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The potential benefits of genetics and genomics to improve beef quality – a review

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Intrinsic quality attributes of beef, and especially its tenderness, depend not only on *post-mortem* factors associated with meat ageing, but also on muscle characteristics of live animals, which themselves depend on genetic, nutritional and rearing factors. Different breeds or different genotypes of the same breed mainly differ by the characteristics of their connective tissue (content and solubility of collagen), content and composition of intramuscular fat and/or the characteristics of their muscle fibres (slow-oxidative, fast-oxidoglycolytic and fast glycolytic). These differences induce mainly differences in meat colour and cooking losses and, to a lesser extent, in flavour and tenderness of beef. Mutation in the myostatin gene induces generalized hypertrophy of muscles, promotes a glycolytic muscle fibre metabolism, and leads to decreased collagen and intramuscular fat contents which favour tenderness and dietary attributes. Simultaneously, however, lower intramuscular fat content is detrimental for flavour. The genetic variability is quite high for intramuscular fat content (marbling), moderate for tenderness and low for flavour and juiciness. The identification of polymorphisms in some key genes which determine characteristics of connective tissue or of muscle fibres has been reported because of their association with beef quality traits. Gene or protein expression profiling thanks to the advent of functional genomics has also allowed the identification of new molecular indicators of tenderness or marbling. Generally, genetic selection in favour of high muscle development and low fat deposition induces an orientation of muscle fibres towards the fast-glycolytic type as demonstrated by biochemical and functional genomic studies.
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Quality is a complex concept. It has been defined by the French Association for Normalization (AFNOR) as "the overall properties of a product (or a service) which confer on it the capacity to satisfy expressed or implicit needs" of end-users (especially consumers in the case of food products). It thus includes intrinsic and extrinsic quality attributes. The first refer to the characteristics of the product itself, while the latter to traits more or less associated with the product such as, for beef, production system characteristics and marketing variables (brand name, labelling, traceability, *etc*). Intrinsic quality attributes of beef include safety, nutritional, technological and sensory aspects. In this paper, we will mainly consider sensory attributes such as tenderness, flavour and juiciness, but also marbling and dietary attributes. Marbling is an important meat quality trait in North America, Asia and Australia. It refers to the appearance of white flecks or streaks of adipose tissue between the bundles of muscle fibres. It is thus closely linked to intramuscular fat content. Dietary aspects are clearly associated with a low intramuscular fat content, a low proportion of saturated and a high proportion of polyunsaturated fatty acids (SFA and PUFA, respectively) in beef, all these factors being supposed to decrease the incidence of obesity and cardiovascular diseases.

It is well-known that intrinsic quality attributes of beef, and especially its tenderness, depend to a great extent on *post mortem* factors (temperature, pH, proteolysis which degrades muscle proteins during the *post-mortem* ageing of beef). But meat characteristics depend also directly on the muscle biology of live animals, which is regulated by genetic, nutritional and rearing factors [Geay *et al*. 2001, Maltin *et al*. 2003]. Among the latter, the genetic factors are of prime importance because genetic improvement is permanent and cumulative when inherited by the next generations.

The importance of genetic factors can be demonstrated by comparing different breeds or different genotypes of the same breed, by investigating the effects of major genes or by studying the polygenic inheritance of beef quality. The advent of high-throughput DNA-sequencing techniques, array technology and protein analysis have increased the efficiency of research in bovine muscle physiology, with the ultimate objective to improve beef quality by either breeding or rearing factors. For genetic purposes, the discovery of new polymorphisms in some key genes has been reported because of their association with beef quality traits. The sequencing of the bovine genome will dramatically increase the number of available gene polymorphisms. For rearing purposes, global gene expression profiling at the mRNA or protein level has already showed that previously unsuspected genes may play a role in muscle development or growth, and new molecular indicators of tenderness or marbling have been or will be reported.

