Factors controlling fatty acid composition and meat quality in pork and other meats

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Summary

This paper reviews the factors controlling fatty acid composition in muscle and adipose tissue of meat animals, with an emphasis on pig muscle. Phospholipid, present in muscle membranes, has a much higher concentration of the major polyunsaturated fatty acid (PUFA) linoleic acid (18:2n-6) than triacylglycerol (neutral lipid), the lipid apparent as white flecks in marbled pork. Phospholipid has a low and constant concentration in muscles (about 400 mg/100 g in longissimus), so the PUFA percentage in lean muscle is high but declines quickly as total muscle fatty acids increase and the proportion of neutral lipid increases. This lipid fraction is high in saturated and monounsaturated fatty acids. Most breed and some diet/feed effects on muscle fatty acid composition are explained by effects on the total amount of fat and therefore the ratio of phospholipid to total lipid. However, the use of diets high in particular fatty acids such as fish oil or linseed (flaxseed) can dramatically change fatty acid composition. Big increases in n-3 PUFA can lead to excessive oxidation of fatty acids during processing and cooking, leading to abnormal odors and flavors in pork. A value of 3% α-linolenic acid (18:3n-3) in total fatty acids has been suggested as an upper limit when feeding linseed. In cattle produced on all-grass diets, the concentration of 18:3n-3 is less than 3% of total fatty acids, and 18:3n-3 contributes positively to beef flavor. Vitamin E (and other antioxidants) prevents excessive PUFA oxidation, being obtained from fresh grass or as a feed additive. Usually pig muscle is oxidatively stable compared with beef and lamb.

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Proceedings of the 61st American Meat Science Association
***Reciprocal Meat Conference** (pp. 1–7)*
June 22–25, 2008, Gainesville, Florida
www.meatscience.org

Introduction

Fatty acid composition is an important part of the nutritional value of meat because of concern that saturated fatty acids (SFA), which are found at high levels in meat, are risk factors for human health. On the other hand, meat contains significant quantities of monounsaturated fatty acids (MUFA) and, in the case of pigs and poultry, polyunsaturated fatty acids (PUFA), which are beneficial nutrients. Recent research in meat animals has explored ways of producing a healthier fatty acid balance by diet and genetic changes. This means increasing the ratio of PUFA to SFA and increasing the proportion of n-3 PUFA in total PUFA. This paper examines the factors controlling fatty acid composition in meat animals and examines the effects of fatty acid composition on meat quality. Most attention will be focused on muscle fatty acids and on pigs.

Effects of Species on Fatty Acid Composition

Typical data for the fatty acid composition of the 3 red meat species are shown in Table 1. Pork is classified as a red meat in some countries, but in others, it is classified as a white meat because it has similarities to poultry, including a high ratio of PUFA to SFA. The data in Table 1 are for total fatty acids in loin muscle cross sections with a small amount of subcutaneous and intermuscular fat attached to the muscle. Crude dissection was used to produce the muscle sample, similar to that which might be done by people removing fat from muscle during a meal. The value for total fatty acid content is therefore higher than if muscle cores from the center of the muscle had been studied. These results reveal some important differences between the species. Linoleic acid (18:2n-6), which is an essential fatty acid derived entirely from the diet, is at much higher concentrations in pigs. This is because this fatty acid, an important constituent of grains and oilseeds and therefore of pig diets, is not broken down during digestion in the monogastric stomach and passes directly from the small intestine to the blood and thereby to the tissues of the animal. Concentrations of other PUFA also tend to be at high concentrations in pigs, including α-linolenic acid (18:3n-3), which is a major constituent of the diet of ruminants, being the main fatty acid in grass and forages. Ruminants hydrogenate PUFA, producing SFA and a

Table 1. Fatty acid composition (% of total fatty acids) and total fatty acid content (mg/100 g of muscle) of loin steaks/chops in pigs, sheep, and cattle (Enser et al., 1996)[1]

Item	Pigs	Sheep	Cattle
14:0	1.3[a]	3.3[c]	2.7[b]
16:0	23.2[b]	22.2[a]	25.0[c]
16:1 *cis*	2.7[b]	2.2[a]	4.5[c]
18:0	12.2[a]	18.1[c]	13.4[b]
18:1 *cis*-9	32.8[a]	32.5[a]	36.1[b]
18:2n-6	14.2[b]	2.7[a]	2.4[a]
18:3n-3	0.95[b]	1.37[c]	0.70[a]
20:4n-6	2.21[b]	0.64[a]	0.63[a]
20:5n-3	0.31[b]	0.45[c]	0.28[a]
n-6:n-3	7.2	1.3	2.1
P:S	0.58	0.15	0.11
Total	2,255[a]	4,934[c]	3835[b]

[a–c]Means with different superscripts are significantly different ($P < 0.05$).
[1]Fifty samples of each species.

range of intermediate fatty acids (e.g., trans fatty acids) for absorption into tissues.

