The Effects of Genetic and Nutritional Factors on Pork Quality* - Review -

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ABSTRACT : Consumers are increasingly quality orientated and an understanding of the factors that influence product quality is a prerequisite to the development of programs to produce quality pork to meet market requirements. Pork quality is comprised of many components and is multi-factorial in nature. This review focuses on genetic and environmental influences on muscle color, water holding capacity, and palatability attributes. The impact of genetic factors such as breed variation and the influence of major genes (the Halothane and Rendement Napole genes), as well as relationships between carcass leanness and quality, are considered. In addition, the effect of nutrition, including vitamins and minerals, feeding level, and dietary energy:protein ratio, on pork quality is reviewed. Finally, the impact of diet on fat composition and quality is summarized. *(Asian-Aus. J. Anim. Sci. 1999. Vol. 12, No. 2 : 261-270)*

Key Words : Pork Quality, Halothane and Rendement Napole Genes, Vitamin, Mineral, Energy, Amino Acid, Feeding Level

INTRODUCTION

Discussion of the issue of pork quality is complicated by two factors. Firstly, there are many aspects to the quality issue, a number of which are not clearly defined and are difficult to measure objectively. In addition, genetics and nutrition are only two of a multitude of factors, many of which are outside of the producer's control, that impact the ultimate quality of pork and in many situations their effects relative to other factors will be small. Nevertheless, both genetics and nutrition can have a significant influence on pork quality, both positive and negative, and an understanding of these impacts is the first steps to developing production programs to optimize quality.

Definitions of pork quality will vary between countries, and within countries between market outlets and between different segments of the swine and meat industries. There have been a number of attempts to define quality, with perhaps the most extensive being that of Hoffmann (1994) who suggested that meat quality could be considered in terms of sensory properties, technological factors, nutritive value and hygienic and toxicological or food safety aspects. This review will focus on water holding capacity, a major factor that affects processing and saleable product yields, and pork color and palatability, factors that have a major bearing on the consumer acceptability of pork.

GENETIC INFLUENCES ON QUALITY

Variation among breeds and genetic lines

One of the most rapid and easiest methods to improve any trait is to import a breed or genetic line with superior characteristics and, consequently, there has been great interest in variation between breeds for quality aspects. A breed that has received considerable attention in this respect is the Duroc. This breed has a number of positive production attributes, including fast growth and hardiness, and it has been used commercially in both sire and dam lines. In addition, the Duroc has high intramuscular fat (IMF) relative to other breeds and there is evidence of a positive association between IMF and eating quality.

Recent studies in North America and Europe have confirmed the advantages of the Duroc relative to other breeds and lines. The National Pork Producers Council has carried out two comparisons, one involving purebreds (NPPC, 1994) and the other terminal sire lines (NPPC, 1995) and these studies are summarized in tables 1 and 2, respectively. These results illustrate the higher growth rates and intramuscular fat levels for the Duroc. Differences among breeds and lines for eating quality and shear force were, however, modest and did not always favor the Duroc. A threshold model has been proposed for the association between IMF and eating quality (Bejerholm and Barton-Gade, 1986; DeVol et al., 1988) with the proposed minimum IMF level for optimum eating quality being between 2 to 3%. A possible explanation for the relatively small differences in eating quality between the Duroc and other breeds in the NPPC studies is that all of the breeds and lines investigated had IMF levels close to or above the proposed threshold (tables 1 and 2).

A study carried out in the United Kingdom (MLC, 1991) compared slaughter pigs with increasing proportions of Duroc and showed an increase in growth rate, backfat thickness and IMF and an improvement in eating quality with increasing Duroc inclusion (table 3). However, the incidence of Pale, Soft, Exudative (PSE) pig meat condition also decreased with increasing Duroc inclusion and a number of authors have shown a negative relationship between PSE and palatability traits

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Table 1. Breed differences in growth, carcass and meat quality (from National Pork Producers Council, 1994)

	Av.daily gain, g	Backfat depth 10th rib (mm)	Loin eye area (cm^2)	Ultimate pH	Intra-muscular Fat (%)	Shear force (kg)	Taste Panel[1]	
							Juiciness	Tenderness
Berkshire	754	29.5	32.8	5.90	3.24	5.79	3.1	3.5
Chester White	735	30.5	34.5	5.86	3.13	5.92	3.3	3.4
Duroc	804	27.2	34.2	5.73	4.29	5.90	3.3	3.4
Hampshire	735	23.4	39.7	5.57	2.63	6.19	3.3	3.3
Landrace	754	26.2	36.7	5.67	2.49	6.38	3.1	3.1
Poland China	758	28.7	34.7	5.74	3.22	6.54	3.1	3.0
Spot	740	28.7	34.9	5.72	3.09	6.51	3.0	3.0
Yorkshire	745	26.7	35.4	5.72	2.48	6.39	3.0	3.1

[1] Higher values = more tender and juicier.

