

SIMULTANEOUS IMPROVEMENT OF MEAT QUALITY AND GROWTH-AND-CARCASS TRAITS IN PIGS

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INTRODUCTION

Breeding for meat quality in pigs has been the topic of much scientific writing over the past two decades. Many authors have focused on correlated responses in meat quality as a result of selection for production traits, but in this paper we focus on direct selection for meat quality in practice. We present historical developments, summarise the current (2002) situation, and finish with thoughts on the role of DNA markers and future developments

STATE OF THE ART AT THE EARLY NINETIES

Given the complexity of meat as a product, a meaningful description of "pig meat quality" (further denoted as "MQ") must be based on a complicated aggregate of traits. Ten years ago this description had arrived at a reasonable level of sophistication in terms of (i) the relevance of these traits for meat-processing industry, retail sector and consumer, (ii) their variation and relationships among each other and with other traits, (iii) their physiological background and genetic characteristics, and (iv) the way this should logically lead to practical selection methods. Various large-scale studies into the quantitative genetics of many MQ traits had been conducted (see Sellier 1998); major genes had been found to be responsible for PSE (the *Hal* gene; Fujii *et al.*, 1991) and "acid meat" (the *RN* gene; Le Roy *et al.*, 1990); the importance of the various muscle fiber types and their glycolytic characteristics for *post mortem* biochemical changes had been discovered (Sosnicki 1987; Fiedler *et al.*, 1991); and features such as water holding capacity (WHC), intramuscular fat content (IMF), colour, tenderness and flavour had been proposed as separate breeding objective traits (Cameron, 1993; Hovenier *et al.*, 1993a).

The distinction between (i) halothane-connected PSE problems and (ii) genetic variation in MQ traits independent of the *Hal* gene, had been recognised by the mid-eighties (e.g. Knap *et al.*, 1985). The recessive allele of the *Hal* gene leads to strongly unfavourable correlations of carcass leanness with traits related to WHC, and hence to unfavourable MQ responses to selection for leanness (as demonstrated by Oksbjerg *et al.*, 2000). But that antagonism is less serious (and often absent) when this allele does not segregate: much of the initially perceived antagonistic difficulty of combining MQ traits into breeding objectives (Steane, 1981) can be removed by changing the population's halothane status.

Of course, this also works the other way around: without proper statistical adjustment, the inclusion of MQ measurements in a selection index for a halothane-susceptible population is not much more than an inefficient way of selecting against the recessive *Hal* allele. Nevertheless, MQ traits in some form or another had been part of the breeding objectives (and selection criteria) of several pig breeding organisations since the mid-seventies (see Lindhe *et*

al., 1980 and further references in Sellier 1998, p. 492), quite apart from all the halothane eradication programs that were started by then (initially motivated much more by stress-induced mortality than by MQ problems). But by the early nineties, the halothane status of many pig populations had been successfully brought under control, and there was little reason to worry much about *Hal* anymore when designing breeding strategies (Lundström, 1990).

So by 1992 the pig breeding sector was well-equipped to implement MQ traits as selection criteria. But apart from the European finalisation of halothane eradication and a careful start with *RN* eradication (earliest in France, e.g. www.france-hybrides.com/j25years_eng.htm), not much seems to have taken place by that time. Exceptions are the national breeding schemes of Finland (Mäntysaari *et al.*, 1994), Switzerland (Schwörer *et al.*, 1994), France (Guéblez and Sellier, 1990), and some German areas (e.g. Karras *et al.*, 1993). But there are two reasons for the general lack of effort to improve MQ through conventional selection, as below.

In the early nineties, some European abattoirs were considering payment systems for slaughter pigs based on in-line measured pH in addition to carcass weight and leanness. But these early initiatives suffered much from the notion that many of the cases of reduced MQ in practice are entirely out of the producer's control (e.g. Ellis and McKeith, 1995), making it unclear how a penalty system for individual carcasses could be made to have the "guidance" effect on the production sector that has been so successful for leanness. The consequence was a lack of drive from the processing industry towards MQ improvement, being the main reason for the slow uptake in the breeding sector : *no pay, no cure*.

