ELSEVIER

Food Chemistry 69 (2000) 397–405

Food Chemistry

www.elsevier.com/locate/foodchem

The use of gene technology for optimal development of pork meat quality

A.G. de Vries [a,*], L. Faucitano [a], A. Sosnicki [c], G.S. Plastow [b]

[a] *PIC Europe, Fyfield Wick, Abingdon OX13 5NA, UK*
[b] *PIC Group, Fyfield Wick, Abingdon OX13 5NA, UK*
[c] *PIC Americas, PO Box 348, Franklin, KY 42135-0348, USA*

Received 20 March 1999; received in revised form 21 August 1999; accepted 31 August 1999

Abstract

The aim of this paper is to discuss the opportunities for gene technology in relation to the quality of pork. After dealing with breed effects and within-breed variation, an overview of major genes and DNA technology is given. It is demonstrated that some of the breed effects can be fully explained from the presence of a single gene with major effect. Within breeds, there is considerable genetic variation in relevant meat quality traits like waterholding capacity and intramuscular fat. Again, part of this variation is due to major genes. As a result, DNA marker technology can play an important role in improving meat quality. Selective breeding based on this technology will also increase the uniformity of the final product. Furthermore, the exploitation of major genes can be highly relevant for differentiation of breeding populations for specific markets. © 2000 Elsevier Science Ltd. All rights reserved.

1. Introduction

The quality of raw pig meat is influenced by a large number of genetic and non-genetic factors. The latter include farm, transport, slaughter and processing conditions. Meat scientists have performed a substantial amount of research on these factors, which has led to considerable quality and compositional improvements. Part of the research has also been dedicated to the genetic background of the pigs, and several studies have revealed the importance of genetic factors (e.g. Sellier & Monin, 1994). This has made the industry aware that both the selective breeding of pigs and the use of gene technology can play an important role in enhancing pork quality (Tarrant, 1998). Moreover, DNA technology can also be used for the prediction of quality traits.

The aim of this paper is to discuss the genetic opportunities for meat quality improvement. After discussing differences between breeds and within breeds, we will focus on identification and exploitation of individual genes based on DNA technology. The present paper deals only with the implications for pork quality, but the potential of the new technology is equally relevant for other species

2. Breed effects

Significant breed effects have been reported for intramuscular fat, waterbinding capacity, colour and tenderness (Sellier & Monin, 1994). Meat from Pietrain and Belgian Landrace pigs can be of inferior quality when compared to Large White or French Landrace (Monin, Talmant, Laborde, Zabari & Sellier, 1986; Touraille & Monin, 1994). Due to a fast pH decline after slaughter, Pietrain and Belgian Landrace meat can be pale, exudative and less tender. However, this breed effect can probably be completely explained through a high frequency of one single gene, the so-called Halothane (HAL) gene (see later under gene effects).

Meat from Hampshire pigs often shows a markedly lower ultimate pH. This leads to a lower waterbinding capacity and higher cooking loss (Monin & Sellier, 1985). On the other hand, this breed is often characterized by higher tenderness (Sellier & Monin, 1994). Again, the specific effect of Hampshire has been found to be related to a single gene (RN), which will be discussed later.

The Large White and Duroc breeds are seen as positive contributors to meat quality. Also meat from Landrace can be of high quality, provided the Halothane gene has been removed. An extra benefit for the

---

* Corresponding author. Tel.: +44-1865-822200.

0308-8146/00/$ - see front matter © 2000 Elsevier Science Ltd. All rights reserved.
PII: S0308-8146(00)00049-2

Duroc in some markets is often the two-fold higher percentage of intramuscular fat when compared to Large White and Landrace pigs (Armero, Flores, Barbosa, Toldra & Pla, 1998; Lo, McLaren, McKeith, Fernando & Novakofski, 1992), which can positively contribute to eating quality. Indeed, as the percentage of Duroc genes increases (0, 25, 50 and 75%) meat is scored by panelists as being more juicy, more tender and with higher pork flavour and lower abnormal flavours (Meat and Livestock Commission [MLC], 1992). Certain studies also report a higher haem pigment content for Duroc (e.g. Garrido, Granados, Lenstra, Álvarez, Bañon, Cayuela & Laencina, 1998).

Several comparisons of meat quality between European and American breeds with Chinese purebred or crossbred pigs revealed that the latter provide more tender, more juicy and tastier products (Suzuki, Kojima, Ikeuchi, Ikarashi, Moriyama, Ishizuka et al., 1991; Touraille, Monin & Legault, 1989). However, the amount of visible fat was judged as excessive in meat from Chinese crossbreds, which counterbalanced the better meat quality. In addition, Ellis, Lympany, Haley, Brown and Warkup (1995) reported no evidence of any beneficial effect of the Chinese Meishan breed on overall meat quality.

Traditional European breeds have been studied in more detail in recent years. Corsican pigs were found to have a better waterbinding capacity than Large White (Casabianca & Luciani, 1989; Goutefongea, Girard, Labadie, Renerre & Touraille, 1983). Iberian pig breeds were studied by Sañudo and Sierra (1989) and Serra et al. (1998). In a comparison with Landrace, the latter study found higher levels for ultimate pH, haem pigment content, intramuscular fat, type I fibres and lower concentrations of polyunsaturated fat. This was accompanied with large differences in age at slaughter and backfat levels. Comparative studies which involved traditional British breeds (Tamworth, Glouchester Spots, Saddleback and others) and improved breeds (Large White, Pietrain, Landrace, Hampshire and Duroc) showed that the latter ones had paler and more watery meat. The meat from Tamworth scored the highest overall sensorial acceptability (Warriss, Kestin, Brown & Nute, 1996).