Table 2. Breed and genetic line differences in growth, carcass and meat quality (from National Pork Producers Council, 1995)

	Av.daily gain, g	Backfat depth 10th rib (mm)	Loin eye area (cm^2)	Ultimate pH	Intra-muscular fat (%)	Shear force (kg)	Taste Panel[1]	
							Tenderness	Juiciness
Berkshire	840^{c}	31.8^{a}	37.0^{c}	5.91^{a}	$2.41b^{c}$	5.74^{ab}	3.50^{a}	3.4
Danbred HD	831^{c}	24.9^{b}	43.5^{a}	5.75^{cd}	2.33^{c}	5.81^{ab}	3.45^{ab}	3.4
Duroc	885^{a}	28.7^{c}	39.6^{b}	5.85^{ab}	3.03^{a}	5.65^{a}	3.38^{ab}	3.3
Hampshire	849^{bc}	25.7^{a}	42.5^{a}	5.70^{d}	2.57^{b}	5.86^{ab}	3.36^{ab}	3.4
NGT Large White	849^{bc}	29.7^{cd}	36.3^{c}	5.84^{ab}	2.15^{c}	6.09^{c}	3.16^{c}	3.4
NE SPF Duroc	894^{a}	28.2^{bc}	41.0^{ab}	5.88^{ab}	2.71^{ab}	5.78^{ab}	3.36^{ab}	3.4
Newsham Hybrid	863^{ab}	24.9^{c}	41.6^{a}	5.82^{bc}	2.25^{c}	6.12^{c}	3.25^{bc}	3.3
Spot	835^{c}	31.5^{d}	37.6^{c}	5.83^{bc}	2.35^{c}	5.91^{bc}	3.16^{c}	3.3
Yorkshire	835^{c}	26.7^{ac}	39.8^{b}	5.84^{ab}	2.33^{c}	6.13^{c}	3.26^{bc}	3.4

[1] Higher values = more tender and juicier.

Means in the same column with different superscripts differ ($p<0.05$).

(e.g. Topel et al., 1976) which suggests that any eating quality advantage for the Duroc may be due, in part, to the lower incidence of PSE associated with this breed.

Table 3. Influence of proportion of Duroc genes on carcass and eating quality traits (from Meat and Livestock Commission, 1991)

Percentage Duroc	0	25	50	75	Approx. LSD[a]
P2 backfat depth (mm)	10.2	11.2	11.7	5.38	0.59
Intramuscular fat (%)	0.70	0.86	1.08	1.27	0.10
Carcasses judged PSE (%)	8.3	5.4	1.6	0.1	4.20
Taste panel[b]:					
Tenderness	4.96	5.03	5.32	5.38	0.25
Juiciness	4.09	4.11	4.18	4.38	0.17
Pork flavor	3.88	3.99	3.96	3.98	0.12

[a] Least significant difference between means, $p<0.05$.

[b] Evaluated using an 8-point scale; lower values=poorer quality.

The genetic line comparisons carried out by the NPPC (tables 1 and 2) focused attention on the Berkshire from a pork quality perspective, with studies showing that this breed produced the best eating quality and lowest shear force of all those evaluated. The Berkshire is being used in programs to produce a high quality product for specific markets, including for export to Japan. However, the growth performance and, particularly, the carcass lean contents of the Berkshire are relatively low (tables 1 and 2) and, therefore, the costs of producing Berkshires will be higher than that of other breeds and lines. This illustrates the dilemma faced by the swine industry in terms of trade-offs between growth and carcass characteristics and, thus, the costs of production, and quality attributes.

Single genes associated with quality

Although there are likely to be a large number of individual genes that impact pork quality, at the present time a relatively small number of genes with major effects on quality traits have been identified; these include the Halothane and Rendement Napole (RN) genes. Interestingly both these genes exert their influence through effects on post-mortem glycolysis and, consequently, either the rate or the extent of the decline in pH after slaughter. The Halothane gene can produce a very rapid decline in muscle pH immediately post mortem when muscle temperatures are still high and this combination results in the PSE condition. In contrast, with the RN gene the rate of pH decline is normal but more extensive, producing a low ultimate pH in the muscle i.e. the acid-meat condition.

The halothane gene

This is so-called because animals homozygous for the recessive form of the gene show a distinctive response when exposed to the anaesthetic gas halothane which is characterized by muscle rigidity and hypothermia. The halothane gene is of interest because it influences all aspects of the production and marketing chain with both beneficial and deleterious effects. The gene is being exploited in commercial programs with, most commonly, heterozygous carrier animals being produced as the slaughter generation.