Relations Between Fatty Acid Composition and Fat Content

In muscle, the fatty acids are located in triacylglycerol, extracted by neutral solvents and termed neutral lipid and phospholipid, extracted using polar solvents. The neutral lipid forms white flecks of marbling fat in older, fatter pigs. Phospholipid is part of the intimate structure of cell membranes and organelles. In pig longissimus muscle, phospholipid is a fairly constant fraction, present at about 400 mg/100 g of muscle. Neutral lipid is much more variable and increases dramatically as total fat increases. Phospholipid has a different fatty acid composition to neutral lipid; in particular, 18:2n-6, the major PUFA in meat, is much higher in phospholipid (about 3× in longissimus), and 18:1 *cis*-9, the main MUFA in meat, is much higher in neutral lipid (again, about 3× in longissimus; Table 2). There are differences between muscles: the white glycolytic longissimus muscle has a relatively low concentration of phospholipid relative to neutral lipid, whereas the red oxidative psoas is much higher in phospholipid relative to neutral lipid (Table 2). These differences in the fatty acid composition of the lipid fractions mean that at low levels of total lipid in muscle, the concentration of 18:2n-6 is high, because phospholipid is a high proportion of total lipid. At high levels of total lipid, the concentration of 18:2n-6 is much lower as phospholipid is swamped by neutral lipid with its higher concentrations of SFA and MUFA. The opposite trends are apparent for 18:1 *cis*-9. When total fat is low, the concentration of this fatty acid is also low, but as fattening proceeds, the concentration of 18:1 *cis*-9 increases, reflecting its higher concentration in neutral lipid.

These trends are shown in Figures 1 to 3. Figure 1 shows the concentrations of neutral lipid and phospholipid in longissimus muscle plotted against the concentration of total fatty acids (i.e., neutral lipid plus phospholipids) in a population of entire male pigs from 4 pure breeds: Berkshire, Duroc, Large White, and Tamworth. Results are from the study of Wood et al. (2004). Large White and Tamworth breeds were low in total muscle fatty acids, whereas Berkshire and Duroc were high. All pigs had predictable levels of neutral lipid and phospholipid in relation to their level of total lipid. The relationship between the percentage of 18:1 *cis*-9 in total fatty acids and the concentration of total fatty acids in muscle is in Figure 2, showing an upward curving graph with Large White and Tamworth pigs in the lower part of the curve and Berkshire and Duroc in the upper part. The relationship between the percentage of 18:2n-6 and total fatty acids is in Figure 3. This is a downward-curving graph, with Large White and Tamworth having high percentages of 18:2n-6 because of low concentrations of total fatty acids and Berkshire and Duroc having low percentages of 18:2n-6 because of high concentrations of total fatty acids. The graphs for psoas showed similar trends, although the ranges of values were different; for example, 18:2n-6 ranged from 25 to 6% of total fatty acids in longissimus and from 30 to 15% in psoas.

Changes in the percentages in total muscle fatty acids of 18:1 *cis*-9 and 18:2n-6 as total muscle fatty acids increases are in general similar for cattle, with 18:1 *cis*-9 increasing and 18:2n-6 declining. This was shown in a study of Angus cross and Holstein-Friesian steers growing from

Table 2. Mean and SD for 18:1 cis-9 and 18:2n-6 (%) in neutral lipid (NL), phospholipid (PL), and total lipid (TL) and concentrations of these lipids in longissimus and psoas muscles (mg/100 g) in 4 pig breeds (Wood et al., 2004).

	NL		PL		TL	
Item	Mean	SD	Mean	SD	Mean	SD
Longissimus						
18:1 cis-9	39.4	2.46	11.0	1.79	31.4	4.56
18:2n-6	8.9	2.86	30.0	2.04	14.8	4.16
Total	1,534	1,121	440	732	1,974	1,177
Psoas						
18:1 cis-9	33.6	3.31	9.4	1.44	23.6	3.43
18:2n-6	14.0	3.55	34.0	1.85	22.2	3.10
Total	851	337	560	101	1,412	399