Breed effects on beef quality

It is well-known that different cattle breeds or genotypes differ in muscle characteristics due to marked differences in their physiology. Consequently, beef may differ in quality depending on the animal genotype. For instance, meat from *Bos indicus* cattle is less tender than that from *Bos taurus* breeds. The lower tenderness is due to reduced proteolysis of myofibrillar proteins in muscles from *B. indicus,* associated with greater activity of calcium-dependent protease inhibitor [Whipple *et al*. 1990b]. It was also demonstrated that beef breeds (Blonde d'Aquitaine and Limousin) were characterized by lower collagen content, and compression and shear force in raw and cooked meat, respectively, compared to dairy (Holstein) or dual purpose (Brown Swiss) breeds. However, texture differences between animals and breeds were shown to decrease with ageing time during storage of beef at 4°C after slaughtering [Monson *et al*. 2004]. In another study comparing two French local breeds (Aubrac, Salers) and two French beef breeds (Limousin, Charolais) no significant differences were found in eating quality due to much higher variation within breeds than between breeds. Slightly higher eating quality was, however, observed in Limousin and Aubrac cattle. Inter-breed differences in beef quality are often less pronounced than those identified within breeds and are overridden by larger differences between muscles or cuts [Dransfield *et al*. 2003].

It is also well known that late-maturing beef breeds (Belgian Blue, Limousin and Blonde d'Aquitaine) deposit more muscles and less fat compared to dairy breeds or early-maturing beef breeds (Angus and Japanese Black cattle). Less intramuscular fat may be detrimental to beef flavour, especially in young animals such as bulls slaughtered at 15-18 months of age. Breed differences reported in the literature are thus often confounded with differences in somatic maturation time, and hence fatness. This prompted some authors to compare quality of beef from steers of four breeds (Angus, Simmental, Charolais and Limousin) showing the same level of intramuscular fat. Under those conditions, meat from Angus and Charolais steers was found pale and with low haem iron content. Beef from Angus and Limousin was more tender. The flavour was similar among breeds while juiciness was the highest in Limousin and the lowest in Angus cattle. The juiciest beef showed the highest drip losses and the lowest cooking losses [Chambaz *et al*. 2003].

Another comparative study was recently carried out on 243 young bulls from eight European beef breeds from Spain, Italy and France. The breeds with higher fattening performance (e.g. Piedmontese) had a lower thawed meat pH after 10 days of ageing, while the local breeds (e.g. Asturiana de la Montaña, Avileña) had higher pH, lower drip losses and, in terms of meat colour, less lightness and yellowness, but greater redness. The highest shear force values were observed for the Spanish local breeds and the Charolais breed on raw meat, but for Marchigiana and Piedmontese on cooked meat. Compression at 20% of maximum compression force stress, which may be related to myofibrillar resistance, did not discriminate breeds, unlike compression

tests at 80% of maximum stress, which is associated with connective tissue resistance. The highest values were observed for the two Spanish local and the Charolais breed, while the lowest for the Piedmonteses [Failla *et al*. 2004]. The two local breeds were also characterized by a more oxidative muscle metabolism and a higher proportion of fast oxido-glycolytic fibres [Jurie *et al*. 2004]. This clearly explains the differences in colour, and probably in pH and in drip losses. However, the differences in toughness are less clear and more complicated to explain since more parametres related to fibre type, proteolysis rate during ageing and collagen characteristics are involved. Another recent study has confirmed that the beef quality of different breeds is mainly related to fat content, cooking losses, and colour (luminosity, redness) due to different muscle fibre types related to the breed [Cuvelier *et al*. 2006].

From a nutritional point of view, a key issue is to increase the proportion of polyunsaturated fatty acids (PUFA) and CLA (conjugated linoleic acid) in beef. The leanest breeds are characterized by a higher PUFA percentage, and CLA content is proportional to intramuscular fat content. Japanese Black cattle are also genetically predisposed to produce lipids with higher monounsaturated fatty acids (MUFA) concentration. However, although significant, these differences are probably nutritionally meaningless due to the low contribution of beef fat to the human diet [reviewed by De Smet *et al*. 2004].