The benefits and disadvantages of producing Halothane carrier progeny can be illustrated by the results of a recent study carried out at the University of Illinois (Leach et al., 1996). In this trial, a Halothane carrier sire line was mated to a negative female line resulting in both Halothane carrier and negative progeny being produced within the same litter. This allows the effects of the gene to be evaluated against the same genetic background. Halothane carriers had a number of advantages over negative animals, including better feed efficiency, improved carcass yield, and increased carcass lean content (table 4). However, carriers had poorer muscle color and water holding capacity (table 4) which would offset any growth and carcass advantage. Interestingly, the eating quality of the carrier and negative animals in the study of Leach et al. (1996) was similar (table 4).

Table 4. Within-litter comparison of Halothane carrier and negative pigs (from Leach et al., 1996)

	Carrier	Negative	Av. SE	Sig[a]
Average daily gain, g	974	964	16.9	NS
Gain:Feed	0.36	0.33	0.005	**
Dressing percentage	75.3	74.4	0.29	***
Weight of fat-free lean in the side, kg	24.7	23.9	0.35	*
Longissimus:				
pH (45 min)	6.4	6.6	0.05	***
Minolta L*	45.7	42.0	1.03	***
Drip loss,%	5.2	3.4	0.43	***
Shear force, kg	3.4	3.4	0.17	NS
Juiciness[b]	7.3	7.6	0.27	NS
Tenderness[b]	9.1	9.2	0.30	NS

[a] NS, *, **, *** = *not significant*, $p<0.05$, $p<0.01$, $p<0.001$, respectively.

[b] Taste panel scores from 0=extremely dry and tough to 15= extremely moist and tender.

However, other studies have shown a negative effect of the Halothane gene on palatability traits (Boles et al., 1991). The economic advantages and disadvantages of the Halothane gene will, to a certain extent, balance and the net effect of the Halothane gene on the overall economics of pork production may be negligible. In addition, because of the increasing importance of quality to the swine sector, a number of national industries and breeding programs have decided to eliminate the gene.

The rendement napole gene

Another single gene that has been shown to affect meat quality is the Rendement Napole (RN) gene, which is also referred to as the Napole or Acid Meat gene or the Hampshire effect, because its effects have largely been observed in purebred and crossbred Hampshire pigs, or commercial lines with Hampshire ancestry. Historically, breed comparison involving the Hampshire have generally shown low ultimate pH values for this breed in comparison with others (Sayre et al., 1963; Jensen et al., 1967; Hedrick et al., 1968). More recently, a comparison of terminal sire breeds and lines carried out by NPPC also showed this phenomenon in US Hampshire populations (table 2; NPPC, 1995). Monin and Sellier (1985), working with Hampshire populations in France, were the first to show that the low ultimate pH or acid meat was the result of elevated glycolytic potential in the muscle. Glycolytic potential (GP), which is an index of the potential of the muscle for glycolysis, is defined as follows.

Glycolytic potential (in μmoles lactate equivalent per gram of muscle tissue)=*2(glycogen+glucose-6-phosphate+glucose)+lactate*

The GP of Hampshires is elevated compared to other breeds (Monin and Sellier, 1985) resulting in an extended decline in pH post mortem (figure 1) and an abnormally low ultimate pH.

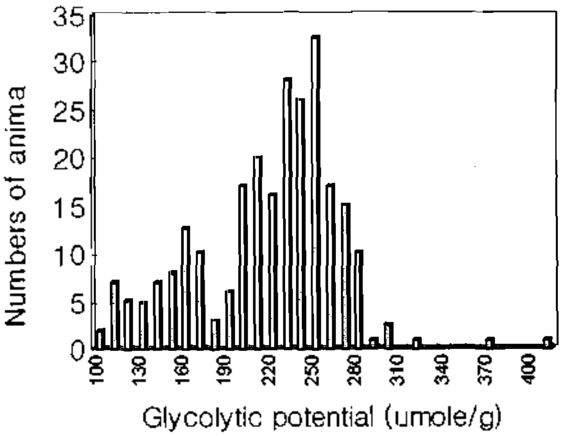

Figure 1. Effect of dietary lysine level on longissimus intramuscular fat (Cisneros et al., 1998)

Naveau (1986) was the first to postulate that there was a major dominant gene associated with this condition and called this the Rendement Napole gene, after the laboratory test for ham curing yield that had suggested the presence of the gene in Hampshire populations. The dominant allele, which produces the acid-meat condition, is designated RN^- and the recessive allele is designated rn+. The existence of this gene was confirmed by Le Roy et al. (1990). Hampshire populations within which the RN gene is segregating show a bimodal frequency distribution for glycolytic potential with a high and a low GP group. This is illustrated by the results of a recent study carried out in our laboratory (Miller, 1998) which are presented in figure 2. In this example, the breakpoint between the high and low GP groups was at approximately 180 μ moles/g. The high GP group (figure 2) contains animals that are homozygous for the dominant allele (RN^-RN^-) and heteroyzgotes (RN^-m+) with the low GP population containing homozygous recessive pigs ($m+m+$).