The second reason is the simple fact that conventional selection for MQ requires observations on dead animals, which in practice leads to sib slaughter schemes. These measurements are quite expensive by themselves (the prediction, with reasonable accuracy, of a breeding objective trait like drip loss is costly in terms of both the required number of measured carcasses and the sophistication of the measurements) and individual carcass identification throughout the abattoir's carcass flow involves surprisingly elaborate (and again costly) logistics. So the selection for such traits results in high data acquisition costs for the breeding organisation, with an unclear return in view of the abovementioned lack of direction from the processing industry.

DEVELOPMENTS OF THE PAST DECADE

Three significant developments with regard to meat quality selection have taken place in the past decade, as follows.

First, the meat processing industry and the retail sector have gone through much consolidation and integration; and processing, quality control, and distribution procedures have become more sophisticated and transparent (e.g. VIV/LEI, 2001; Windhorst, 2001). At the same time, consumer awareness of food quality has become a major factor in agribusiness. As a result, MQ has received more specific attention from the processing and retail sectors, and this is now passed on to the production and breeding tiers of the pyramid. This does not necessarily mean that individual carcasses will be penalised for insufficient MQ in the foreseeable future; the in-line identification problems mentioned in the previous section still prevail and it seems more likely that abattoirs will collect their MQ measurements on a group level (e.g. Paterson, 2000).

Second, DNA tests have been developed that allow for a much more effective eradication of undesirable alleles, such as for the *Hal* gene (HAL-1843TM, as licensed from the Innovations Foundation, Toronto, Canada, owner of the trademark) and the *RN* gene (Milan *et al.*, 2000).

Breeders that had not started or completed their eradication programs were able to do so much more efficiently than before, most notably in north America like www.babcockswine.com/babcockgenetics.htm and www.pic.com/usa/products/pic327mq (see Danavl, 2000 and Anonymous 2001 for examples on *RN* from Europe). In fact, many sire lines that are nowadays marketed as "meat quality lines" seem to derive this label mainly from lacking these two unfavourable alleles (e.g. www.genetiporc.com/Main/EngU/Site/REmain.asp and http://www.france-hybrides.com/maxterqu_eng.htm), not entirely surprising considering the size of the allele substitution effects compared to conventional selection responses. However, additional MQ genes are now being identified (our PICmarq™ programme includes more than 15 such markers) and used for selection (see below).

Third, much population-specific applied research has been done to follow up the initial quantitative genetics work. Many breeding organisations are now well-informed about the genetic MQ characteristics of their own populations. Breeding objectives and selection procedures can then be designed and monitored without the need to rely on external parameters. This has resulted in many more breeding organisations including MQ traits in their breeding objectives and selection indices. See Danavl (2000), Wuensch *et al.* (1998) and www.vns.or.at for examples from Europe, and www.pic.com/usa/resources/tech_updates/GEN_2_1bw.pdf for an American one as per 1997. Realised selection response is gradually being reported too, e.g. by Danavl (2000, table 5) where the response of pH seems to be essentially flat, similar to the above mentioned Finnish system (Mäntysaari *et al.*, 1994). Note that MQ traits have often been included as "restricted index" traits with zero desired gain (e.g. Morel *et al.*, 1988 ; Iansen and Sehested, 1989), especially where economic values could not reasonably be quantified.

BREEDING OBJECTIVES

Drip loss has an objective economic value. The abattoir pays for the purge but cannot sell it, which constitutes a true financial loss. In addition, the processing and retail sectors experience a financial loss through continued disappearance of saleable matter, and because consumers have the tendency to reject meat with too much purge. But the latter feature is difficult to quantify, and all other MQ traits suffer from that same drawback, making it difficult to implement them as breeding objective traits because their economic values are unclear. Von Rohr *et al.* (1996) present a "contingent valuation" approach based on querying industry representatives for "different prices to carcasses within different quality classes". Alternatively, desired gains procedures are being implemented.

Moreover, many of these traits have intermediate optima. For example, NPPC (1998) presents optimum ranges of 5.6 to 5.9 units for muscle pH, 2 to 4 % for IMF, 3 to 5 on a six-point linear scale for muscle colour, and a "robust pork flavour". With (genetic) change of average population levels over time, this results in continuously shifting marginal economic values (Hovenier *et al.*, 1993b), requiring frequent re-assessment of breeding objectives. A related issue is the drive towards uniformity; for example, Paterson (2000) states that current USA standard deviations of ultimate pH, *post mortem* pH decline and L* colour intensity should be halved "to produce innovative pork products that consistently satisfy [USA] consumer demands".