Monogenic inheritance of beef quality: the double-muscling character

The double-muscling phenotype (DM) is characterized by general hypertrophy of muscles (+25%). Simultaneously, DM cattle display reduction in the size of the other organs (-40%) and have less fat and bone than conventional ones. DM is also characterized by increased stress susceptibility, reduced fertility, severe calving difficulties (dystocia), and low calf viability [reviewed by Bellinge *et al*. 2005]. The overall increase in muscle mass, which is due to an increase in the number of muscle fibres (hyperplasia) and to a lesser extent to fibre enlargement (hypertrophy), differs between muscles. DM animals show a higher proportion of lean meat than conventional cattle. Their meat is pale and tender, mainly due to an elevated proportion of white fast-twitch glycolytic fibres and lower collagen content. The meat of DM animals shows reduced flavour due to much lower content of intramuscular fat. Lastly, in DM cattle hormonal and metabolic status related to lower plasma concentrations of triiodothyronine, insulin and glucose is different from that of conventional cattle [Hocquette *et al*. 1999].

The DM phenotype is controlled by the *mh* (muscle hypertrophy) gene, mapped to the centromeric end of *Bos taurus* chromosome (BTA) 2. Grobet *et al*. [1997] showed that the myostatin gene maps to the *mh locus*. Mice with knocked-out myostatin (GDF-8) gene exhibit double-muscling. Myostatin is known to be a growth factor that inhibits myoblast proliferation and hence regulates muscle development and growth [reviewed by Kambadur *et al*. 2004 and Bellinge *et al*. 2005]. Mutations disrupting

myostatin lead to the DM phenotype in cattle and can be explained by a higher rate of myoblast proliferation. However, DM in European cattle breeds is characterized by allelic heterogeneity and many independent mutations have been observed. Several loss-of-function mutations have been identified within the three exons of the coding region of myostatin [Grobet *et al*. 1997]. They include either (i) deletions such as the 11-bp deletion of nucleotides in exon 3 referred to nt821(del11) in Belgian Blue DM [Grobet *et al*. 1997] or (ii) amino acid changes such as the C313Y mutation within exon 3 in Piedmontese and Gasconne breeds or (iii) the Q204X mutation in Charolais [reviewed by Kambadur *et al*. 2004]. The mutations result in the production of either an out-of-frame truncated or a full-length inactive myostatin protein. Interestingly, Blonde d'Aquitaine cattle do not display any of these mutations, but do show characteristics similar to DM cattle [Listrat *et al*. 2001].

The features of muscles of DM cattle already appear during their foetal development. Indeed, it was recently shown that myostatin promotes the differentiation of multipotent mesenchymal cells into the adipogenic lineage and inhibits myogenesis [Artaza *et al*. 2005], which explains why double muscled cattle show a greater muscle mass and less intramuscular fat than normal ones. Myostatin expression is detectable from day 16 of pregnancy in bovine embryos [reviewed by Kambadur *et al*. 2004] and is regulated throughout gestation [Deveaux *et al*. 2003]. At day 100 of foetal life, homozygous DM foetuses display enlarged muscles [Deveaux *et al*. 2001] and an increased total number of muscle fibres. This is due to increased proliferation of myoblasts as observed in primary cells cultured from DM foetuses [Picard *et al*. 1998, Deveaux *et al*. 2001]. The higher proportion of fast-twitch glycolytic fibres (type IIX) results from higher proliferation rates of the second generation of myoblasts [Deveaux *et al*. 2001]. Accordingly, myostatin expression was found in the latest differentiating cells from the second generation [Deveaux *et al*. 2003]. In addition, muscle contractile and metabolic differentiation of DM foetuses is delayed compared to that of normal animals [Gagnière *et al*. 1997] since DM muscles express fewer mature myosin heavy chains at the same gestation age during the first two-thirds of foetal life [Picard *et al*. 1995]. More precise studies were conducted in order to understand the molecular mechanisms by which myostatin affects muscle growth and differentiation. It was found that a higher expression of the growth hormone receptor (which regulates IGF I and IGF II expression) – Listrat *et al*. [2005] – and a higher level of IGF-II mRNA level in skeletal muscles at the end of gestation – Listrat *et al*. [1999] – occurred in DM foetuses compared to normal animals.

DM cattle are thus a very interesting model to study the effects of one major gene in interaction with other gene(s), and to understand how increased muscular mass may be associated with lower intramuscular fat and collagen contents.