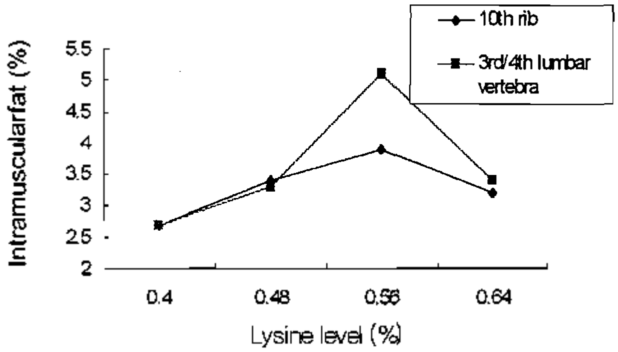

Figure 2. Bimodal frequencyb distribution of glycolytic potential in a population of pigs within which the RN gene is segregating (Miller, 1998)

Animals with high GP have elevated muscle glycogen levels, which have been shown to be up to 70% greatere in high compared to low GP animals. Following slaughter, this glycogen is converted into lactic acid producing the abnormally low pH in the muscle. At these low pH levels, the muscle approaches its isoelectric point at which there are no electric charges on the muscle proteins and, consequently, the water holding capacity of the muscle is dramatically reduced.

Recently, Miller (1998) carried out a literature review of the effects of the RN gene and the results of this are summarized in tables 5, 6, and 7. The net effect of the reduced water holding capacity associated with the RN^- allele is to increase drip, purge, and cooking losses and reduce curing and processing yields (table 5). In addition, muscle color is generally paler for high GP compared to low GP animals (table 5). However, the RN^- allele also has positive effects on quality with a number of studies showing a reduction in shear force and improvements in tenderness and juiciness for animals with high GP (genotypes RN^-RN^- and/or RN^-m+) compared to low GP pigs (genotype $m+m+$) (table 6). High GP animals also seem to have small advantages in growth rate, backfat thickness, loin eye area, and carcass lean content compared to those with low GP (table 7). Thus, the RN gene has both positive and negative effects with the major trade off being between reduced water holding capacity and improved

Table 5. Published estimates of the effects of the Napole gene on meat quality traits (Results relate to the difference between genotypes)

Authors	Genotypes Compared	pH[a]	Drip loss (%)	EEL[b]	WHC[c]	FOP[d]	Napole yield (%)[e]
Enfalt et al., 1997	RN^-m^+-m^+m^+	-	0.6*	-0.1	-	-	-4.7***
Sutton, 1997	RN^-m^+-$m+m^+$	-0.18***	2.53***	-	-4.82***	-	-3.63**
Lundrom et al., 1996	RN^-m^+-m^+m^+	-0.12***	1.1***	1.4***	-	5.6***	-6.5***
LeRoy et al., 1996	RN^-m^+-m^+m^+	-0.22***	-	3.4***	-3.0*	-	-7.9***
	RN^-RN^--m^+m^+	-0.20***	-	2.5***	-2.8*	-	-8.4***
Enfalt et al., 1994	Hamp-York	-0.13***	1.9***	0.9	-	2.1**	-5.9***
Monin and Sellier, 1985	Hamp-York	-0.13*	-	3.7*	-	11.0*	-

[a] Ultimate pH of the longissimus, [b] Muscle reflectance, [c] Water holding capacity (%), [d] Fiber optic probe, [e] A measure of processing yield.

*,**, *** = $p<0.05$, $p<0.01$, $p<0.001$, respectively.

Table 6. Published estimates of the effects of the Napole gene on eating quality traits (Results relate to the difference between genotypes)

Authors	Genotypes Compared	Cooking loss (%)	Shear force (kg)	Tenderness[a]	Juiciness[a]	Flavor[a]	Acidity[a]
Sutton, 1997	RN^-m^+ - m^+m^+	3.53***	-0.27**	-	-	-	-
Lundstrom et al., 1996	RN^-m^+ - m^+m^+	3.0*	-0.2*	-0.1	-	-	0.4**
LeRoy et al., 1996	RN^-m^+ - m^+m^+	0.10**	-	-1.27**	-0.68	0.87*	-
	RN^-RN^- - m^+m^+	0.09**	-	0.45**	-0.25	1.42*	-
Enfalt et al., 1994	Hamp-York	2.8***	-0.3**	-	-	-	-
Monin and Sellier, 1985	Hamp- York	2.1*	-	-	-	-	-

*, **, *** = $p<0.05$, $p<0.01$, $p<0.001$, respectively.