In spite of these conceptual difficulties, breeding objectives have been extended with MQ traits in practice (see above), focusing on the [pH – WHC – colour] complex and on IMF. Generally

these make up about 10 % of the total variance of the aggregate objective. In the current literature, Danavl (2000, p. 44) is at the low side of the range (pH makes up 5 % in dam lines, 8 % in sire lines), the Austrian national breeding scheme at the high side (IMF and a WHC indicator make up 15+15 % in its dam lines, 10+20 % in Pietrain; www.vns.or.at as per 2000).

SELECTION PROCEDURES

Traditionally, MQ breeding value estimation has relied on sib slaughter schemes for its data collection (Lindhe *et al.*, 1980 ; Lundström *et al.*, 1989) which used to involve labour-intensive dissection work. With rationalisation of abattoir processes this becomes evermore difficult to arrange on a routine basis, and many breeding companies focus now on some kind of exploitation of in-line MQ measurements, preferably on crossbred commercial animals to deal with genotype by environment interactions at the same time. The logistics of such a program are by no means easy (see above) and the measured animals must have close genetic ties to the purebred selection candidates for the process to be genetically effective; nevertheless, once the infrastructure is in place this is a powerful information-generating tool. Alternatively, *in vivo* measurement of muscle characteristics has received much attention; the observation of muscle fiber characteristics on the selection candidate itself has obvious genetic advantages, but up to now the *post mortem* processes are predicted poorly (e.g. Cameron *et al.*, 1998).

Breed differences in MQ traits are large (Sellier 1998, table 16.14) and commercially relevant. Duroc, Hampshire and Berkshire lines are commonly marketed as "meat quality lines" (e.g. www.qgenetics.com), and several industry lines have been based on these breeds. But the discovery of the *Hal* and *RN* genes has encouraged the approach of examining single gene effects rather than breed effects. It has also allowed breeding organisations to make use of a wider range of breeds after a change of allele frequencies through selection and/or introgression. Of course, MQ traits constitute the classical case of a system where marker-assisted selection is at its most efficient : traits which cannot be measured on the selection candidate and only at high costs on its relatives, and which depend on reasonably well-documented biochemical pathways so that candidate genes are relatively straightforward to postulate. Marker information can be obtained at a very young age so that animals can be pre-selected before performance testing, a distinct advantage over sib slaughter schemes. Meuwissen and Goddard (1996) suggest that conventional selection responses can be increased by more than half, and that this type of response can be sustained when markers are identified continually, adding new markers to the selection criterion as existing ones begin to reach fixation.

MARKER-ASSISTED SELECTION

Several scientific groups are exploring genes that influence MQ, currently using more than 20 resource populations involving wild boar and a wide variety of domestic pig breeds. Up to now this has resulted in MQ-associated QTL and marker genes on chromosomes 1 to 4, 6, 7, 12 and 15 (e.g. Fouilloux *et al.*, 1997 ; Soumillion *et al.*, 1997 ; Andersson-Eklund *et al.*, 1998 ; De Koning *et al.*, 1998 ; Ernst *et al.*, 1998 ; Monin *et al.*, 1998 ; Parr *et al.*, 1999 ; Beuzen *et al.*, 2000 ; Bidanel *et al.*, 2000 ; Óvilo *et al.*, 2000 ; Pérez-Enricso *et al.*, 2000 ; Renard and Mourot 2000 ; Malek *et al.*, 2001ab). Interesting candidate genes are the fatty acid binding protein genes (*FABP* ; Gerbens *et al.*, 1998ab), associated with IMF and only partially related to subcutaneous fat content. These tests have been patented (Gerbens 1997 ; see

www.ipg.nl/organisation.htm) and should permit selection for IMF based on *FABP* genotype while overall body fat is controlled by conventional selection.

More R&D projects are underway, often international consortium projects with an industry-wide contribution to knowledge (see for example www.qualityporkgenes.com which involves IRTA, INRA, the Rowett Institute, the National University of Ireland, Galway and PIC). But as with quantitative genetic parameter estimation, the best approach to discover practically relevant DNA markers is to search for them directly in the breeding population. This requires again some form of routine sib slaughter system; any data collected that way will then serve multiple purposes : (i) to produce sib information for conventional breeding value estimation, as above, (ii) to detect markers, (iii) to validate markers from experimental populations and test candidate genes (significant markers can then be directly included in the selection process), and (iv) to monitor the breeding population to keep the intermediate-optimum breeding objectives (see above) under control.

