intake, leptin regulates energy balance in the body, lipogenesis, thermoregulation and body weight (Houseknecht et al., 1998). In sheep, several mutations of the leptin gene were identified. Studies by Boucher et al. (2006) demonstrated that a mutation located in intron 2 (A103G) had a negative effect on muscle growth. The authors observed a reduction in *longissimus dorsi* muscle thickness and an increase in loin eye fatty tissue weight in the Dorset breed. Moreover, the A103G mutation was associated with increased shear force, pH, and cross-sectional area (CSA) of the slow-twitch oxidative fibers. Studies conducted on different sheep breeds confirmed that SNPs in the *LEP* gene in sheep significantly influenced the fat content in carcasses, muscle growth, meat quality traits (Boucher et al., 2006; Hajihosseinlo et al., 2012; Sadeghi et al., 2014). On the other hand, analysis of the association between this gene and meat content demonstrated discrepant results in different breeds (Barzehkar et al., 2009). In the Shal breed, this mutation increased cold-carcass weight, while in the Zel breed, the same mutation reduced slaughter weight, cold-carcass weight and meat content (Barzehkar et al., 2009). The results obtained by different authors showed that the leptin gene influenced important quality traits of sheep meat; however, these data should be confirmed on large numbers of animals of different breeds.

Table 1. Candidate genes and their association with meat production traits in sheep

| Gene symbol | Gene name | DNA variant | Effect on production traits | Breed | Reference |
|---|---|---|---|---|---|
| 1 | 2 | 3 | 4 | 5 | 6 |
| *CLPG* | *Callipyge* | Mutation in *CLPG locus*: A→G transition that affects a muscle-specific control element located in the middle of the 90-kb *DLK1-GTL2* intergenic region | Association with muscle hypertrophy (especially in the hindquarters) and carcass fatness; Impact on feed efficiency and daily feed intake | American Dorset | Jackson et al., 1997 |
| *Carwell locus* | the rib-eye muscling *locus* (REM), *Carwell* | Has not been identified so far | Association with muscle hypertrophy – *longissimus dorsi* muscle; | Australian Poll Dorset | Nicoll et al., 1998 |
| | | | Carwell phenotype increases the rib-eye area – about 11% and weight of the *longissimus dorsi* muscle – about 7% | British Texel | McEwan et al., 2000 |
| *MSTN (GDF8)* | myostatin | G6723A in 3'UTR region | Mutation creates new complementary binding site for miRNA, increases muscularity; | Belgian Texel | Clop et al., 2006 |
| | | | Effect on meat and fat content in lamb carcasses; Association of four microsatellite markers and muscling and fatness | Texel sheep | Kijas et al., 2007 |
| | | -41 (C→A),<br>-781 (G→A),<br>-956 (T→C),<br>6223 (G→A) | Haplotypes impact average daily gain | Meat and Multi-Prolific Chinese Merino Fine Wool, Huyang, Kazak, Beltex, Dorper and Beltex × Huyang | Gan et al., 2008 |
| *CAST* | calpastatin | *CAST/Msp*I, *CAST/Nco*I polymorphic sites in intron1 | Association with live weight gain, carcass weight and *longissimus dorsi* shear force; | Dorset Down, Dorset Down × Coopworth | Palmer et al., 1998, 1999 |
| | | CAST/*Msp*I in intron 1 | Impact on daily gain birth to weaning | Kurdi sheep | Nassiry et al., 2006 |

Table 1 – contd.

| 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|
| *FABP4 (A-FABP)* | fatty acid binding protein 4 | g.A282G in intron 1 | Associated with meat tenderness, marbling score, intramuscular fat content in *longissimus dorsi* | Small-Tailed Han sheep, Tan sheep, Inner Mongolia sheep | Xu et al., 2011 |
| *DGAT1* | diacylglycerol acyltransferase 1 | 487 T>C in exon 17 | The T allele had a positive effect on tenderness, IMF content and marbling score | Small-Tailed Han sheep, Tan sheep, Inner Mongolia sheep | Xu et al., 2009 |
| | | A103G in intron 2 | Decrease of muscles thickness and loin eye area; increased shear force, pH, association with subcutaneous fat | Suffolk, Dorset | Boucher et al., 2005 |
| *LEP* | leptin | A113G in intron 2 | Increase of fat-tail percent, total body fat weight | Iranian sheep breeds (Shal, Zandi, Zel) | Barzehkar et al., 2009 |
| | | PCR-SSCP polymorphism in exon 3 | Associated with birth weight, weaning weight, average daily gain | Makooei sheep | Hajihosseinlo et al., 2012 |
| *TNNC2* | fast skeletal muscle troponin C | Indel GTTA>GT-A in intron 1 | Association with meat tenderness, marbling score, pH and carcass weight | Small-Tailed Han sheep, Tan sheep, Inner Mongolia sheep | Xu et al., 2008 |