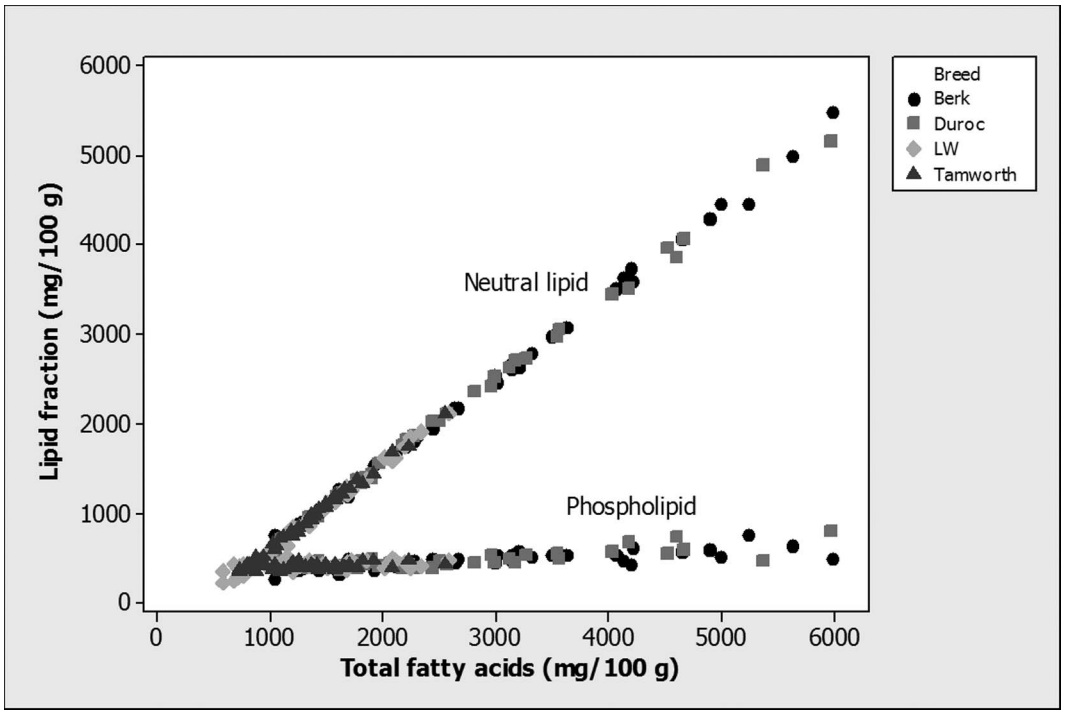

Figure 1. Concentrations of neutral lipid and phospholipid fatty acids (mg/100 g) plotted against total fatty acids (mg/100 g) in longissimus muscle of 4 pig breeds (Wood et al., 2004). Berk = Berkshire; LW = Large White.

6 to 24 mo of age by Warren et al. (2008a). However, the concentrations of these fatty acids in the 2 lipid fractions are different between the species, with cattle having a higher percentage of 18:1 *cis*-9 in phospholipid (13 to 28% in Warren et al., 2008b) and a lower percentage of 18:2n-6 in phospholipid (18 to 22% in Warren et al., 2008b). The contrast between cattle and pigs was particularly marked in neutral lipid, cattle having a similar value to pigs for 18:1 *cis*-9 but much less 18:2n-6, 0.7 to 2.8%, in Warren et al. (2008b). In this sense, cattle conserve