The recent identification of new alleles of the *RN* gene (*PRKAG3*) illustrates this. Analysis of glycolytic potential in our breeding populations suggested a major gene effect in *rn*⁺ carrier lines, and subsequently a QTL found at this position on chromosome 15 in an experimental cross (Malek *et al.*, 2001ab) pointed to this gene as a likely candidate. The gene was sequenced in several lines to identify polymorphisms for possible use as markers in association studies using samples from a routine sib slaughter system. Several alleles were found in our breeding populations, associated with variation in muscle pH and colour (Ciobanu *et al.*, 2001). Another example is the calpastatin locus (*CAST*), associated with shear force and taste-panel tenderness (Ciobanu *et al.*, 2002). Once such effects are identified, markers are validated to identify pleiotropic effects and to calculate economic values (e.g. Short *et al.*, 1997); as expected, several markers impact both MQ and growth performance, e.g. *MC4R* (Jungst *et al.*, 2001 ; Kim *et al.*, 2000 ; Emnett *et al.*, 2001ab). Markers are then incorporated in line improvement programmes (see Table 1), taking into account the factors described above.

The use of genetic fingerprinting to establish the origin or quality of meat (e.g. DNA-TraceBack™, Biopsytec™) will likely increase

as genotyping costs fall. Tests have also been developed for the breed origin of meat (see Plastow, 2000), most useful where the market associates quality with a particular breed, e.g. Berkshire for "black pork" in Japan. The use of markers in breeding programs will also help to reduce variation in carcass composition and MQ traits, enhancing uniformity.

FUTURE DEVELOPMENTS

The exploitation of (physiological and DNA) markers in combination with controlled environmental conditions will allow for customisation of breeding programs and pig/carcass

Table 1. Examples of marker effects on MQ traits in crossbred slaughter pigs

Gene	n ^A	Trait	Effect ^B	P < ...
<i>RN</i>	300	ham pH	D	0.17 0.0001
<i>PRKAG3</i>	540	ham pH	A	0.055 0.001
<i>MC4R</i>	718	loin pH	A	0.03 0.1
		backfat (mm)	A	0.5 0.05
<i>CAST</i>	448	shear force (kg)	A	0.14 0.01
<i>MQ35</i> ^C	548	loin pH	A	0.07 0.001

^A separate data sets; ^B Additive, Dominant; ^C one of >15 PICmarq™ MQ tests.

differentiation for specific markets. For example, high IMF is required for certain types of dry cured ham, whereas a variety of cooked ham products require low IMF levels. In the long term processors and retailers will likely abandon in-line end product quality control, instead specifying series of alleles, along with environmental controls, that are to be present or absent in each product. Such a set of customised genes will initiate the prediction of leanness and MQ of specified products. MQ measurements can then be minimised to a sample size sufficient to statistically ensure that each product complies with the end user's quality specifications. R&D emphasis will then be on the discovery of networks of genes that determine specific MQ traits. Functional genomics using cDNA microarrays (containing thousands of genes) and proteomics (analysis of protein content of samples) will allow for the analysis of gene expression and gene products in muscle or meat, and for relating this to leanness and MQ. Increasingly sophisticated process control techniques will be used within a production framework to evaluate the environmental interaction with genetics to reduce end product variability. A breeding organisation that is part of such a network must then (i) establish breeding objectives, selection criteria and molecular genetic technology, as above; this includes research into muscle differentiation and protein deposition, and functional genomics and proteomics, (ii) implement guidelines for on-farm management of production and pre-slaughter stress (which interacts strongly with ultimate MQ), (iii) work with its downstream customers on statistical process control procedures for pre-slaughter handling and post-slaughter processing to minimise quality variation, and on development of in-line MQ measurement equipment, and (iv) implement procedures to electronically identify groups of carcasses, to evaluate these for weight, leanness and MQ, and to use that information in quality assurance procedures to monitor and minimise quality variation (Klont *et al.*, 2001). And finally, the payment for slaughter pigs (either individual or group-based) should come to reflect the value of desirable vs. undesirable leanness and MQ.

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