Polygenic inheritance of beef quality

Comprehensive research was initiated in the early nineties by the US Meat Animal Research Center, Nebraska, taking advantage of their extensive Germ Plasm Evaluation project. The systematic measurement of beef production traits and beef quality simultaneously provided the first estimates of genetic parametres on a large sample of animals. Complementary results have been obtained in US Universities of Colorado, Texas, Louisiana and Florida (reviewed by Burrow *et al*. [2001]) while other reports were published by Kim *et al*. [1998] and Riley *et al*. [2003]. The animals were mainly steers intensively fattened in feedlots and slaughtered at the mean age of 15 months. A wide diversity of breeds was analysed, including *Bos indicus* crosses. Another set of novel results was obtained by the Cooperative Research Center for the cattle and beef industry, in Australia [Reverter *et al*. 2000, 2003, Johnston *et al*. 2003]. Temperate and tropically adapted breeds were studied in different finishing conditions, feedlot or pasture, temperate or tropical zone. Steers and heifers were slaughtered at the age of 20 to 30 months, due to a long growing period on pasture before fattening, especially in the tropics.

The meat quality attributes were measured by panels scoring tenderness, juiciness and flavour of cooked meat. Steaks were grilled to an internal temperature of 70°C. Genetic variation was estimated in 10 publications. The mean heritability coefficient *(h^2)* for the tenderness score was 0.24, while for juiciness and flavour scores as low as 0.11 and 0.09, respectively. However, the genetic correlation coefficients *(r_G)* between the three scores appeared very high (0.84 to 0.91 on average) suggesting the panel could not really be used to discriminate between the quality attributes. A larger number of studies included shear force, that is a mechanical measure of the texture of cooked (70°C) meat, either grilled (US) or cooked in water bath (Australia). Moreover, the mean h^2 appeared high (0.26, n = 14) as well as the mean r_G with tenderness score (-0.84). Shear force appeared therefore as an objective alternative for measuring of and selecting for meat tenderness.

However, other predictors of meat quality were sought for an indirect selection for meat quality genetic merit. Nine studies included the measurement of fat content. It was shown that intramuscular fat content heritability is much higher (h^2 = 0.49), and that intramuscular fat content is on average positively correlated with tenderness (r_G = 0.41, n = 4) or negatively with shear force (r_G = -0.50, n = 5). As marbling score in these animals was genetically highly correlated with lipid content (r_G = 0.91, n = 4), selection based on the former may lead to a correlated improvement in tenderness (r_G = 0.46, n = 7) or a decrease in toughness (r_G = -0.50 with shear force, n = 8). This relationship drives most of the efforts dedicated to improving meat quality in the USA and Australia. Currently, research has been directed towards the development of live scanning for fat content as a selection tool [Reverter *et al*. 2000, Hassen *et al*. 2001, Sapp *et al*. 2002]. However, marbling is positively correlated to the carcass fatness (r_G = 0.36, n = 6, as reviewed by Koots *et al*. [1994]) and the indirect improvement of

tenderness through selection on the basis of intramuscular fat content or marbling will have counterproductive effects on carcass quality.

As calpastatin, a major regulator of calpain proteolytic activity during ageing when beef is stored at 4°C after slaughtering, was shown to account for a significant proportion of variation in beef tenderness [Whipple *et al.,* 1990a], its activity was measured in four studies. There is high mean heritability ($h^2 = 0.44$), and significant genetic correlation with tenderness ($r_G = -0.61$) and shear force ($r_G = 0.48$). However, this activity is not easy to measure and is unreliable for selection. So, research is directed towards seeking molecular polymorphisms in the calpastatin or calpain genes related to tenderness variability.

Only few investigations have been conducted upon the genetic variation of beef colour measurement [Aass 1996, Johnston *et al*. 2003]. The parametres of lightness (L*) and redness (a*) are moderately heritable ($h^2 = 0.22$ and 0.15, respectively).