3. Within breed variation

Within a breed, there is still variation in meat quality between individual pigs. Part of this variation is of genetic origin. Geneticists quantify this proportion by looking at differences between and within families, and refer to this as the degree of heritability (h^2). Higher values indicate a stronger importance of genetic factors, lower values a stronger influence from environmental factors. The first heritabilities for pig meat quality traits were reported in the early sixties (Duniec, Kielanovski & Osinska, 1961), and since that time numerous h^2 estimates have been published for all important meat quality attributes, including eating quality (for review see Cameron, 1990; De Vries, Van der Wal, Long, Eikelenboom & Merks, 1994; Hovenier, Kanis, Van Asseldonk & Westerlink, 1993; Wood, 1990) as well as muscle fibre characteristics (Larzul, Lefaucheur et al., 1997). According to Wood (1990), there is moderate genetic variation for some traits (i.e. drip loss, intramuscular fat content and colour), but little opportunity exists to improve eating quality attributes such as flavour, texture or juiciness.

Selection for improved meat quality within lines has been limited by the absence of relevant measures that can be taken on live pigs. However, the existence of major genes together with the development of DNA technology may overcome this problem.

4. Major genes

Geneticists consider that a gene can be defined as a major gene, when the difference between the mean value of the individuals homozyguous for this gene and that of individuals not carrying this gene, is equal or superior to one phenotypic standard deviation of the trait of interest (Sellier & Monin, 1994). Genes with such large effects can usually be detected by analyzing phenotypic data across families where the gene segregates. This approach is referred to as segregation analysis. Sellier and Monin reviewed two important major genes that affect pig meat quality: Halothane and RN. After a short update on these two genes, two more recent examples for pigs will be provided.

4.1. Halothane sensitivity gene

The Halothane gene is also referred to as the porcine stress syndrome (PSS) gene, and has been studied and discussed extensively. Thorough reviews are given by Simpson and Webb (1989) and Sellier and Monin (1994), and results of Larzul, Le Roy et al. (1997) and a review of Hermesch (1997) add interesting material to the discussion. The gene started to become relevant for breeders when Christian (1972) speculated the existence of monogenic variation in stress-susceptibility and when Eikelenboom and Minkema (1974) showed that PSS could be triggered by halothane gas. Since then, many comparisons regarding meat quality were done, and most studies showed major differences in pH, colour and waterbinding between stress positive and negative pigs. These differences were directly related to a large difference in PSE (pale soft exudative meat) incidence between the two genotypes, which can be explained by the different muscle metabolic profile. Indeed, fibre areas are shown to be larger and capillarization (cap/ mm^2) lower in stress-positive pigs, which lead to higher lactate formation in the muscle (Essen-Gustavsson, Karlstrom & Lundstrom, 1992; Klont, Lambooy & Logtestjin, 1993). Pommier and Houde (1993) showed that the PSE condition does not result directly from the Halothane gene, but the gene often exacerbates the problem.

Since 1991 we can accurately separate all three Halothane genotypes [instead of just reactors (nn) from non-reactors (NN and Nn)] with the Hal1843™ [1] DNA test. This test was developed from the work of Fujii et al. (1991) who found the causative mutation for porcine stress syndrome in the gene encoding the fast-twitch fibre ryanodine receptor isoform or calcium release channel (RYR1 or CRC1). Once it was possible to easily detect heterozyguous animals, more detailed work on the effect of this mutation was possible.

A major discussion at present is whether carriers have acceptable meat quality compared to the animals that are completely free of the gene. This is very relevant, since the gene definitely improves carcass lean content, but reduces meat tenderness and juiciness (Ellis, Brewer, Sutton, Lan, Johnson & McKeith, 1998; National Pork Producers Council [NPPC], 1994). No general conclusion from this discussion is possible, since the optimum approach depends on slaughter conditions and the type of processing (e.g. cooked vs. dried vs. fresh). The best strategy for breeding organizations is to make sure that all the dams of the slaughter pigs are free of the Halothane gene, whereas the HAL-status of the sires can be tailored to specific carcass requirements

4.2. RN^- gene

The RN^- gene was first suggested by Naveau (1986) as being responsible for 'acid meat', and later confirmed by segregation analysis in two French composite lines of pigs (Le Roy, Naveau, Elsen & Sellier, 1990) as a gene with dominant inheritance. The gene is named after the Rendement Napole (RN) test, which predicts cooking yield. The dominant allele leads to a decreased technological quality due to a lower meat protein content and reduced ultimate pH. The latter is a result of an increased glycogen content in the white (fast-glycolytic) fibres. For (low phosphate) cooked ham processing, the yield of RN^- carriers is 5–6% lower, and moreover these hams can have extremely high slicing losses. So far, the gene has been found segregating only in populations with Hampshire influence, but because of its dominant inheritance and the widespread use of Hampshire derived sires, the gene is very relevant for breeders.

Milan, Le Roy, Woloszyn, Caritez, Elsen and Gellin (1995) found that the gene is located on chromosome 15 and later DNA marker studies (Looft, Reinsch, Rudat & Kalm, 1996; Mariani, Lundström, Gustafsson, Enfält, Juneja & Andersson, 1996; Milan et al., 1996) mapped the gene more accurately. The most recent published results place RN^- between Sw2053 and Sw936, a bracket of approximately 8 centimorgans (Milan et al., 1996). Based on the map position, a commercial DNA-marker test for detecting the gene was developed and validated (De Vries, Timm, Wilson, Keller & Plastow, 1997). The test successfully predicted large differences in ultimate pH and phosphate free ham processing yield. The study also showed that the yield differences completely disappeared when phosphate was used. Although the test is an excellent tool to quickly reduce the incidence of the gene, its complete elimination requires a DNA probe that detects the causative mutation. Milan and colleagues have subsequently refined the map position of the RN gene and have developed new markers that may be useful for this elimination (pers. comm.).

4.3. Intramuscular fat

Intramuscular fat (IMF) has been identified as playing a role in eating quality of pork. Janss, Van Arendonk and Brascamp (1994,1997) performed a segregation analysis on meat quality data of F2 crosses between Meishan and Dutch pig strains. They detected a recessive major gene for IMF, originating from Meishan. Animals with two copies of the gene had an average of 3.9% IMF in the loin, whereas carriers and homozyguous negative animals had 1.8%. Research is underway to look at the existence of this gene in purebred populations, e.g. Duroc (Monin, Sellier & Bonneau, 1998). This could eventually lead to DNA tests that allow better control of the marbling level of pork. Breeders will then have a large influence on the level of this trait, since its heritability is around 50% (Cameron, 1990; De Vries et al., 1994; Hovenier et al., 1993). The challenge is to achieve a higher IMF without increasing the levels of the other fat depots (subcutanuous, abdominal and intermuscular). More attention to this is given in the Candidate Gene section of this paper (H-FABP gene).