[a] Taste panel: lower scores = better quality.

Table 7. Published estimates of the effects of the Napole gene on growth and carcass traits (Results relate to the difference between genotypes)

Authors	Genotypes compared	Av. daily gain (g)	Slaughter yield (%)	Carcass length (cm)	Backfat depth (mm)	Loin eye area (cm^2)	Carcass lean (%)
Enfalt et al., 1997	RN^-rn^+ - rn^+rn^+	26.0**	-0.2	0.1	-1.2	-	1.0
LeRoy et al.,1996	RN^-rn^+ - rn^+rn^+	50.0*	-	0.16	-1.3*	3.3	1.0
	RN^-RN^- - rn^+rn^+	10.0*	-	0.20	-2.1*	2.9	0.9

eating quality. In practice, this gene may be exploited in situations where a high eating quality product is desired but eliminated from populations where the meat is principally used for cured and processed products.

Sutton (1997) studied the interaction between the Halothane and RN genes by comparing animals with high and low glycolytic potential that were either Halothane carriers or negatives. This study showed that pigs that were Halothane carriers with high GP produced meat that was paler and had lower water holding capacity than any of the other combinations of these two genes. This result in not unexpected given the rapid drop in pH early post mortem associated with the Halothane gene and the extended decline in pH resulting from the presence of the RN^- allele.

Estimates of the frequency of the dominant allele (RN^-), which have largely been derived in European populations, have generally been high. For example, Enfalt et al., (1994; 1997) reported frequencies of 0.72 and 0.61, respectively, in Swedish Hampshire populations. A recent study involving samples of pigs from US Hampshire breeders, produced an estimate of the frequency of the RN^- allele of 0.64 (Miller, 1998), which is within the range found in European populations. Because this is a dominant gene, the RN^- allele can be eliminated by using only homozygous recessive animals (rn+rn+) as replacement breeding stock. However, the only method currently available to identify these animals is using glycolytic potential values determined on a biopsy muscle sample taken in the live animal. In addition, a large enough population needs to be tested to allow the development of the bimodal frequency distribution for the population to identify the breakpoint between animals with low or high GP. Several research groups are trying to identify the specific gene involved and eventually develop a DNA-based test to genotype animals. The RN gene has been localized to an area of chromosome 15 (Milan et al., 1995) and a number of microsatellite markers linked to the RN locus have been reported (Mariani et al., 1996), but to date the gene has not been located.

Association between pork quality and carcass leanness

The swine industry has been remarkably successful at reducing backfat levels and increasing carcass lean content. For example, in the United Kingdom average backfat thickness levels, measured at the P2 position, have been halved over the last 20 years, being reduced from in excess of 20 mm to current levels of approximately 11 mm (MLC, 1997). Similar trends have been observed in other countries although the extent of the decline has often been less extreme. Improvements in carcass leanness have been achieved through a combination of genetic selection, improved nutrition and, in the case of the UK, the use of entire males.

Programs to reduce carcass fat levels have been so successful that the question "Are pigs too lean" has frequently been asked, and there are major concerns within the meat sector that the quality of pork from lean carcasses is inferior, particularly in terms of palatability attributes. Intramuscular fat levels (IMF) decline with increasing carcass leanness and can be very low in lean carcasses (less than 1%) and there is a general belief that eating quality and IMF are positively related.

What evidence is there that eating quality is negatively associated with carcass leanness? As previously discussed, there is circumstantial evidence that breeds and lines with low carcass and intramuscular fat produce tougher, drier meat (tables 1 and 2). However, as already pointed out, there are other aspects that affect meat quality that also differ between breeds and thus confound any evaluation of the association between IMF and quality.A number of studies have been carried out in the UK to investigate the eating quality of lean compared to fatter pigs. Wood et al. (1986) compared lean (8 mm P2 backfat) and fat (16 mm P2 backfat) pigs and showed a small difference in taste panel juiciness scores in favor of the fatter animals but little difference in tenderness or other palatability traits (table 8).

Table 8. Influence of backfat thickness on eating quality of pork loin chops (from Wood et al., 1986)

	Backfat thickness (P2, mm)		
	Lean (8)	Fat (16)	SED[a]
Intramuscular fat (%)	0.55	0.96	0.037***
Tenderness[b]	1.0	1.1	0.37
Juiciness[b]	1.0	1.3	0.07**
Flavor liking[b]	1.5	1.7	0.15
Pork flavor[b]	0.6	0.9	0.14
Overall acceptability[b]	0.7	1.0	0.23

[a] Standard error of the difference (SED); *,**,*** = $p<0.05$, $p<0.01$; $p<0.001$, respectively.

[b] Evaluated using a 15-point scale; -7 to +7; lower values = poorer quality.

