Prospects for the genetic improvement of meat and eating quality – where do we go from here?

Rex Walters

UPB Genetic World

Introduction

Reputable pig breeding programmes have been very successful in reducing production costs over the last twenty years through significant genetic progress in a wide variety of traits including growth, feed conversion, reduced backfat thickness and, over the last decade, litter size and litters per sow per year [1] . However, with some notable exceptions, genetic progress in many meat and eating quality traits has been largely non-existent. The reasons for this are:

1. The genetic potential for lean growth remains under-exploited for many markets – currently there is no indication of a plateau in this trait. For these markets it remains important economically to maximise lean potential through on-going genetic improvement (and through the matching of nutrition to genetic potential). Unfortunately, as indicated later in this presentation, there are often negative genetic relationships (correlations) between production traits and quality traits.

2. The lack of payment systems to reward better quality in the majority of markets.

3. Logistical problems of data collection and recording.

4. The high costs involved with the measurement and collection of accurate data.

However, consumer awareness about ‘quality’ and the increasing change in the industry away from supply to demand driven production has highlighted the importance of pork quality. Genetics has a major potential role to deliver real benefits for the future in meat and eating quality.

Genetic overview

The performance of an animal may be divided between the genetic component (the genotype) and all the other factors, such as feed, housing, management, health, etc (the environment):

Phenotype = Genotype + Environment

At its simplest, it is possible to estimate the percentage of the phenotype that is under genetic control as the heritability. The higher the heritability, the greater the genetic control. Heritabilities vary between traits, as the Table below indicates:

Type of trait	Trait	Heritability
Production traits	Litter size	10
	Growth rate	30
	Feed conversion	29
	Backfat	37
	Lean %	51
Meat technological quality	pH1 (30-60 minutes post slaughter)	16
	pHu (24 hours post slaughter)	21
	Meat colour	28
	Water-holding/Drip	15
	Meat quality index	20
Meat sensory quality	Tenderness (by instrument)	26
	Tenderness (by taste panel)	29
	Flavour (by taste panel)	9
	Juiciness (by taste panel)	8
	Overall acceptance (by taste panel)	25
	Intra-muscular fat (marbling)	45
Fat quality	% lipid in meat	48
	% linoleic acid in fat	55
	Ratio saturated:unsaturated fat	50
	Backfat firmness	42
Product quality	Boar taint	54
	Seasoning loss (dry-cured ham)	?
	Muscle fibre characteristics	?

Source: references [2,3,4]

Note that many meat and eating quality traits have moderate to high heritability meaning that there is potential for genetic progress in the traits.

However, it is also important to look at the totality in a selection programme and to understand the relationships between the traits. The geneticist is interested in the genetic correlations between traits that indicate what will happen during selection for a particular characteristic. Some of the main genetic relationships are shown below:

	Selection for:		
	Lower backfat	**More lean**	**Faster growth**
Meat colour	↓↓	↓↓	↓
Marbling (IMF)	↓↓	↓↓	↑
Drip-loss	↓	↓	**0**
Tenderness	↓↓	↓↓	**0**
Juiciness	↓↓	↓↓	**0**
Flavour	↓↓	↓↓	↑

↓↓ = Strong reduction in quality: ↓ = Some reduction in quality ↑↑ = Some increase in quality: ↑ = Some increase in quality 0 = Probably little change

Source: references [2,3,4]

Note the antagonistic relation between all the meat and eating quality traits with increasing lean and reduced fatness! This largely answers why quality has been often difficult to improve over the past twenty years as most payment methods remain based on lack of backfat or high lean percentage. However, despite these problems there have been some notable success stories over recent years which are outlined in the next section.

Progress to date

Pale soft exudative (PSE) pork

Colour variation in pigmeat can be wide, from very dark red to very light pink. The former colour is usually due to dark firm dry (DFD) meat, a non-genetic effect, caused by prolonged stress in the animal resulting in depletion of muscle glycogen and the retention of a high pH in the muscle after slaughter. The condition can normally be controlled by careful pre-slaughter handling in which fighting, aggression and poor handling do not occur. Very light meat is called pale, soft, exudative meat (PSE) – it results from very rapid post mortem acidification of muscle. Typically, the rate of pH fall is higher than 1 pH unit per hour instead of the usual 0.2 to 0.5. In addition, ultimate pH must be lower than 5.7. When both conditions are met, protein denaturation is important and both colour intensity and water holding capacity are decreased. More than thirty years ago the main cause of PSE was established to be due to a recessive gene [5]. The HAL gene has 2 alleles, N (normal, dominant) and n (sensitive, recessive). The nn pigs present frequencies of sudden death and PSE meat much higher than the NN pigs. The n allele is completely recessive for mortality but not for meat quality. The heterozygous pigs are intermediate between the homozygous pigs for most meat quality traits, particularly tenderness. However the n allele is advantageous regarding muscular development and muscle percentage. This effect is additive, i.e. the heterozygotes are intermediate between both homozygotes. In the 70's and 80's many national and breeding company organisations undertook expensive halothane gas testing programs to manage the incidence of the gene. However, in 1991 the actual mutation (an amino acid substitution in the calcium-release channel called the ryanodine receptor RYR1) was discovered in Canada [6]. This allowed the development of a simple and relatively cheap DNA test meaning that pig breeders can now guarantee the genotype of any animal tested.