4.4. Androstenone

Another trait with a high heritability is the level of androstenone (Willeke, 1993), which is one of the causes of the so-called 'boar taint' problem in meat from entire males (Bonneau, 1998). Applying segregation analysis, Fouilloux, Le Roy, Gruand, Renard, Sellier and Bonneau (1997) found a major gene for androstenone level in LW populations that were selected on this trait. The

---

[1] The HAL-1843™ is licensed from the Innovations Foundation, Toronto, Canada, owner of the trademark.

gene giving rise to a low androstenone level was dominant, and carriers of this gene had 3 standard deviation (SD) units lower level than non-carriers (0.33 vs. 0.90 ppm). In the same data set, the authors also found a major gene for the development of the bulbo-urethral glands. The size of these glands are seen as a good indicator of the sexual maturity status of boars (Fouilloux et al.).

Earlier work in France (Bidanel et al., 1996) showed a large gene effect on androstenone level in an F2 generation of Meishan with Large White. This gene effect was linked with the major histocompatibility complex of the pig (SLA). Linkage with SLA haplotypes was also shown with male genetical tract development in work by Rothschild, Renard, Sellier, Bonneau and Vaiman (1986).

Boar taint is not only caused by androstenone, but also by skatole. Genetic work on skatole levels is limited. However, this trait also shows some genetic variation, and Lundström et al. (1994) suggested, based on work in experimental Yorkshire lines, that the genetic effect on skatole may be due to a major gene with a recessive mode of inheritance. They expect that the expression of the gene depends on certain environmental conditions like diet composition and hygiene.

4.5. Muscle fibre traits

Muscle fibre types differ phenotypically in that they express different subsets of myofibrillar isoform genes with different ATPase activities as well as different types and levels of metabolic enzymes. The different myosin heavy chain isoforms are coded for by separate genes, some of which are preferentially expressed in fast skeletal muscle and in slow skeletal muscle (see review by Goldspink, 1996). The number of myofibers is prenatally determined, so the maximal number of myofibers available for meat production is formed during embryonic myogenesis, which seems to be under the genetic control of the MyoD gene family (Buckingham, 1992). The reader is referred to the Te Pas, De Vries and Visscher (1994) review for more detailed information on the MyoD gene family muscle regulatory mechanism.

According to Fiedler, Rehfeldt and Ender (1991) and later Larzul, Lefaucheur et al. (1997) the measurements of muscle fibre characteristics (such as fibre type distribution and cross-sectional areas) might be used for selection purposes, as these traits are moderately heritable (0.2–0.6) and correlated with lean growth and meat quality traits (i.e. ultimate pH, colour and drip loss). A higher proportion of type IIB fibres in leaner lines was recently shown by Brocks, Hulsegge and Merkus (1998).

Pig breeding programmes including selection for growth performance traits may negatively affect meat quality. In a 5 year survey (1983–1988) of meat quality traits recorded in 4 breeds (Large White, Landrace, Hampshire and Duroc) present in the Danish population, Barton-Gade (1990) recorded a decrease in pigment content (paler meat), which she assumed was due to a change in fibre composition towards a greater % of glycolytic fibres (type IIB). Likewise, a 5 percentage points lower frequency of slow twitch (type I) and a consequently lower meat tenderness score was recorded in genetically-improved Danish Landrace (anno 1995) when compared to ‘old’ Danish Landrace (anno 1976) (Petersen, Henckel & Støier, 1997).

5. DNA technology

The evidence for major genes reported in the previous section was originally obtained using segregation analysis, i.e. without any DNA marker information. Afterwards molecular studies were performed to detect the location of these genes on the genetic map. In practice, and except for alleles of very large effect, DNA studies are required to dissect the genetic nature of most traits of economic importance. In this section an overview of the latest results is given. The first part deals with DNA markers that are closely linked with major genes. The second part deals with mutations in targeted functional genes referred to as the candidate gene approach.

5.1. DNA markers

Markers can be used to localize genes responsible for qualitative traits like coat colour (e.g. Johansson Moller, Chaudhary, Hellmén, Höyheim, Chowdhary & Andersson, 1996), and they can also be used to detect genes with substantial effects on quantitative traits like growth rate, IMF, etc. In this case the approach is referred to as QTL (Quantitative Trait Locus) mapping.

In pigs, the QTL mapping approach normally uses families created from crosses based on divergent lines e.g. Large White with wild boar or Chinese Meishan. Indeed, this approach has been used in relation to intramuscular fat (IMF). Having identified a major gene for IMF using segregation analysis (Janss et al., 1994, 1997), this group went on to QTL mapping, using microsatellite markers. They recently reported evidence for suggestive linkages with markers on chromosome 1 and a marker on chromosome 3 (De Koning, Janss, Van Arendonk, Van Oers & Groenen, 1998). The same region on chromosome 1 was also identified as containing a QTL for backfat. The latest analysis from this group has also identified QTLs for this trait on chromosomes 4 and 7 (M. Groenen, pers. comm.). In a recent study on Iberian×Landrace progenies a QTL for intramuscular fat was found on chromosome 6 (Óvilo et al., 1999).

A number of pig populations are now being used or have been created for the purposes of searching for meat quality QTLs. These include crosses between the following breeds: Wild Boar, Large White, Meishan, Landrace, Pietrain, Iberian pig, Duroc, Mangalitsa and Berkshire (De Vries, Sosnicki, Garnier & Plastow, 1998).

Traits measured include carcass composition, fat and lean distribution as well as meat quality measures such as waterbinding, shear force and intramuscular fat content and taste panel assessment. Some of the first results were published by Andersson-Eklund et al. (1998) from the Wild Boar×Large White population. For meat quality they did not find any QTL which reached the genome-wide significance threshold, however, significant QTLs for carcass characteristics, such as loin eye area and lean meat %, were detected. The largest QTL was on chromosome 4 and is likely to be a pleiotropic effect of the previously reported QTL for backfat and growth (Andersson et al., 1994).