However, the IMF content of pigs in this study was low, being under 1% even for the fatter carcasses. The threshold model for the effect of IMF on eating quality that has previously been discussed (Bejerholm and Barton-Gade, 1986; DeVol et al., 1988), suggests that a minimum of 2 to 3% IMF is required for optimum palatability. However, the study of Bejerhom and Barton-Gade (1986) used different genotypes to create the range of IMF levels to investigate associations with eating quality and DeVol et al. (1988) selected pigs of different IMF levels from the slaughter line.

Therefore, in both of these studies the level of IMF was confounded with other factors, particularly genotype, and it is not certain if this same threshold level for IMF exists within a breed or genetic line.

Relatively few studies have investigated the genetic correlations between carcass lean and eating quality. However, estimates of the genetic correlations between backfat thickness and IMF on the one hand and palatability traits on the other have generally been unfavorable (Jensen et al., 1967; Cameron, 1990; Lo et al., 1992) suggesting that genetic selection for improved carcass lean content will produce a correlated reduction in pork tenderness and juiciness.

Published heritability estimates for eating quality traits have generally been in the range from 0.23 (Cameron, 1990) to 0.45 (Lo et al., 1992) for tenderness, and from 0.12 (Lo et al., 1992) to 0.19 (Jensen et al., 1967) for juiciness, suggesting that direct selection for eating quality, particularly tenderness, would produce a relatively rapid improvement. However, the obvious problem is measuring eating quality, particularly in the live animal. Achieving a genetic improvement in eating quality as a correlated response to selection for a trait that is easier to measure is another option. In this respect, the genetic correlations presented above would suggest that selection for increased IMF would produce a correlated improvement in pork tenderness and juiciness. The heritability of IMF is high, with estimates ranging from 0.49 (Schworer et al., 1987) to 0.86 (Jensen et al., 1967). However, it is not currently technically feasible to measure IMF in the live animal. Research is in progress to investigate the potential for real-time ultrasound scanning to predict IMF levels in cattle and pigs. However, given that the optimum level of IMF for pork is likely to be within a relatively narrow range of 2 to 3%, it is uncertain if this technique will work in pigs. There is evidence that there are single genes with a relatively large effect on IMF (Gerbens et al., 1998) and in the longer term selection for these genes is likely to be feasible and may be the most appropriate approach to increasing IMF levels in populations with low carcass fat levels.

Nutritional influences on quality

A number of nutritional approaches to improving the color, water holding capacity and eating quality of pork have been studied. These have included evaluation of the role of specific dietary ingredients and the impact of feeding level and of dietary energy:protein ratio.

Vitamins and minerals

Interest in antioxidants, particularly vitamin E, and their role in pork quality stems from their potential impact on product shelf life and muscle color and water holding capacity. Lipid oxidation results in an increase in unacceptable flavors and odors and reduces the shelf life of products. In addition, oxidation of the phospholipids in the sub-cellular membranes can disrupt the integrity of the cell wall and increase moisture loss.

The effect of dietary vitamin E on lipid oxidation and color and water holding capacity of pig meat has been reviewed by Buckley et al. (1995) who concluded that dietary vitamin E was effective in reducing lipid oxidation and improving muscle color and water holding capacity. Two recent studies that have investigated the effect of vitamin E on water holding capacity are summarized in table 9. The study of Cheah et al. (1995) showed a significant reduction in drip loss as a result of feeding supplementary vitamin E (500 mg/kg of feed) to both Halothane negative and carrier animals. In contrast, Cannon et al. (1996) found no effect of supplementary vitamin E (100 mg/kg feed) on drip loss for storage periods of up to 56 days post mortem. One possible explanation for the difference in response observed in these two studies is the lower level of vitamin E used by Cannon et al. (1996) and these authors suggested that their lack of response may have resulted from the low-tocopherol concentrations found in the muscle of treated pigs.

Table 9. Impact of Dietary Vitamin E Supplementation on Drip Loss from Longissimus Chops

Study	Supplementary Vitamin E level (mg/kg)	Other Treatment	Drip loss (%) Control	Drip loss (%) Supplemented
Cheah et al., 1995	500	Halothane genotype:		
		Nigative	6.9	3.2
		Carrier	9.1	5.0
Cannon et al., 1996	100	Days of storage:		
		0	5.01	4.76
		14	3.81	3.30
		28	2.96	2.68
		56	2.35	2.40

The other nutrient that has been implicated for potentially reducing lipid oxidation in pork is Selenium, which is a component of the enzyme glutathione peroxidase. However, there is little evidence to suggest that providing pigs with additional selenium above that required for normal health and growth performance shows any benefit in terms of meat quality.