In France, a study was conducted to estimate the predictive value of different muscle characteristics on the phenotypic variability of meat quality attributes of young Charolais bulls slaughtered at 17 months of age [Renand *et al*. 2001]. With this type of animal and a low cooking temperature (55°C), it was shown that tenderness depends mainly on muscle fibre size and collagen characteristics and is poorly related to intramuscular fat content. Genetic parametres of these muscle characteristics were estimated [Youssao *et al*. 2004] to be of a moderate heritability ($h^2 = 0.17$ to 0.34). Genetic correlations with carcass traits were also estimated showing that selection seeking leaner carcasses will decrease fat and pigment contents, decrease the muscle fibre size and improve collagen solubility. As a consequence, we may expect improved tenderness, but colour and flavour may be affected negatively. Indeed, from a biochemical point of view, genetic selection for muscle growth capacity induced a lower intramuscular fat content and a lower activity/expression level of some indicators of muscle oxidative metabolism (e.g. mitochondrial enzymes), especially in oxidative muscles. However, Hocquette *et al*. [2004] showed a muscle-specific response of metabolic characteristics to the selection process. Positive correlations between carcass fatness, muscle triglyceride content, and a marker of adipocyte differentiation (the expression of the *A-FABP* gene) were shown [Hocquette *et al.,* 2004].

Genetic markers of beef quality

With regard to beef quality, information on genetic markers is still very limited. Indeed, genetic variation has been proved to be rather high for these traits and should enable genetic markers to be detected and then used to increase beef quality through marker-assisted selection (MAS). During the past ten years, considerable efforts have been engaged to detect QTLs for beef quality especially in the USA or in Canada, and several studies on this topic have also been performed in Australia, Europe and Japan. These were recently reviewed by Kühn *et al*. [2005] and were mainly focused on tenderness and on the amount and the composition of intramuscular fat. Several

of them investigated meat quality in *Bos taurus* x *Bos indicus* crosses, where a very marked difference in meat quality traits, particularly toughness, is known to exist.

Tenderness

Several studies independently identified a QTL on BTA29 with an effect on tenderness, either in *Bos taurus* and *Bos indicus* crosses or in crosses between *Bos taurus* breeds [Schmutz *et al*. 2000, Casas *et al.* 2005; reviewed by Kühn *et al*. 2005]. Page *et al*. [2002] suggested that genetic variants of the calpain 1 *(CAPN1*) gene, which is located in the same chromosomal region, are the functional background of this QTL because two SNPs – in exons 9 and 14 – were associated with variations in tenderness measured by a shear force test on *Longissimus dorsi*. It should be noted that these two polymorphisms correspond to amino acid substitutions A316G and I530V, and that three combinations (alleles or haplotypes) have been described. Other QTLs with impact on beef tenderness traits were identified on BTA4, 5, 9, 11, 15, and 20, but have not been confirmed in independent studies nor is there evidence for a gene within the QTL region that could be considered as a strong candidate. On the contrary, polymorphisms in two genes – *CAST* (calpastatin) and *LOX* (lysyl oxidase) – both located on BTA7, where no QTL for tenderness has been reported, have been associated with an effect on the beef tenderness trait [Barendse 2002a]. For *CAST*, two SNPs located in the 3'UTR region and a microsatellite located in the 5' region were reported (reviewed by Kühn *et al*. 2005): only two haplotypes have been shown to be associated with improved tenderness and it was suggested that the known markers are in linkage disequilibrium with a causative mutation that has not yet been identified.

Marbling

As reviewed by Kühn *et al*. [2005], several QTLs for marbling were reported and located on BTA2, BTA3 and BTA27. Interestingly, the myostatin gene lies on BTA2 where the QTL was detected [Casas *et al*. 1998]. However, it seems unlikely that this gene is involved in the variation shown in all studies because some of these did not include breeds known to be carriers of double muscling. Other QTLs on BTA5, 8, 9, 10, 14, 16, 17, 23, and 29 were also reported, but have not yet been confirmed. In contrast to the galore of studies investigating the amount of intramuscular fat, there is only one report describing *loci* with impact on the composition of the intramuscular fat [Taylor *et al*. 1998], but the study was restricted to the investigation of a single chromosome (BTA19) and to the comparison of *Bos taurus* and *Bos indicus* alleles. Genetic markers associated with intramuscular fat deposition or marbling were reported, and are located on chromosomes BTA5 and BTA14, where QTLs for these traits were suggested elsewhere. On BTA5, the polymorphic microsatellite *loci* – CSSM34 and ETH10 – which are 20 cM apart, are associated with marbling scores in the Angus, Shorthorn, and Wagyu cattle [Barendse 2002b]. The diacylglycerol-O-acyltransferase 1 (*DGAT1*) and the thyroglobulin (*TG*) genes are both located in the centromeric region of BTA14. An Ala232Lys polymorphism of the *DGAT1* gene has