*DGAT1* (diacylglycerol acyltransferase 1) is another interesting gene which, in cattle, affects important traits of milk production, such as the content of fat, protein, lactose and the number of somatic cells in milk. Many studies are currently under way which investigate the association between the *DGAT1* gene and meat quality traits in different species (Giusti et al., 2013; Borges et al., 2014; Renaville et al., 2015), including sheep. Studies by Xu et al. (2009) revealed the impact of the silent mutation in exon 17 (Ala487Ala; T>C) of the *DGAT1* gene on important quality traits of lamb. Authors indicated that TT genotype was associated with increase of marbling score and intramuscular fat (IMF) content as well as with lower shear force and drip loss rate.

The association between meat productive traits and the *TNNC2* gene encoding the protein troponin had been also studied. Troponin C plays a key role in the complex of troponin proteins responsible for the regulation of stripped muscle contractions, suggesting that this protein may be linked with quality traits of meat. In sheep, studies by Xu et al. (2008) demonstrated a single nucleotide polymorphism in intron 1 which influenced carcass weight and several meat quality traits: *m. longissimus thoracis* and *m. lumborum* shear force, water-holding capacity, marbling and pH value. Sheep with the TT genotype were characterized by improved meat tenderness and marbling, but lower carcass weight. An overview of associations between different candidate genes and meat production traits in sheep is shown in Table 1.

**Whole-genome association of meat production traits in sheep**

Nowadays, the genetic progress in sheep breeding is achieved by several approaches including BLUP (best linear unbiased prediction) generated breeding values in combination with sire-referencing schemes (Lewis and Simm, 2000). The animal breeding and selection methods are assisted by MAS selection based on haplotype analysis, mapping of single genes or QTLs, detection of copy number variation (CNV), genome-wide association study (GWAS) or genomic selection. The production traits in animals can be genetically correlated with each other and the strength of this association is estimated by genetic correlation value. Production traits can be genetically related when in linkage (*loci* determined different characteristic are mapped near each other on the same chromosome) or pleiotropy (Solovieff et al., 2013). Thus, the modern genetic methods focus on identification of QTLs associated with important traits and facilitate the application of genomic selection and GWAS.

To date, in SheepQTLdb database have been annotated 175 QTLs related with carcass traits, 33 with meat composition, 6 with meat color and 5 with meat texture (Hu et al., 2016). New capabilities enable the estimation of breeding value based on computed tomography (CT) technique (for example for muscle area or subcutaneous fat thickness measurements) and identification of genomic regions associated with assessed traits (Cavanagh et al., 2010). On the other hand, the use of genome-wide association studies (GWAS) to estimate the correlation between the frequency of alleles/genotypes of panel of markers and different phenotypes has been proven to be the most accurate approach compared to other methods (Hirschhorn and Daly, 2005). The first GWAS research was performed in sheep in 2011 by Johnston et al. who searched the genetic basis of horn type in a wild sheep population. In 2013, Zhang et al. using high throughput genotyping technology (Illumina OvineSNP50 BeadChip) identified several genes involved in growth processes and meat production traits in sheep. Similarly, Gholizadeh et al. (2015) used the genotyping on the Illumina ovine SNP 50K BeadChip assay in order to determine the most casual polymorphisms affecting body weight traits in sheep. Authors analyzed such traits as weight at birth, weaning, six months and twelve months and mapped SNPs or genomic regions significantly associated with body weight traits. Both studies confirmed that GWAS is an excellent genome-wide method used to identify the genetic basis of economically important production traits in animals.