Although there have been successes in identifying QTL, for example for backfat on chromosome 4, for fat androstenone level on chromosome 7 and for meat pigment content on chromosome 6 (Óvilo et al., 1999; Milan et al., 1998), it is not trivial to make use of the results within commercial breeding programmes. Many workers in this field conclude that it is necessary to identify the gene or genes underlying the QTL. This is a substantial task, as the QTL region is usually relatively large and may contain many genes. Identification of the relevant genes thus remains a significant hurdle in farm animals, although the development of improved comparative maps will allow better use of information from 'gene-rich' species such as mouse and human. In the short term projects are underway to determine how such initial QTL findings can be used in commercial populations. For example, the EC Biotechnology Project entitled "Transferring QTL technology to the pig breeding industry (PigQTech) — a demonstration project", coordinated by Leif Andersson at the Swedish University of Agricultural Sciences, aims to produce a route map to assist animal breeders to exploit genome mapping information. The project involves SCAN Genetics (Sweden), a Spanish breeder, Copaga and PIC as well as the Roslin Institute, Centre UdL-IRTA and the University of Barcelona.

An alternative to the above approach would be to use markers to introgress favourable QTLs identified in a non-commercial genotype (such as the wild boar) into a commercial line (Visscher, Haley & Thompson, 1996). In this respect, it is interesting to note the recent findings from several of the PiGMaP groups with respect to backfat QTL. They have identified a QTL on chromosome 7 where the 'lean' allele is contributed by the Meishan and the 'fat' allele is from the Large White component of the cross (Haley, pers. comm.; Milan et al., 1998; Moser, Muller, Beeckman, Yue & Geldermann, 1998; Rothschild, pers. comm.). This type of effect has been found in plant species and is a potentially useful finding as we think of how to use these new tools to manipulate meat quality.

5.2. Candidate genes

The candidate gene approach can be relatively straightforward compared to the QTL approach. For example, we have used polymorphisms in candidate genes to look for associations across populations. When associations are identified the resulting marker can potentially be used directly in breeding programmes. This approach has been used very successfully for the Estrogen Receptor (ESR) gene and litter size (Short et al., 1997).

An example for a candidate gene for meat quality is provided by the gene for heart fatty acid binding protein (H-FABP). Gerbens, Rettenberger, Lenstra, Veerkamp and Te Pas (1997) identified polymorphisms in this gene and found these to be associated with variation in IMF in the Duroc (Gerbens, Van Erp, Meuwissen, Veerkamp & Te Pas, 1998). H-FABP maps to pig chromosome 6 and not to the QTL regions identified by De Koning et al. (1998), (see the section on Major Genes). A comparison of the homozygous haploid classes found that they differed by about 15% of the mean value. More recently, this group has found a larger effect on IMF with the related gene adipocyte FABP (FABP4. Gerbens, Jansen, et al., 1998). In addition, the effect appears to be independent of backfat and so offers promise for the manipulation of IMF by Marker Assisted Selection (MAS). These candidate gene markers have now been included in a joint analysis with the QTL analysis of Janss and co-workers (Wageningen University) and it will be interesting to see if the variation in IMF in the crosses can now be explained more completely (see above).

Another relevant candidate gene approach is the research on calpain, calpastatin and cathepsin (B, B+L and H). In beef and sheep, there are many reports of the role of the calpain system, a set of calcium dependent proteases and their inhibitor calpastatin, both in vivo and post-mortem in protein turnover. See, for example, the excellent review of Koohmaraie (1996). Interestingly, Ernst, Robic, Yerle, Wang and Rothschild (1998) have reported the identification of three polymorphic sites in the pig calpastatin gene. Many studies are also in progress to investigate the possible influence of pig genetic on cathepsin (B, B+L and H) activity, which play a key role in the seasoned product (i.e. dry-cured ham) proteolysis. Higher activities of cathepsins B and B+L were found in English and Dutch Large White sires compared to Belgian Landrace and Belgian Landrace×Landrace sires. On the other hand, activity of cathepsin H was higher in Belgian Landrace and Belgian Landrace×Landrace sires than in Duroc, English and Dutch Large White sires (Armero, Barbosa, Toldrá, Baselga & Pla, 1999). No significant differences were recorded in cathepsin B activity between breeds (Duroc, Large White and Landrace) by Russo et al. (1998), but a large within breed variation was reported in combination with a moderate heritability (0.23–0.28).

Other markers which have been generated for meat quality based on the candidate gene approach include myogenin (increased muscle fibre number, which may impact overall pork quality) (Soumillion, Erkens, Lenstrá, Rettenberger & Te Pas, 1997) and the dominant KIT gene leading to white coat colour in pigs (Johansson Moller et al., 1996).

A shortcoming of the candidate gene approach can be that the number of candidates is increasing substantially as more and more genes are being identified. For example, in Hwang, Loftus, Mandrup and Lane (1997) at least 30 genes affecting fat tissue development are described.

6. Discussion

6.1. From breeds to genes

The early work on genetic effects on meat quality focused on breed differences, and those differences are still very relevant. However, a number of specific breed effects, have more recently been found to be caused by single major genes (e.g. Halothane in Pietrain, RN gene in Hampshire). This has encouraged the approach of examining single gene effects, rather than breed effects. It has also allowed the breeding organizations to make use of a wider range of breeds, as it is possible to change the frequency of favourable or unfavourable genes through selective breeding. With a combination of backcrossing and selection, it is even possible to move a foreign favourable gene into a breed. The latter procedure is referred to as gene introgression. Even more dramatic changes might be derived with genetic engineering, but that approach would be very controversial, especially in relation to meat quality changes.

6.2. Exploitation of major genes for meat quality

Improving meat quality is not just about changing levels of traits like tenderness or marbling, but it is also about increasing uniformity. The existence of major genes provides excellent opportunities for improving meat quality, since it allows large steps to be made in the desired direction (e.g. improving technological yield of ham process by selecting against RN^- gene in pigs). Secondly, it will help to reduce variation, since we can fix relevant genes in our products. Another aspect is that major genes allow differentiation for specific markets. For example, in certain types of dry cured ham a high IMF is required, whereas other products like cooked ham require a low amount of IMF. For the future it is expected that processors and retailers will specify a whole series of genes that have to be present or absent for each product that they process or sell.