been shown to have an effect on intramuscular fat deposition in German Holstein and Charolais cattle [Thaller *et al*. 2003] and an association between one *TG* haplotype, based on two SNPs, and marbling has been reported [Barendse 2002b]. No association between both markers and carcass composition was found, however, in *Bos indicus* cattle by Casas *et al*. [2005]. It seems that the markers have independent effects, because no statistically significant linkage disequilibrium was detected. Several SNPs in the leptin (*LEP)* gene have been described, and two of them located in exon 2 were reported to affect fat content of carcass [Buchanan *et al*. 2002] and feed intake [Lagonigro *et al*. 2003]. The fatty acid composition of beef has generally an impact on the softness of the fat and/or on its flavour. In Wagyu cattle, Taniguchi *et al*. [2004] identified an association between a polymorphism in the stearoyl-CoA desaturase *(SCD)* gene and the monounsaturated fatty acid content as well as the melting point of intramuscular fat.

SNP identification

Other efforts are being devoted to the identification of SNPs in a large set of candidate genes with a view to evaluating their association with meat quality data measured across a wide range of genetically divergent breeds. Within the context of an EU-funded project (GeMQual, *www.gemqual.org*), a list of about 500 candidate genes that may be expected to affect muscle development, composition, metabolism or meat ageing and hence the quality of meat has been established based on knowledge of their physiological role. Coding and non-coding regions from about 400 of these candidates have been sequenced to reveal polymorphisms [Levéziel *et al*. 2003]. So far, a total of about 375 SNPs identified in 156 genes have been genotyped in 450 bulls that have been studied for meat characteristics in the project. The expected results should provide an indication of the genes that may have an effect on meat quality traits and that will be targets for further studies.

The potential benefits of genomics

Scientists used to study one gene at a time, in isolation from the broader context of other genes. Nowadays, they have access to gene networks and interaction thanks to the development of transcriptomics and proteomics which allow the high-throughput detection of genes and proteins differentially expressed between breeds and genotypes. A great number of studies dealing with functional genomics in cattle have been published so far (reviewed by Hocquette *et al*. 2005 and Lehnert *et al*. 2006]. All those related to the genetic effects on beef meat quality will be reported here.

Differentially expressed genes associated with marbling

Differential-display polymerase chain reaction has allowed the identification of a known gene (*NAT1*, a translational suppressor) by comparing muscles with different intramuscular fat contents from different finishing periods on high-grain

feeding [Childs *et al*. 2002]. *NAT1* was not previously suspected to play a role in fat deposition. Putative functional genes were found to be differentially expressed (e.g. ATP citrate lyase) or, surprisingly, not differentially expressed (e.g. PPARγ) between extreme animals [Childs *et al*. 2002]. Transcriptomic studies identified some genes (*e.g.* 12-lipoxygenase, prostaglandin D synthase) as key candidates involved in the control of fat accumulation in ruminants [Cho *et al*. 2002]. Wang *et al*. [2005] showed that the genes which are more expressed in muscles from Japanese Black cattle (which produce marbled beef) compared to Holsteins are associated with the thyroid hormone pathway, unsaturated fatty acid synthesis and fat deposition, including previously identified *A-FABP* [Hocquette *et al*. 2004].