**Nutritional factors influencing lamb meat quality**

The feeding system is an important factor decisive for lamb meat quality. Feeding intensity can influence fat content in lamb carcasses (Borys et al., 2011). The relationship between muscle (protein) and fat content in carcasses determines the marbling and tenderness of meat. The meat content can be enhanced by increasing protein deposition, reducing fat deposition or both. The amount of protein deposited by the sheep is dependent on factors both related and unrelated to feeding. The main feeding-related factors influencing protein deposition include energy supply and appropriate protein content in rations, aimed at providing a sufficient amount of indispensable amino acids to maximize protein deposition. The main amino acids limiting protein deposition in muscle tissue are lysine, methionine, cysteine, tryptophan, and in some cases, isoleucine and valine (Nimrick et al., 1970). It should be remembered that the amino acid supply in the diet depends on the animals' age, sex, physiological conditions, the season, etc. Some meat quality traits such as tenderness can be improved by using the growth compensation reaction (Warner et al., 2010; Pannier et al., 2014). This feeding strategy is used mostly in pig rearing but is also applied in sheep and consists of a limited energy supply in the initial period of fattening, simultaneously with a protein supply at the normal level. This feeding technology improves meat texture and tenderness, while the limited energy supply does not adversely affect slaughter parameters: carcass weight, carcass yield and primal cuts (Murphy et al., 1994; McPhee et al., 2008; Borys et al., 2011). Currently, this method is not often used in sheep feeding due to the small scale of sheep meat production. Apart from feeding-related factors, demand for amino acids is determined by genotype (breed), sex, health condition and environmental factors.

Marbling is beneficial for the tenderness, juiciness and tastiness of meat. Fat deposition in muscles usually accompanies intermuscular, subcutaneous and visceral fat deposition (McPhee et al., 2008). Larger amounts of such fats in the carcass are undesirable. It is also known that fat is first deposited around the kidney and intestines, then subcutaneously, and finally as inter- and intramuscular fat. Therefore, it is difficult to produce carcasses containing a great deal of intramuscular fat and small amounts of other fats. It should be reminded that the degree of marbling is strongly correlated with general fat content in the carcass (McPhee et al., 2008; Pannier et al., 2014). The above-mentioned nutritional treatments aim to produce the dietetic lamb meat characterized by high taste qualities, being a good source of health-promoting substances, among others unsaturated fatty acids, especially *n-3* PUFA, CLA, vitamins of the E and B groups, carnitine and micronutrients (Fisher et al., 2000; Alvarez et al., 2014; Ikem et al., 2015). Fatty acid composition in muscle tissue largely depends on the type of the diet, especially the type of dietary fat. The studies conducted so far on ruminants have focused on dietary modification of meat composition and have tested the effect of supplemental oil plant seeds, sea fish oils, protected fats, animal fat and some plant oils (Baranowski et al., 2007; Choi et al., 2007; Chen et al., 2008). Improvement of fatty acid composition in tissues depended on the amount and type of supplementary fat and duration of dietary supplementation. Studies on lambs compared feeding rations supplemented with forage *vs.* unsupplemented rations and demonstrated higher contents of *n-3* PUFA and reduction of the *n-6/n-3* ratio in the forage-fed group (Aurousseau et al., 2004; Nuernberg et al., 2008). Supplementation of fodder with high-energy feedstuffs, i.e. fats, provides animals with a sufficient level of dietary energy. Another reason why sheep rations are supplemented with fat is to change the fatty acid composition in milk or to enhance the content of polyunsaturated fatty acids of the *n-3* family in carcass lipids (Radunz et al., 2009). However, the introduction of polyunsaturated fatty acids in the form of plant oils or plant seeds oil requires technology for protecting these fatty acids from hydrogenation in fermentation processes occurring in the rumen. This process can be prevented by the use of formaldehyde. On the other hand, in many countries including Poland, fodder supplementation with formaldehyde for domestic animals is prohibited. High-temperature processing of fodder is another method to prevent protein decomposition and fat hydrogenation in the rumen (McKinnon et al., 1991). Proper preparation (by heating at 120–130°C) of flaxseed and rapeseed makes the nutrients less soluble and thus less prone to degradation by the rumen microflora. Studies by Barowicz and Brejta (2000) on ruminants demonstrated that the digestion of fat from heated rapeseed and flaxseed was shifted to the small intestine and that high-temperature treatment disabled protein and fat digestion.