The RN/Napole/Acid meat/Hampshire gene

Another muscle quality condition associated with an abnormal pattern of pH fall is found in pigs having the dominant RN gene, which is most common in the Hampshire breed. In this case the initial pH fall is normal but the absolute fall is more extensive which reduces the technological yield when meat is cured. The meat tends to be paler with a higher drip loss than normal but tenderness may be improved. The problem was first highlighted in France in the 70's where ham manufacturers drew attention to the fact that meat from pigs with Hampshire blood presented a very serious defect of technological quality. This defect was called "acid meat" and resulted in a major decrease in processing yield. Economical penalties followed, as some abattoirs began to reject affected pigs.

By the mid 80's the causal mechanism was found to be a dominant gene [7], which was named RN as it was defined by its effect on the "Rendement Napole", an estimator of the cooked ham processing yield. At that stage the thinking was that the RN gene had 2 alleles or forms, rn+ (normal, recessive) and RN- (acid meat allele, dominant). The RN- allele leads to a large increase in muscle glycogen, a decrease in pH in the white muscles of the carcass, a decrease in cooked ham processing yield and a decrease of 5 % of the protein content in white muscles (very important in processed ham production). At the same time, the RN- gene affects colour (paler), taste (more pronounced) and tenderness. The effect on the latter remains controversial as French research suggests that RN- meat is tougher while Swedish research indicates a trend of RN- meat to be more tender [8,9]. The probable reason for this difference is related to differences in cooking temperatures in the two countries.

In 2000, a molecular test was developed [10] to identify the different genotypes (there are now known to be five genotypes since the discovery of a third allele, rn*, [11] which is similar to rn+ in its effect on quality traits), allowing management of the gene in populations. In Sweden, the favourable effects of the gene on sensory quality have lead to a concentration of the gene for high quality meat production. However, in the US and France, the gene is considered undesirable and is being reduced in affected populations.

Breed effects

Breed effects are well documented. Unfortunately, current pig classification systems are imperfect as there are significant biases for different genetic populations. The Duroc confers advantages in meat colour, fat firmness, marbling and tenderness (however, at least 50% or more Duroc genes are required in the slaughter generation for these differences to be readily identified) but at the cost of reduced feed efficiency, increased fatness and skin quality defects [12]. The Hampshire link to the RN gene is referred to above with its different national emphasis. There is also interest in some 'old' breeds such as the Berkshire for their apparent good eating quality – in Japan a premium is paid for Berkshire pork and a gene test is available to ensure 'purity' [13]. To date the reason for the advantage is not clear, though fatness per se appears to be only part of the story. Finally, in Spain and Italy, there is competition to be 'world champion' for the production of the very best air-dried cured ham. Some people favour

Prosciutto di San Daniele from Italy while others favour Jamon iberico from Spain, particularly 'de Bellota' where the unique black Iberian pigs are fed on acorns and herbs.

General breeding programmes

Outside the testing for the HAL and RN genes, various programmes have tried in different ways to maintain quality. Two main approaches have been used. The first is the use of sophisticated selection indices that either use 'restricted gains' or 'desired gains', where traits are maintained at a minimum value, or by trying to take account of antagonistic relationships by modelling of economic values and multi-trait relationships. The second approach involves large-scale sib-based slaughter programmes, such as those implemented in Finland, Switzerland, France and parts of Germany. The latter are very expensive and are criticised in some markets for being not cost effective. In the long-term it is hoped that reliable biopsy and scanner techniques can be developed to give good objective measures of meat and eating quality in live pigs.

Where do we go from here?

There are several areas for further exploitation of quality characteristics:

1. Genotype validation.
2. Increasing inclusion of meat and eating quality in breeding programmes.
3. Molecular technologies.
4. Boar taint.
5. Muscle fibres.

These are discussed in more detail below:

Genotype validation

An important step is to determine which genotypes fit best for a particular type of production and/or market. Usually this will involve using different terminal sires in specific nutritional environments and then following the carcase through the abattoir and on to specific assessments of meat and eating quality [14].

Increasing inclusion of meat and eating quality in breeding programmes

Increasingly breeding programmes are including some measures of quality into their BLUP programmes – with the moderate to high heritabilities for many of the traits it is possible to forecast some genetic progress. However, the more traits included in the breeding goal, the lower the progress in individual traits. This necessitates excellent accuracy in the evaluation of economic values. To date this has been difficult due to the threshold values (penalties incurred commercially at specific and, often changing, points) for many traits, the lack of effective cooperation between the various parts of the production chain and problems of monitoring individual pig identification post slaughter.