The double-muscling character

Potts *et al*. [2003] compared gene expression in DM and normal 31-33 day-old bovine embryos by using suppressive subtractive hybridization. They identified genes encoding transcription factors, modulators of protein synthesis and degradation, proliferation or metabolism, and three of the differentially-expressed genes were physically mapped to BTA5, very close to the Warner Bratzler shear force at day 14 *post mortem* interacting QTL peak. This is a first step towards understanding the link between muscle hypertrophy and the superior tenderness of beef produced by double-muscled animals. Another study was conducted in order to compare the expression profile of muscle genes in the *semitendinosus* of double-muscled *vs* non-double-muscled 260-days-old foetuses using muscle-dedicated oligochips. Differential expression of several gene categories was found. Genes involved in slow contractile properties (e.g. *TNNC1*, *TPM3*, *MYH7*), extracellular matrix (e.g. collagen I and III) and ribosomal proteins (e.g. *RPL3*, *RPL23*, *RPS24*, *RPS20*) were found to be under-expressed in the double-muscled foetuses, thus explaining why muscles of double-muscled animals are faster and less oxidative and contain less collagen than muscles of normal animals. On the other hand, genes related to cell cycle regulation (e.g. *p21cip1*, *E2F1, CTBP1*), DNA metabolism and regulation of transcription (e.g. *HMGB1*, *mcm6*, *HDAC4*, *MEF2A*, *MyoD*), and protease (e.g. furin, *TIMP4*) were found to be over-expressed in the double-muscled foetuses. Interestingly, the expression of three differential genes (*C1QTNF3*, *SIX3* and *FOXC2*) was also found in double-muscled cows, suggesting the putative involvement of these genes in the maintenance of muscle hypertrophy. Further work is needed to understand their physiological implication in the development and modulation of muscle mass [Cassar-Malek *et al*. 2006]. The orientation towards fast glycolytic type muscles in DM cattle was confirmed by Bouley *et al*. [2005] who compared the proteome of *semitendinosus* muscle of DM and normal animals. In that muscle, the expression of proteins was affected including proteins belonging to other pathways than contraction and metabolism, or of unknown function such as sarcosin, SR53G, and heat shock protein p20.

Polygenetic inheritance of muscle growth potential

A recent study compared gene expression in muscles from Charolais bulls divergently selected for muscle growth. Besides known genes (encoding mitochondrial enzymes and *A-FABP*), other novel genes such as *LEU5* (a tumour suppressor), sarcosin (a muscle-specific gene involved in human hypertrophic cardiomyopathy) and a heat shock protein have been demonstrated to be less expressed in muscles from animals with a high than with a low muscle growth potential [Sudre *et al*. 2005]. Some of these genes were also previously detected as being differentially expressed throughout muscle development [Sudre *et al*. 2003]. In addition, other recent transcriptomic studies confirmed that selection conducted in favour of higher muscle growth potential induces a higher expression of genes involved in muscle traits related to glycolytic metabolism (e.g. lactate dehydrogenase A) or fast contraction (e.g. tropomyosin beta and myosin heavy chain 2x) – Cassar-Malek *et al*. [2005]. As for DM cattle [Bouley *et al*. 2005], proteomic studies have also demonstrated the under-expression of slow troponin T isoforms and the over-expression of fast troponin T isoforms as well as of other proteins abundantly expressed in fast glycolytic muscles [Picard *et al*. 2005].

Advantages and limitations of genomics

As already described, functional genomics is nowadays providing catalogues of muscle genes regulated by various factors, but sometimes without any real information about gene function. A reasonable approach is thus to consider a microarray experiment as exploratory data analysis, with a view to identifying potentially interesting genes which are worthy of further studies. We must, however, bear in mind that gene expression differs markedly between muscle types [Cassar-Malek *et al*. 2005]. This may be due, among other factors, to the fact that the muscle tissue is a composition of many cell types (including myofibres, connective tissue fibroblasts and adipocytes) which differ in their proportions between individual muscles. So, we do not know which cell population is responsible for the observed changes. Another problem is that genomics simply scores mRNA or protein levels. In fact, it is quite difficult to identify the causal genes, which are also called master controllers (and which regulate the expression of groups of genes). Unfortunately, as transcription factors and cell regulators are often expressed at low levels, they cannot be detected easily with genomic approaches. A final problem is that arrays do not have universal genome coverage in cattle, which is a major limitation for the discovery of new genes. Despite these limitations, genomics may help to identify genes, especially those which show significant changes in expression in different environments, suggesting that their expression level depends mainly on genetic factors. Furthermore, the tremendous progress in animal models (from yeasts to laboratory rodents) will help in identifying master controllers. This is comparative genomics currently changing the face of biology. A cost-benefit analysis should be seriously considered, however, before any practical application is introduced [Walsh and Henderson 2004].