It should be remembered that C18 fatty acids, i.e. linoleic and linolenic acids, are biohydrogenated in the rumen and 60–95% of these acids are transformed into stearic acid (Doreau and Ferlay, 1994). Another way to preserve plant fats from decomposition in the rumen is to supplement fodder with calcium, sodium or magnesium salts of fatty acids from plant oils. This procedure protects about 40–60% of the linoleic and linolenic acid in the rumen (Ngidi et al., 1990). Fats in the form of soap are not degraded as much as they are in an unprotected form in the neutral pH of the rumen, but are efficiently digested enzymatically in the acid pH in the abomasa and absorbed in the intestine. It was shown that the use of calcium salts of fatty acids from flaxseed oil in sheep feeding increased MUFA content, linolenic acid (C18:3) level and reduced the *n-6/n-3* ratio in intramuscular fat (Zsedely et al., 2012). It was also demonstrated that the polyunsaturated fatty acids EPA and DHA were biohydrogenated in the rumen to a lesser extent compared to others and were able to reach the duodenum unchanged.

Sheep of dairy breeds are often used for the production of light lambs for slaughter. Meat from the carcasses of such lambs is characterized by high nutritional values and palatability. This was confirmed by Margetín et al. (2014), who demonstrated also favorable content of saturated and unsaturated fatty acids and their relative proportions in the meat obtained from carcasses of lambs reared traditionally compared with the artificial rearing. The impact of feeding system on the fatty acid composition of meat was explained. The source of protein and energy in the diet also has an effect on fatty acid deposition in lamb tissue. Alpha linoleic acid (ALA) is the major dietary fatty acid for pasture-fed ruminants since it constitutes over 50% of total fatty acids in grass and grass products (Wood et al., 2008). The incorporation of linoleic acid (LA) from concentrate diets and ALA from pasture diets into lamb fat deposits in the study of Bas and Morand-Fehr (2000) led to higher synthesis of ALA and lower levels of oleic and linoleic acid in lambs fed the pasture system, compared with lambs fed the concentrate diet. Studies on the modification of fatty acid composition in meat and milk have been carried out for the past decade and longer. The conjugated linoleic acid (CLA) occurring naturally in ruminant-derived products deserves special attention. The biological activity of CLA isomers reveals a variety of health-promoting aspects, such as prevention of atherosclerosis, anticancer and immune-stimulating properties, and improvement of lipid metabolism (Koba and Yanagita, 2014). The addition of rapeseed, plant oils rich in linoleic acid and fish oils to the animals' rations increased CLA content in tissues and milk, though this was not always confirmed by study results. However, supplementation of rations with protected fish oil was proven to enhance CLA in lamb (Schumacher-Strabel et al., 2001).

Recent studies have indicated that, apart from CLA derived from the rumen, there exists a dominating desaturation mechanism in which trans-11-octadecenoic (vaccenic) acid desaturase is responsible for CLA synthesis. Therefore, proper feeding creates an opportunity to increase CLA levels in ruminant products and, in this way, to enhance their health-promoting value for the customer (Dervishi et al., 2010). The administration of protected fat in the diet of sheep, among others, calcium salts of palm oil, algae, linseeds or fish oil increases the fatty acids of the *n-3* family in the meat and milk, reduces the ratio of *n-6/n-3* (Demirel et. al., 2004; Hopkins et al., 2014), and may also cause an increase of fatty acid oxidation in the meat and lower its quality (Diaz et al., 2011).

Grasses and legumes, especially red clover, occurring in pastures are a rich source of unsaturated fatty acids, especially linoleic and α-linolenic acids (Shen et al., 2007). Lipase present in forage plant leaves is responsible for the first stage of lipolysis, which occurs during grazing in pastures. Red clover is characterized by a much lower level of lipolytic activity than grass, which is dependent on the effect of the enzyme polyphenol oxidase (PPO). Lee et al. (2010) suggested that the protective effect of PPO consisted of the reduction of bio-hydrogenation and denaturation of plant-derived unsaturated fatty acids by promoting the formation of lipid-protein-phenol complexes.