Some of the major genes can be fixed or eliminated just by using phenotypic data. These data can be derived in simple or more complicated ways, e.g. like the RN gene through biopsis. For other genes, it will be essential to use molecular genetic technology. The elimination of Halothane (HAL) carriers is a good example of this requirement, as full HAL elimination was previously only possible by using expensive progeny testing. The other advantage of the DNA technology is that markers close to relevant genes or tests that identify mutations in candidate genes allow us to also exploit genes with smaller effects (e.g. H-FABP gene for IMF).

For a proper exploitation of major genes it is critically important to know what type of meat we want to select for. This is not a trivial issue, as meat is processed and used in many different ways. One possible solution is that breeding companies need to be able to provide choice. The HAL gene can be used as a nice example. Some breeding organisations provide HAL-negative Pietrain boars, next to HAL-positive boars. Breeding organisations can provide such a choice in two ways: (1) fixing the gene in one base line and eliminating the gene in another line, and (2) maintaining segregation of the gene and performing DNA tests on the potential breeding animals that are used at a commercial level. In the first option there are high initial costs for DNA tests, but thereafter the only extra costs are the maintenance and improvement of multiple lines within a breed. In the second option, there are no costs of maintaining multiple lines but DNA tests have to be performed continuously on potential breeding animals.

6.3. Potential of DNA marker assisted selection

Information at the DNA level can help to fix a specific major gene, but it can also assist the selection of a quantitative trait for which we already select. Molecular information in addition to phenotypic data can increase the accuracy of selection and therefore, the selection response. The size of the extra response in such a Marker Assisted Selection (MAS) scheme has been considered by many workers from a theoretical point of view. In general terms, MAS is more beneficial for traits with a low heritability and which are expensive to measure phenotypically. The results obtained depend, of course, very much on the assumptions made in the models. Gibson (1994) and others have shown that there is a short term benefit in using MAS, but that in some cases this can lead to a long term penalty.

However, this is over a relatively long time frame. More recently Meuwissen and Goddard (1996) considered a different set of assumptions and in particular looked at the impact for traits such as reproduction and meat quality that are difficult to progress using traditional methods. Their results are extremely encouraging, showing that for traits such as meat quality, where the trait is measured after slaughter, an additional response of up to 64% could be achieved. Importantly, they also pointed out that this type of response could be sustained if new markers could be continually identified. For example, new markers would be added to the selection index as old markers begin to reach fixation.

In the meantime we anticipate that significant progress will be made by utilising candidate genes and searching for population wide linkage disequilibrium, using tools such as Amplified Fragment Length Polymorphism (AFLP). This technology is an extremely powerful tool for revealing useful polymorphisms in commercial populations. For example, we have used AFLP and bulk segregant analysis to find markers for coat colour (Plastow, Kuiper, Wales, Archibald, Haley & Siggens, 1998) which are useful for ensuring white skin for slaughter pigs in markets such as the UK and Italy. We believe that this approach is applicable for other traits, an example of its application would be the generation of simple markers for QTL identified using microsatellite based QTL mapping. Such markers would then enable use without the need for family information as was the case originally for coat colour and RN^-.

Work is also underway in other species, particularly, sheep, deer and beef cattle. Taylor and Davis (1997) have recently reviewed the prospects for beef cattle, and this provides a good indication of what might be achievable. They indicate that projects are underway to identify QTLs affecting growth and carcass attributes of beef cattle in Australia, Japan and Belgium as well as in the US (MARC and Texas A&M). The first results of the Texas A&M group indicate that QTLs were detected for nearly all of the traits examined. In particular, they report a QTL influencing the proportion of unsaturated and saturated fatty acids in adipose tissues, four QTLs that appear to influence marbling and another four that influence measures of tenderness.

6.4. Practical implementation of selection for meat quality

The best approach to genetically improve meat quality is to find relevant DNA-markers directly in the populations under selection. For this reason, meat quality measurements should be performed continuously on the nucleus populations of breeding organizations. Since a full assessment of meat quality can only be done after slaughter, the data have to be collected on culled animals and cannot be obtained on potential breeding animals.

The phenotypic meat quality data will not only enable the detection of relevant DNA markers, but will also be used to validate markers from experimental populations or to test candidate genes. Significant markers or genes will be included straight away in the selection process. An advantage of the molecular information is that we can obtain it already at very young age, which means that animals can be preselected based on DNA markers before the growing performance test. This is a great advantage for the overall testing and selection system.

The continuous collection of meat quality data from nucleus lines is expensive. However, its use is not limited to DNA marker research. The data also allow the breeding organization to monitor their nucleus lines, which is important for optimizing the breeding direction. Furthermore, the data can be used directly in the selection process as phenotypic information on relatives (culled litter mates and half-sibs) of potential breeding animals.

7. Conclusions

There are clear breed effects on meat quality, which in some cases are fully related to the presence of a single gene with major effect.

Within breeds, there is considerable genetic variation in important meat quality traits, which again is partly caused by major genes.

DNA technology provides excellent opportunities to improve meat quality in selection schemes within lines.

Selection on major genes will not only increase average levels of quality but also decrease variability (i.e. increase uniformity). On the other hand, major genes can be exploited for differentiation for specific markets.

References

Andersson, L., Haley, C. S., Ellegren, H., Knott, S. A., Johansson, M., Andersson, K., et al. (1994). Mapping quantitative trait loci for carcass and meat quality traits in a wild boar×Large White intercross. *Science, 263*, 1771–1774.

Andersson-Eklund, L., Marklund, L., Lundström, K., Haley, C. S., Andersson, K., Hansson, I., et al. (1998). Mapping quantitative trait loci for carcass and meat quality traits in a wild boar×Large White intercross. *Journal of Animal Science, 76*, 694–700.

Armero, E., Barbosa, J. A., Toldrá, F., Baselga, M., & Pla, M. (1999). Effects of terminal sire type and sex on pork muscle cathepsins (B, B+L and H), cysteine proteinase inhibitors and lipolytic enzyme activities. *Meat Science, 51*, 185–189.