Conclusions

Genetic selection in some countries (e.g. in France or Belgium) was applied in favour of high muscle and low fat deposition to produce leaner meat. Indeed, this has been successful in increasing growth rate of beef cattle. However, this type of genetic selection has clearly induced an orientation towards the fast-glycolytic muscle type as has recently been shown by biochemical, transcriptomic and proteomic approaches in both double-muscled cattle and divergently selected Charolais bulls. This is important because nowadays, consumers seek meat of high and consistent quality and the concept of quality includes now not only eating quality, but also nutritive and dietary value as well as any other consideration important for consumers. In this context, the orientation of the muscle type towards the fast-glycolytic type may favour tenderness and dietary quality, being simultaneously detrimental for flavour due to a reduction in intramuscular fat content. In addition, increasing knowledge in muscle biochemistry has shown that breeds differ in connective tissue and fibre characteristics with potential consequences on both tenderness and flavour.

The advent of genomics will undoubtedly increase our knowledge of the genes involved in determining beef quality. The major outcomes are (i) the development of DNA tests to improve beef quality by genetic selection, and (ii) the identification of molecular markers to predict the ability of animals to produce beef with quality traits desirable for the consumers. It is, however, important to emphasize that most, if not all of the results published so far need to be confirmed and widen before the markers reported are used in practice, because the associations have been observed on a limited number of individuals, breeds and breeding systems [Renand *et al*. 2003]. Undoubtedly, further progress will be made in the future since the entire bovine genome sequence is now available (http://www.hgsc.bcm.tmc.edu/projects/bovine/) and SNP markers at high density are being identified. Future efforts will have to be made to collect phenotypic data on large numbers of animals, especially for traits which are not currently routinely measured. Then, as the availability of SNP markers increases, the genotyping costs decrease and functional genomics develops, clear evidence will be obtained of useful molecular markers.

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Genetyka i genomika jako czynniki doskonalenia wołowiny

S t r e s z c z e n i e

Zasadnicze cechy jakości wołowiny, a zwłaszcza jej kruchość, zależą nie tylko od czynników oddziałujących po uboju, związanych z przechowywaniem mięsa, ale także od cech przyżyciowych. Te ostatnie determinowane są czynnikami genetycznymi, a także żywieniem i innymi warunkami wychowu i opasania. Poszczególne rasy bydła bądź genotypy w obrębie rasy odbiegają od siebie właściwościami tkanki łącznej (zawartość i rozpuszczalność kolagenu) oraz poziomem i składem tłuszczu śródmięśniowego, jak również proporcją między poszczególnymi typami włókien mięśniowych (wolno kurczących się – oksydatywnych, szybko kurczących się – oksydatywno-glikolitycznych i szybko kurczących się – glikolitycznych). Różnice te są źródłem zróżnicowania barwy mięsa i strat, do jakich dochodzi podczas jego przyrządzania (obróbka termiczna), a w mniejszym stopniu decydują także o smaku i kruchości mięsa. Mutacja w genie miostatyny determinuje hipertofię (przerost) mięśni i wzrost ich glikolitycznego metabolizmu, prowadząc także do spadku poziomu w nich kolagenu i tłuszczu śródmięśniowego. Zwiększa się przy tym kruchość i ulegają poprawie właściwości dietetyczne mięsa. Jednocześnie jednak zmniejszenie zawartości tłuszczu śródmięśniowego wpływa ujemnie na smakowitość mięsa. Zmienność genetyczna zawartości tłuszczu śródmięśniowego (marmurkowatości) jest znaczna, podczas gdy umiarkowana charakteryzuje kruchość, a niewielka – smak i soczystość mięsa. Z cechami jakości wołowiny wiąże się polimorfizm genów kluczowych z punktu widzenia cech tkanki łącznej i proporcji ilościowych między poszczególnymi typami włókien. Badania z zakresu genomiki funkcjonalnej umożliwiły profilowanie ekspresji genów lub białek, a nadto pozwoliły na zidentyfikowanie nowych molekularnych wskaźników kruchości i marmurkowatości mięsa. Jak wykazały badania z zakresu biochemii i genetyki funkcjonalnej, selekcja bydła, zmierzająca w kierunku zwiększenia mięsności i zmniejszenia zawartości tłuszczu w tuszy zmienia metabolizm włókien mięśniowych w kierunku zwiększenia metabolizmu glikolitycznego.

Wykorzystano 64 pozycje piśmiennictwa.