Fattening of lambs on compound feeds containing cereal seeds resulted in an increased content of linoleic acid (C18:2) in meat, while feeding the animals on grass or silage rich in linolenic acid caused an enhancement of *n-3* fatty acids (Fisher et al., 2000; Turner et al., 2014). When animals were fed compound feeds supplemented with cereal seeds, the population of microorganisms in the rumen changed and PUFA hydrogenation was inhibited, leading to the absorption of reduced amounts of saturated fatty acids and lower levels of their deposition in tissues (Wood et al., 2008).

Consequently, and unexpectedly, the level of *n-6* fatty acids increased in relation to that of *n-3* fatty acids, which was disadvantageous for consumers' health. Meat from lambs fed rations composed of compound feed supplemented with cereal seeds contained elevated levels of linoleic acid (C18:2), which during cooking undergoes abrupt oxidation, yielding a number of by-products, mostly 2-undecanal and hexanal, giving a characteristic rancid flavor to lamb (Young et al., 1997). Other products dominating in meat during cooking included diketone 2,3-octanedione and tetrahydro-2,5-dimethylfuran. Lamb meat from animals fed grass in daily rations was characterized by the presence of diketone 2,3-octanedione and 3-methylnonanoic acid. α-linolenic acid (C18:3) derived from fish, flax and rape oil was the precursor of long-chain *n-3* fatty acids. Oxidation of these acids imparted a fishy flavor to meat which was unacceptable to consumers. The carriers of this objectionable flavor included α-linolenic (C18:3), eicosapentaenoic (C20:5) and docosahexaenoic (C22:6) acids. British studies estimated that 3% of these acids in the entire pool of meat lipids was the upper limit acceptable to consumers (Enser et al., 1998). On the other hand, comparative work aimed at assessing which meat was preferred by consumers, i.e. meat rich in *n-3* or in *n-6* acids, revealed that meat containing more *n-6* acids, derived from linoleic acid (C18:2), was tastier (Enser et al., 1998).

Fisher et al. (2000) and Sanudo et al. (2000) compared lambs of different breeds finished under various production systems for flavor intensity as measured by sensory panelists in three countries. Forage-fed lambs had higher levels of *n-3* fatty acids and concentrate-fed lambs had higher levels of *n-6* fatty acids. Panelists from the United Kingdom preferred forage-fed lamb; whereas, panelists from Spain preferred concentrate-fed lamb. Priolo et al. (2002) evaluated finishing lambs on grass pastures or concentrates and found that concentrate-fed lambs had lower, less intense, livery off-flavor rating. Tenderness, firmness and juiciness are closely associated with water content in muscle tissue and with stearic (C18:0) and linoleic (C18:2) acid levels. Stearic and linoleic acid have different melting temperatures, approximating 69.6°C and –5°C, respectively, which influence meat compactness and firmness (Zygoyiannis et al., 1985). Thorough studies on the effect of fatty acid composition on meat flavor demonstrated a positive correlation of this parameter with saturated and monounsaturated fatty acids and a negative correlation with unsaturated fatty acids. Stearic acid (C18:0) and oleic acid (C18:1) have the positive impact on flavor of lamb meat but linoleic (C18:2) and arachidonic acids (C20:4) worsen it (Fisher et al., 2000; Wood et al., 2008).

Enrichment of polyunsaturated fatty acids in lamb is desirable for consumers' health because these acids improve the dietary value of meat, but excessive amounts in animals' fat have adverse effects on meat's sensory characteristics (flavor, aroma) and its stability during storage (Nute et al., 2007). Such meat and its products are characterized by decreased stability due to the greater vulnerability of polyunsaturated fatty acids to oxidation, even after freezing. Meat colour also undergoes unfavorable changes due to myoglobin transformation into methmyoglobin, which is dependent on heme iron contained in the hemoglobin and myoglobin occurring in meat (Igene et al., 1979). Iron is thought to be among the main factors responsible for the taste, as there is a close relationship between its content and the development of foreign flavors (Yancey et al., 2006).