Armero, E., Flores, M., Barbosa, J.-A., Toldra, F., & Pla, M. (1998). Effects of terminal pig sire types and sex: On carcass traits, meat quality and sensory analysis of dry-cured ham. *Proceedings 44th International Congress on Meat Science and Technology, Barcelona, 2*, 904–905.

Barton-Gade, P. A. (1990). Danish experience in meat quality improvement. *Proceedings 4th Congress of Genetics Applied to Livestock Production, Edinburgh, UK, 15*, 511–520.

Bidanel, J. P., Milan, D., Chevalet, C., Woloszyn, N., Caritez, J. C., Gruand, J., et al. (1996). Chromosome 7 mapping of a quantitative trait locus for fat androstenone level in Meishan×Large White F2 entire male pigs. *Book of abstracts 47th Annual Meeting EAAP, Wageningen Pers, Wageningen, 2*, 610.

Bonneau, M. (1998). Use of entire males for pig meat in the European Union. *Meat Science, 49*, S257–S272.

Brocks, L., Hulsegge, B., & Merkus, G. (1998). Histochemical characteristics in relation to meat quality properties in the *Longissimus lumborum* of fast and lean growing lines of Large White pigs. *Meat Science, 50*, 411–420.

Buckingham, M. (1992). Making muscle in mammals. *Trends in Genetics, 8*, 144–149.

Cameron, N. D. (1990). Genetic and phenotypic parameters for carcass traits, meat and eating quality in pigs. *Livestock Production Science, 26*, 119–135.

Cassabianca, F., & Luciani, A. (1989). Caractéristiques de la viande de porc Corseissu d'elevage extensif. 1. Qualités technologiques de la viande. Colloque Production Porcine en Europe Méditerrane, Ajaccio.

Christian, L. L. (1972). A review of the role of genetics in animal stress susceptibility and meat quality. In R. G. Cassens, F. Giesler, & Q. Kolb, *Proceedings Pork Quality Symposium* (pp. 91–115). Wisconsin: University Wisconsin.

De Koning, D. J., Janss, L. L. J., Van Arendonk, J. A. M., Van Oers, P. A. M., & Groenen, M. A. M. (1998). Mapping major genes affecting meat quality in Meishan crossbreds using standard linkage software. *Proceedings 6th World Congress Genetics Applied to Livestock Production, 26*, 410–413.

De Vries, A. G., Timm, H. H., Wilson, E. R., Keller, V., & Plastow, G. S. (1997). An effective DNA-marker test for the 'acid meat' problem. *Book of abstracts 48th Annual Meeting EAAP, Vienna, Wageningen Pers, Wageningen, 3*, 340.

De Vries, A. G., Sosnicki, A., Garnier, J. P., & Plastow, G. S. (1998). The role of major genes and DNA technology in selection for meat quality in pigs. *Meat Science, 49*(Suppl. 1), S245–255.

De Vries, A. G., Van der Wal, P. G., Long, T., Eikelenboom, G., & Merks, J. W. M. (1994). Genetic parameters of pork quality and production traits in Yorkshire populations. *Livestock Production Science, 40*, 277–289.

Duniec, H., Kielanovski, J., & Osinska, Z. (1961). Heritability of chemical fat content in the loin muscle of baconers. *Animal Production, 3*, 195–198.

Eikelenboom, G., & Minkema, D. (1974). Prediction of pale, soft, exudative muscle with a non-lethal test for the halothane-induced porcine malignant hyperthermia syndrome. *Tijdschrift Diergeneeskunde, 99*, 421–426.

Ellis, M., Brewer, M. S., Sutton, D. S., Lan, H. Y., Johnson, R. C., & McKeith, F. K. (1998). Aging and cooking effects on sensory traits of pork from pigs of different breed lines. *Journal of Muscle Foods, 3*(9), 281–291.

Ellis, M., Lympany, C., Haley, C. S., Brown, I., & Warkup, C. C. (1995). The eating quality of pork from Meishan and Large White pigs and their reciprocal crosses. *Animal Science, 60*, 125–131.

Ernst, C. W., Robic, A., Yerle, M., Wang, L., & Rothschild, M. F. (1998). Mapping of calpastatin and three microsatellites to porcine chromosome 2q2.1–q2.4. *Animal Genetics, 29*, 212–215.

Essen-Gustavsson, B., Karlstrom, K., & Lundstrom, K. (1992). Muscle fibre characteristics and metabolic response at slaughter in pigs of different halothane genotypes and their relation to meat quality. *Meat Science, 31*, 1–11.

Fiedler, I., Rehfeldt, C., & Ender, K. (1991). Muscle fibre characteristics: new selection criteria. *Tierzuchter, 43*, 444–445.

Fouilloux, M. N., Le Roy, P., Gruand, J., Renard, C., Sellier, P., & Bonneau, M. (1997). Support for single major genes influencing fat androstenone level and development of bulbo-urethral glands in young boars. *Genetics Selection Evolution, 29*, 357–366.

Fujii, J., Otsu, K., Zorzato, F., De Leon, S., Khanna, V. K., Weiler, J. E., et al. (1991). Identification of a mutation in porcine ryanodine receptor associated with malignant hyperthermia. *Science, 253*, 448–451.

Garrido, M. D., Granados, M. V., Álvarez, D., Bañon, S., Cayuela, J. M., & Laencina, J. (1998). Pork quality of pig crossbreeds Large White, Landrace, Hampshire, Pietrain and Duroc. *Proceedings 44th International Congress Meat Science and Technology, Barcelona, 1*, 74–275.

Gerbens, F., Jansen, A., Van Erp, A. J. M., Harders, F., Meuwissen, T. H. E., Rettenberger, G., et al. (1998). The adipocyte fatty acid-binding protein locus: characterization and association with intramuscular fat content in pigs. *Mammalian Genome, 9*, 1022–1026.

Gerbens, F., Rettenberger, G., Lenstra, J. A., Veerkamp, J. H., & Te Pas, M. F. W. (1997). Characterization, chromosomal localization, and genetic variation of the porcine heart fatty acid-binding protein gene. *Mammalian Genome, 8*, 328–332.