Feeding elevated levels of vitamin D3 (up to 7.5 million IU per day) for 5 to 10 days prior to slaughter has been shown to improve the tenderness of beef with reductions in shear force of 7 to 20% at 7-days post mortem for treated animals (Swanek et al., 1997). A possible mode of action for this tenderness improvement is via a stimulatory effect of vitamin D_3 on muscle calcium levels and, consequently, on the muscle protease enzymes that are involved in post-mortem tenderization. We tested the effect of high dietary vitamin D_3 levels in swine in a preliminary study in our laboratory and failed to show any beneficial effect on tenderness (Enright et al., 1998). However, drip loss was substantially reduced and muscle color was improved for the treated animals compared to controls, suggesting a large effect on water holding capacity. The cause of these improvements has not been established and further research is required to validate these findings and further investigate any impact of supplementary vitamin D_3 on meat tenderness.

Two recent studies have highlighted the potential to improve meat quality through nutritional approaches immediately prior to slaughter that modify post-mortem glycolysis. A study carried out in Australia has shown a large effect of dietary magnesium supplementation of pigs on pork quality (D'Souza et al., 1998) in terms of reduced drip loss, improved color and a lower incidence of PSE condition for treated animals compared to controls. Magnesium reduces plasma cortisol and catecholamine concentrations and may act to reduce the animal's glycolytic response to pre-slaughter stress. Similarly, Kremer et al. (1998) showed that feeding sodium oxalate to pigs for 4 hours immediately pre-slaughter slowed the post-mortem decline in pH and decreased water loss from the muscle during a 12-day storage period. Sodium oxalate inhibits pyruvate kinase and, consequently, reduces the rate of post-mortem glycolysis.

There has also been interest in the administration of oral electrolytes in the last few days prior to slaughter to alter the acid-base balance of the animal. In particular, the use of oral sodium bicarbonate, an alkaline salt, has been evaluated as a technique to reduce the incidence of PSE. One study (Ahn et al., 1992) has shown a delayed post mortem pH decline in pigs given sodium bicarbonate orally immediately prior to slaughter. However, this study and that of Boles et al. (1994) failed to show any positive benefit of sodium bicarbonate treatment on pork color or drip loss.

Feeding level and dietary protein:energy ratio effects

A number of studies carried out in the United Kingdom have shown an eating quality advantage for pigs reared under ad libitum compared to restricted feeding. The results from two of these studies are presented in table 10.

Table 10. Effect of ad libitum and restricted feeding regimens on eating quality[1]

Advantage of ad libitum over restricted feeding		
Trait	Trial A[a]	Trial B[b]
Tenderness	0.30***	0.47*
Juiciness	0.26***	0.19*
Flavor	0.00	- 0.05
Odor	0.12	0.02
Overall acceptability	0.19***	

[1] 8-point scale; lower values=poorer quality; *, *** = $p<0.05$, $p<0.001$, respectively.

[a] Source: Ellis et al., 1996, [b] Source: Warkup et al., 1990.

The feeding regimes were imposed between approximately 30 kg live weight and 80 to 85 kg in the case of the study of Warkup et al. (1990) and from 30g to between 80 and 120 kg in the study of Ellis et al. (1996). The degree of feed restriction imposed was similar in both trials at approximately 82% of ad libitum intake.

The results of these studies (table 10) suggest a small but significant improvement in tenderness and juiciness from ad libitum feeding. The mechanisms for any improvement in palatability resulting from ad libitum feeding has not been established but could result from the improved growth rate and/or increased intramuscular fat levels in ad libitum compared to restrict fed animals. Warkup and Kempster (1991) proposed a theoretical model in which increases in intramuscular fat levels and/or lean growth rates are associated with improvements in tenderness and juiciness. This model has not been validated but raises an issue over the extent to which eating quality can be improved by manipulating the growth curve of the animal.

In contrast to these positive associations between growth performance and palatability, other research has shown little effect of either feeding level or growth rate on eating quality. In a recent study, Wood et al. (1995) found no effect of ad libitum compared to restricted feeding (80% of ad libitum intake between 25 and 95 kg live weight) on eating quality characteristics. In addition, a recent collaborative study carried out by Purdue University and the University of Illinois found little difference in tenderness and juiciness between pigs of the same genotype that were grown at widely different rates. This calls into question the influence of feeding level and growth rate on eating quality. The issues relating to genetically low levels of IMF and to the relationship between IMF and eating quality have been discussed previously in this paper. In the short term, the easiest method to increase IMF levels is via nutrition and a number of studies have shown substantial increases in intramuscular fat from feeding protein-deficient diets to pigs (table 11). However, most of these trials were carried out during both growing and finishing phases and the protein-deficient diets also produced substantial increases in carcass fat levels and reductions in feed efficiencies and would be uneconomic in most situations. The impact of short-term feeding of protein-deficient diets on IMF levels is less well established. Cisneros et al. (1996) produced a 2 percentage units increase in IMF from feeding a protein-deficient diet for approximately 5 weeks prior to slaughter (table 11). In a follow up study, Cisneros et al. (1998) investigated the interaction between the level of protein deficiency and time of feeding of protein deficient diets on longissimus IMF. The results of this study suggested that a minimum feeding period of 5 weeks was required to elicit a consistent response in IMF and that there was an optimum protein level to produce the maximum response (figure 2). Feeding protein levels above or below this optimum level