Moreover, oxidation of carcass fat makes it softer and aggravates its unfavorable features, such as reduced oxidative stability during storage, rancid flavor, and change in color. These objectionable processes can be prevented by using antioxidants, preferably natural, of which the most important are: vitamin E (α-tocopherol), β-carotene and vitamin C (ascorbic acid) (Wulf et al., 1995; Alvarez et al., 2014) and natural polyphenols (Lee et al., 2010). Vitamin E plays a role in the neutralization of free radicals in cells, thus counteracting cell damage caused by oxidants. The higher the levels of vitamin E present in tissues, the more efficient this protective mechanism is. The above-mentioned properties of vitamin E are preserved for some time after slaughter. Dietary vitamin E is accumulated in adipose and muscle tissue. Antioxidant vitamins, especially vitamin E and carotenoids, have beneficial effects on meat color. The meat from lambs receiving vitamin E supplements or grazing in pastures is characterized by a greater lightness of color (L*) and higher redness (a*); thus meat color changes occur more slowly during storage and the bright red color is retained longer (Turner et al., 2002). Higher vitamin E levels in muscles enhance the water-holding capacity in cells and reduce water leakage during storage, thereby significantly influencing storage opportunities and sensory meat characteristics (López-Bote et al., 2001). Vitamin E improves sensory meat attributes, such as aroma and flavor, and enhances its dietetic value. Selenium produces similar effects on muscle metabolism and cooperates with vitamin E via glutathione peroxidase to remove free radicals from cell membranes.

It can be concluded that there is a conflict between the dietetic and shelf life values of meat from lambs enriched with polyunsaturated fatty acids. By increasing *n-3* and *n-6* fatty acid contents, we improve the dietetic value of meat, but we have to be aware of the increased vulnerability to oxidation and all its negative consequences. Most of the secondary metabolites of fatty acid and cholesterol oxidation in meat are not entirely harmless to human health and should be monitored in order to make food products worthy of being called ‘safe’.

The macro- and micro-minerals play an important role in the diet of sheep. Mineral nutrition recommendations are included in a series of standards for example: NRC (2007), ARC (1985), the IZ-INRA (2009) which are used by sheep farmers from different regions or countries. An important element in determining the quantity and quality of mineral additives used for sheep is the quality and composition of the pasture sward which is determined by a number of factors such as: soil composition, the weather pattern or the length of the vegetation period. The quality of the pasture, among others, the phase of growth and nutrient content in plants plays a particularly important role in the diet of sheep, especially in the initial period of grazing when sheep are exposed to the occurrence of hypomagnesemic tetany, a syndrome associated with low level of magnesium in the blood, which is caused by the intake of young green grass rich in protein and potassium, and poor in magnesium (Martens and Schweigel, 2000). An important rule in the mineral nutrition of sheep is assurance of adequate amounts of the particular minerals which should be in the right proportion to each other. Following amounts are recommended by the standards: IZ-INRA – content of Ca and P in the dry matter of feed should be between 7.3 and 2.9 g/kg DM; according to American NRC standards: 4.6 and 2.4 g/kg; and according to British ARC: 5.5 and 2.8 g/kg. Special attention should be paid to the supplementation of the ration with micronutrients. It is recommended to use salt licks enriched with iodine. Iodine is responsible for the proper neurohormonal functioning of the thyroid gland. Thyroid hormones control basal metabolism and heat production, cell differentiation and growth of tissues such as brain, central nervous system and lung. Selenium and vitamin E supplementation is applied in fattening of lambs to higher body weight and sheep during lactation, which has a positive impact on the growth of lambs and the quality of their meat (Davis et al., 2006; Kojouri and Shirazi, 2007). In addition, the sheep are vulnerable to shortages of cobalt, its deficit leads to disequilibrium in the synthesis of vitamin $B_{12}$ and significantly affects the course of the protein and energy metabolism of the rumen microorganisms (Kawashima et al., 1997). Sheep are also susceptible to the deficiencies of copper, the absorption of which is closely related to the level of molybdenum in the feed (Pott et al., 1999). A symptom of copper shortages are problems with growth and development of bones and nervous system disorders (enzootic ataxia).

## Conclusions

Sheep production and meat quality traits are mainly influenced by genetic and nutritional factors, which is documented by many results of scientific research. Continuation of research work in this field is highly desirable to improve the effectiveness of sheep production and consumer demand for highly valuable and healthy sheep and lamb meat.

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