Gerbens, F., Van Erp, A. J. M., Meuwissen, T. H. E., Veerkamp, J. H., & Te Pas, M. F. W. (1998). Heart fatty-acid binding protein gene variants are associated with intramuscular fat content and back fat thickness in pigs. *Proceedings 6th World Congress Genetics Applied to Livestock Production, 26*, 187–190.

Gibson, J. P. (1994). Short-term gain at the expense of long-term response with selection of identified loci. *Proceedings 5th World Congress Genetics Applied to Livestock Production, 21*, 201–204.

Goldspink, G. (1996). Muscle growth and muscle function: a molecular biological approach. *Research Veterinary Science, 60*, 193–204.

Goutefongea, R., Girard, J. P., Labadie, J. L., Renerre, M., & Touraille, C. (1983). Utilisation d'aliments grossiers pour la production de porcs lourds Interaction entre type génétique, sexe et mode de conduite. 2. Qualité de la viande et aptitude á la transformation. *Journées de la Recherche Porcine en France, 15*, 193–200.

Hermesch (1997). Genetic influences on pork quality. In P. D. Cranwell, *Manipulating pig production* (Vol. VI, pp. 82–90). Australian Pig Science Association.

Hovenier, R., Kanis, E., Van Asseldonk, Th., & Westerink, N. G. (1993). Breeding for pig meat quality in halothane negative populations — a review. *Pig News and Information, 14*, 17N–25N.

Hwang, S. S., Loftus, T. M., Mandrup, S., & Lane, M. D. (1997). Adipocyte differentation and leptin expression. *Annual Review Cell Development and Biology, 13*, 231–259.

Janss, L. L. G., Van Arendonk, J. A. M., & Brascamp, E. W. (1994). Identification of a single gene affecting intramuscular fat in crossbreds using Gibbs sampling. *Proceedings 5th World Congress Genetics Applied to Livestock Production, 18*, 361–364.

Janss, L. L. G., Van Arendonk, J. A. M., & Brascamp, E. W. (1997). Bayesian statistical analyses for presence of single genes affecting meat quality traits in a crossed pig population. *Genetics, 145*, 395–408.

Johansson Moller, M., Chaudhary, R., Hellmén, E., Höyheim, B., Chowdhary, B., & Andersson, L. (1996). Pigs with the dominant white coat colour phenotype carry a duplicate of the KIT gene encoding the mast/stem cell growth receptor. *Mammalian Genome, 7*, 822–830.

Klont, R., Lambooy, E., & Logtestjin, J. G. (1993). Effect of preslaughter anaesthesia on muscle metabolism and meat quality of pigs of different halothane genotypes. *Journal of Animal Science, 71*, 1477–1485.

Koohmaraie, M. (1996). Biochemical factors regulating the toughening and tenderization processes of meat. *Meat Science, 43*(193), S193–S201.

Larzul, C., Lefaucheur, L., Ecolan, P., Gogue, J., Talmant, A., Sellier, P., et al. (1997). Phenotypic and genetic parameters for *longissimus* muscle fiber characteristics in relation to growth, carcass and meat quality traits in Large White pigs. *Journal of Animal Science, 75*, 3126–3137.

Larzul, C., Le Roy, P., Gueblez, R., Talmant, A., Gogué, J., Sellier, P., et al. (1997). Effect of halothane genotype (NN, Nn, nn) on growth, carcass and meat quality traits of pigs slaughtered at 95 kg or 125 kg live weight. *Journal of Animal Breeding and Genetics, 114*, 309–320.

Le Roy, P., Naveau, J., Elsen, J. M., & Sellier, P. (1990). Evidence for a new major gene influencing meat quality in pigs. *Genetic Research in Cambridge, 55*, 33–40.

Lo, L. L., McLaren, D. G., McKeith, F. K., Fernando, R. L., & Novakofski, J. (1992). Genetic analyses of growth, real-time ultrasound, carcass, and pork quality traits in Duroc and Landrace pigs: I. Breed effects. *Journal of Animal Science, 70*, 2373–2386.

Looft, Chr., Reinsch, I., Rudat, I., & Kalm, E. (1996). Mapping the porcine RN gene to chromosome 15. *Genetics Selection Evolution, 28*, 437–442.

Lundström, K., Malmfors, B., Stern, S., Rydhmer, L., Eliasson-Selling, L., Mortensen, A. B., & Mortensen, H. P. (1994). Skatole levels in pigs selected for high lean tissue growth rate on different dietary protein levels. *Livestock Production Science, 38*, 125–132.

Mariani, P., Lundström, K., Gustafsson, U., Enfält, A. C., Juneja, R. K., & Andersson, L. (1996). A major locus (RN) affecting muscle glycogen content is located on pig chromosome 15. *Mammalian Genome, 7*, 52–54.

Meuwissen, T. H. E., & Goddard, M. E. (1996). The use of marker haplotypes in animal breeding schemes. *Genetics Selection Evolution, 28*, 161–176.

Milan, D., Le Roy, P., Woloszyn, N., Caritez, J. C., Elsen, J. M., & Gellin, J. (1995). The RN locus for meat quality maps to pig chromosome 15. *Genetics Selection Evolution, 27*, 195–199.

Milan, D., Woloszyn, N., Yerle, M., Le Roy, P., Bonnet, M., Riquet, J., et al. (1996). Accurate mapping of the acid meat RN gene on genetic and physical maps of pig chromosome 15. *Mammalian Genome, 7*, 47–51.

Milan, D., Bidanel, J. P., Le Roy, P., Chevalet, C., Woloszyn, N., Caritez, J. C., et al. (1998). Current status of QTL detection in Large White×Meishan crosses in France. *Proceedings 6th World Congress Genetics Applied to Livestock Production, 26*, 414–417.

Meat and Livestock Commission. (1992). Second Stotfold Pig Development Unit Trial Results, MLC, Milton Keynes.

Monin, G., & Sellier, P. (1985). Pork of low technological quality with a normal rate of muscle pH fall in the immediate post-mortem period: the case of the Hampshire breed. *Meat Science, 13*, 49–63.