Molecular technologies

With the advances in genomics there is now much attention on quality traits. The genomic approach has very significant advantages over conventional techniques. Firstly, DNA information can be obtained on all pigs eligible for selection whereas traditional selection has to rely on carcass information obtained on relatives thus making selection programs less effective. Secondly, DNA-information can be collected early in the life cycle of the pig whereas collection of phenotypic meat quality trait data can only occur after the animal has died.

Since 1990 crosses between genetically widely diverging breeds, such as wild boar, Pietrain, Meishan, Iberian, Large Whites and Landraces have been used to identify genetic markers. However, the majority of these markers are microsatellites (small lengths of DNA repeated through the genome) or non-coding DNA, rather than the functional genes themselves so that the actual effects of the markers have been inconsistent, small, difficult to repeat and of unpredictable benefit in pure lines. It is probable that the best approach to discover practically relevant DNA 'tests' is to search for them directly in the breeding population. In the long term the final challenge will be to unravel the complex interactions between genes.

Many genes are now linked to meat and eating quality traits and the list is growing very fast. For example, the Table below shows a sample of scientific reports in the past 12 months that have reported significant new knowledge on a gene:

Gene	**Name**	**Traits**	**Reference**
CBG	Cortisol-binding globulin	pH, colour, drip-loss, tenderness	[15]
FABP4	Fatty-acid binding protein 4	Intramuscular-fat	[16]
LXRA/B	Liver X receptors alpha/beta	Loin area, intramuscular fat	[17]
MC4R	Melanocortin receptor 4	pH, colour, fatty-acid profile	[18]
ME1	Malic enzyme 1	pH	[19]

In some cases, commercial DNA tests are available for the gene, but they add a significant cost to a breeding programme. For example, a single sampling and test for H-FABP currently costs about US$50. Luckily the costs of genetic fingerprinting and single microarray plates (a test for many hundreds of genes in one sample) are expected to fall very significantly over the next few years.

As well as selection for better quality, molecular technologies also allow the tracing of meat through the production chain and the authentication of genotype – such as the Berkshire in Japan and for specialist high added-value products such as Jamon iberico. Selection for specific genes will also reduce genetic variation. Interestingly, even cloning cannot produce complete phenotypic uniformity – for example, for a meat quality trait with a heritability of 25%, some 75% of the variation will remain due to non-genetic influences.

Boar taint

The abnormal odour that affects the meat from some entire boars is due to the compounds androstenone and skatole accumulating in fat tissue. Of course, Improvac is one solution to the problem in many countries. However, the genetic solution to the problem has been helped by the recent development of a set of 32 markers and 18 different candidate genes in Canada [20]. Unfortunately the association with specific markers varies between different genotypes and it is clear that even more markers and candidate genes are needed before a final cost-effective across-breed test will be available [20].

A further development in this area is the possibility of a major break-though in semen-sorting which would allow the production of cost-effective and reliable single-sex litters.

Muscle fibres

Tenderness is arguably the most important component of eating quality. From selection experiments it is known that selection for lean growth aids tenderness due to increased post-mortem activity of the proteolytic enzymes such as calpastatin. Among other important aspects involved are pH post-slaughter, drip loss, intramuscular fat and the proportion of different muscle fibre types.

There are four main fibre types – 1, IIa, IIb and IIx. A greater abundance of IIa and IIx are implicated in better water-holding and colour as well as tenderness. A large number of IIb fibres reduce these quality characteristics. The Duroc breed has a lower percentage of IIb fibres than other breeds and this has been suggested as a key component in the above average eating quality of Duroc meat.

As well as fibre type, it is now evident that enlarged fibres result in impaired tenderness. Typically large fibres are found in pigs of low birth weight, so that there is a direct genetic relationship between birth weight and tenderness [21,22]. The outcome may be that birth weight becomes an important BLUP trait for meat quality as well as growth reasons.

The heritability of muscle fibre type and size is reported as ranging between 12 and 25% [23]. This explains why recent simulation studies have suggested that meat and eating quality could be improved by the inclusion of muscle fibre characteristics. This is clearly an area for further investigation.

Finally, several muscle regulatory genes (including members of the myogenic factor group such as MyoD and MyoG and Myo3) are being studied for their effects on fibre characteristics [24,25].

Postscript

If conventional and molecular genetic approaches are to supply real benefits and improvements in meat and eating quality it will be increasingly important for the different parts of the production chain to cooperate. There will need to be dialogue, exchange of information and accurate data collection and interpretation. Most important, there should be some reward to breeders and producers for expensive genetically in-build meat quality and eating quality advantages! This, rather than the complex biology, is probably the most important factor in deciding 'where we go from here'.

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