Table 11. Influence of feeding protein deficient diets on intramuscular fat content of the longissimus

Dietary protein/lysine level (%)		Intramuscular fat (%)		Weight range (kg)	Source
Adequate	Deficient	Adequate	Deficient		
18.5/0.96	13.1/0.64	1.5	2.5	to 103	Essen-Gustavsson et al., 1994
17.6/0.81	11.9/0.48	1.4	3.5	25-98	Castell et al., 1994
25.0	10.0	3.4	9.4	30-90	Goerl et al., 1995
16.0/0.82	12.0/0.55	5.5	11.2	10-100	Kerr et al., 1995
20.5/1.05	16.6/0.70	1.2	2.4	30-90	Blanchard et al., 1998
14.0/0.56	10.0/0.40	3.8	5.7	80-110	Cisneros et al., 1996

resulted in a reduction in the level of IMF within the muscle (figure 2). In this study, pigs on the lowest level of protein (0.4%) had a reduced feed intake relative to the other treatments and this is the probable explanation for the relatively modest response in IMF. This suggests that the response of IMF to low protein will be sensitive to the interaction between protein level and feed intake.

Fat quality

The quality of the fat, in terms of its physical and nutritive characteristics, is closely related to its fatty acid composition. One of the major concerns is soft fat, which results from a high proportion of unsaturated fatty acids in the fat depots. From a meat sector perspective, soft fat is a disadvantage because it can cause processing problems, particularly during cutting, grinding and slicing operations. In addition, the potential for lipid oxidation resulting in the development of off-flavors increases as the unsaturated fatty acid content of fat depots increase. On the other hand, there is a general belief that the consumption of unsaturated compared to saturated fatty acids is better from a human health standpoint.

In the pig, many of the dietary fatty acids are absorbed intact and are deposited directly into the fat depots (Wood et al., 1994, Masakazu, 1990). Thus, the fatty acid composition of the fat depots are closely related to the fatty acid profile in the dietary fat. This is particularly the case for leaner animals in which a greater proportion of the fatty acids in carcass fat are derived from the diet and a smaller proportion from *de novo* synthesis within the animal.

Fat composition and quality are receiving increasing attention because of the increasing leanness of pigs and an increased use of dietary fat supplementation both to increase the energy density of the ration and to suppress dust levels within the building. In addition, the widespread use of commercial high-oil corn varieties has also highlighted the issue of fat quality.

The unsaturated fatty acid that has received considerable attention is linoleic acid (C18:2) which is not synthesized by the pig or significantly modified before being deposited in the fat tissue. Linoleic acid is relatively high in conventional fat sources used for pigs and increases in dietary levels of C18:2 are closely mirrored by increase in C18:2 concentrations in the fat depots and an increasing softness of the fat. In the UK and elsewhere, this has led to a general recommendation that the concentration of linoleic acid in finisher diets should not exceed 1.6 per cent. However, this recommendation should be reviewed in the light of changes in the fatness level of pigs and nutritional practices.

Another issue relating to fatty quality is that of fishy taints in the meat that can be a problem when high levels of fish oil are fed to pigs. Fish oil is high in polyunsaturated fatty acids such as C20:5 and C22:6 (Irie and Sakimoto, 1992) that are susceptible to oxidative rancidity and the development of off-flavors. The relationship between the fatty acid composition of the intramuscular fat and eating quality traits was investigated by Cameron and Enser (1991) who showed that higher levels of unsaturated fatty acids were generally associated with poorer scores for eating quality. The negative associations between unsaturated fatty acid concentrations and flavor scores most likely resulted from increased lipid oxidation and rancidity.

CONCLUSIONS

The issue of meat quality is of increasing importance in all areas of the world and has many different components. Although post-farm factors will have a major influence on the ultimate quality of pig meat, there is increasing evidence that production practices and particularly genetic and nutritional factors can be extremely important in this respect. However, attempts to improve pork quality by changing genetics and/or nutrition will only be successful if they are accompanied by the adoption of appropriate practices by the other sectors in the chain. In other words, improving pork quality will require a "total quality management" approach involving all of the swine industry. At present, attempts to improve meat quality are restricted by the inability to measure quality on the slaughter line and, consequently, reward producers for producing high quality pork.

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