Monin, G., Talmant, A., Laborde, D., Zabari, M., & Sellier, P. (1986). Compositional and enzymatic characteristics of the *Longissimus dorsi* muscle from Large White, halothane-positive and halothane-negative Pietrain and Hampshire pigs. *Meat Science, 16*, 307–316.

Monin, G., Sellier, P., & Bonneau, M. (1998). Trente ans d'évolution de la notion dequalité de la carcasse et de la viande de porc. *Journées de la Recherche Porcine en France, 30*, 13–27.

Moser, G., Muller, E., Beeckman, P., Yue, G., & Geldermann, H. (1998). Mapping QTLs in F2 generations of Wild Boar, Pietrain and Meishan pigs. *Proceedings 6th World Congress Genetics Applied to Livestock Production, 26*, 478–481.

National Pork Producers Council. (1994). Pork quality genetic evaluation summary. Des Moines.

Naveau, J. (1986). Contribution a l'étude du determinisme genetique de la qualité de la viande porcine. Heritabilité de Rendement technologique Napole. *Journées de la Recherche Porcine en France, 18*, 265–276.

Óvilo, C., Pérez-Enciso, M., Barragán, C., Plop, A., Toro, M., Rodriguez, M. C., et al. (1999). Busqueda de QTLS en el cromosoma 6 para grasa intramuscular y pigmentos en un cruze F2 iberico×Landrace. *Proc. 8th Jornada sobre Producción Animal (ITEA), 20*(1), 240–242.

Petersen, J. S., Henckel, P., & Støier, S. (1997). Muscle physiological traits and meat quality in Danish Landrace pigs *anno* 1976 and 1995. *Book of abstracts 48th Annual Meeting EAAP, Vienna, Austria*, p. 44.

Plastow, G. S., Kuiper, M., Wales, R., Archibald, A. L., Haley, C. S., & Siggens, K. W. (1998). AFLP for mapping and QTL detection in commercial pigs. *Proceedings 6th World Congress Genetics Applied to Livestock Production, 26*, 209–212.

Pommier, S. A., & Houde, A. (1993). Effect of the genotype for malignant hyperthermia as determined by a restriction endonuclease assay on the quality characteristics of commercial pork loins. *Journal of Animal Science, 71*, 420–425.

Rothschild, M. F., Renard, C., Sellier, P., Bonneau, M., & Vaiman, M. (1986). Swine lymphocyte antigen (SLA) effects on male genital tract development and androstenone level. *Proceedings 3rd World Congress Genetics Applied to Livestock Production, 11*, 197–202.

Russo, V., Butazzoni, L., Baiocco, C., Davoli, R., Nanni Costa, L., Schivazappa, C. et al. (1998). Heritability of muscular cathepsin B activity in Italian Large White pigs. *Book of abstracts 49th Annual Meeting EAAP, Warsaw, Poland*, pp. 290.

Sañudo, C., & Sierra, I. (1989). *Cruziamentos y produccion intensiva in cerdo iberico. 3. Calidad de la carne*. Colloque Production Porcine en Europe Méditerrane, Ajaccio.

Sellier, P., & Monin, G. (1994). Genetics of pig meat quality: a review. *Journal of Muscle Foods, 5*, 187–219.

Serra, X., Gil, F., Pérez-Enciso, M., Vàzquez, J. M., Gispert, M., Diaz, I., et al. (1998). A comparison of carcass, meat quality and histochemical characteristics of Iberian (Guadyerbas line) and Landrace pigs. *Livestock Production Science, 56*, 215–223.

Short, T. H., Rothschild, M. F., Southwood, O. I., McLaren, D. G., De Vries, A., Van der Steen, H., et al. (1997). Effect of the estrogen receptor locus on reproduction and production traits in four commercial pig lines. *Journal of Animal Science, 75*, 3138–3142.

Simpson, S. P., & Webb, A. J. (1989). Growth and carcass performance of British Landrace pigs heterozygous at the halothane locus. *Animal Production, 49*, 503–509.

Soumillion, A., Erkens, J. H., Lenstra, J. A., Rettenberger, G., & Te Pas, M. F. W. (1997). Genetic variation in the porcine myogenin gene locus. *Mammalian Genome, 8*(8), 564–568.

Suzuki, A., Kojima, N., Ikeuchi, Y., Ikarashi, S., Moriyama, N., Ishizuka, T., et al. (1991). Carcass composition and meat quality of Chinese purebred and European×Chinese crossbred pigs. *Meat Science, 29*, 31–41.

Tarrant, P. V. (1998). Some recent advances and future priorities in research for the meat industry. *Proceedings 44th International Congress on Meat Science and Technology, Barcelona, 1*, 2–13.

Taylor, J. F., & Davis, S. K. (1997). Gene mapping projects with beef cattle — an international perspective. In B. J. McGuirk, *Bovine gene mapping* (pp. 46–53). London: Milk Development Council.

Te Pas, M. F. W., De Vries, A. G., & Visscher, A. H. (1994). The MyoD family and meat production — a review. *Proceedings 40th International Congress on Meat Science and Technology*, The Hague, NL, S-VII, 8.

Touraille, C., & Monin, G. (1984). Comparaison des qualités organoleptiques de laviande de porcs de trois races: Large White, Landrace français, Landrace belge. *Journées de la Recherche Porcine en France, 16*, 75–80.

Touraille, C., Monin, G., & Legault, C. (1989). Eating quality of meat from European×Chinese crossbred pigs. *Meat Science, 25*, 177–186.

Visscher, P., Haley, C. S., & Thompson, R. (1996). Marker assisted introgression in backcross breeding programs. *Genetics, 144*, 1923–1932.

Warriss, P. D., Kestin, S. C., Brown, S. N., & Nute, G. R. (1996). The quality of pork from traditional pig breeds. *Meat Focus International, 5/6*, 179–183.

Willeke, H. (1993). Possibilities of breeding for low 5α-androstenone content in pigs. *Pig News and Information, 14*, 31N–33N.

Wood, J. D. (1990). Consequences for meat quality of reducing carcass fatness. In Wood & Fisher, *Reducing fat in meat animals* (pp. 344–389). Elsevier Science Publishers.