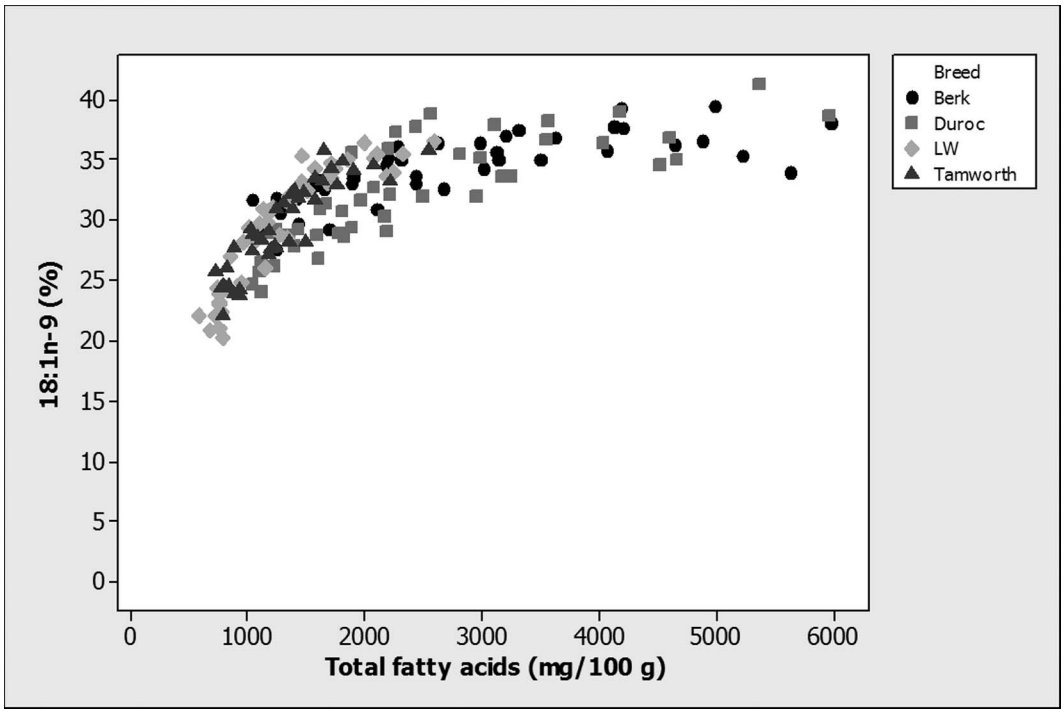

Figure 2. Percentage of 18:1 cis-9 in total fatty acids of longissimus muscle plotted against total fatty acids (mg/100 g) in 4 pig breeds (Wood et al., 2004). Berk = Berkshire; LW = Large White.

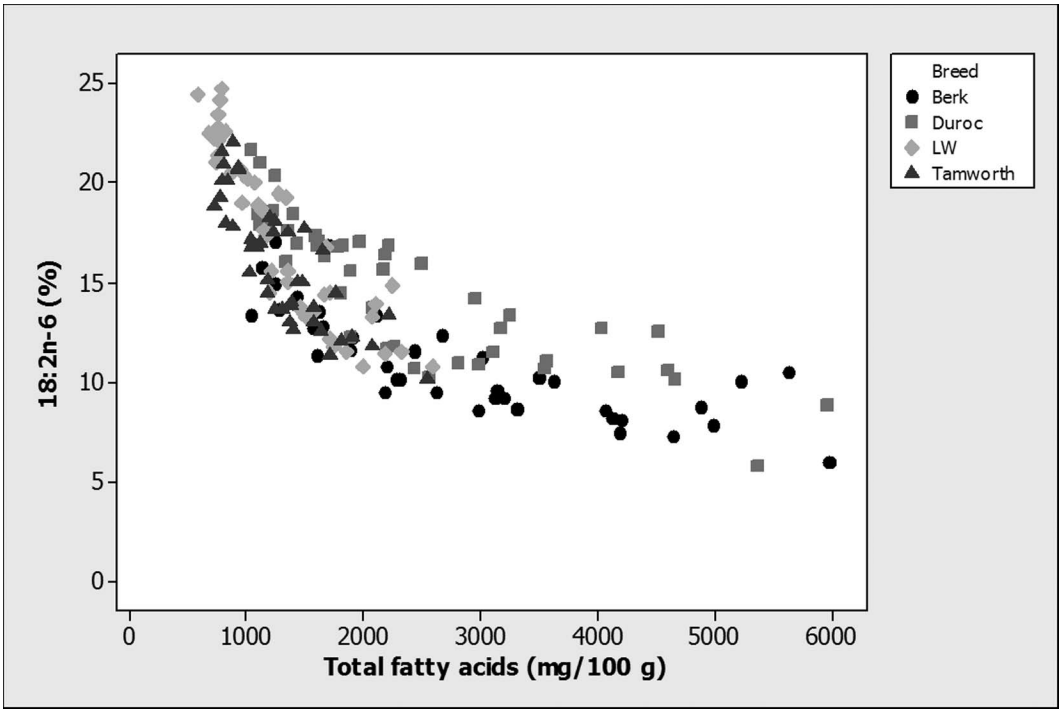

Figure 3. Percentage of 18:2n-6 in total fatty acids of longissimus muscle plotted against total fatty acids (mg/100 g) in 4 pig breeds (Wood et al., 2004). Berk = Berkshire; LW = Large White.

18:2n-6 in phospholipid rather than storing it in neutral lipid where it is available for oxidation.

Adipose tissue is composed mainly of 1 lipid class triacylglycerol (neutral lipid). It contains the same fatty acids as neutral lipid in muscle, with low concentrations of long-chain PUFA because of the very low concentrations of phospholipid. These long-chain PUFA are undetectable in cattle adipose tissue. As fattening proceeds in the pig, the same trends in the percentages of 18:1 *cis*-9 and 18:2n-6 are seen as in muscle (i.e., an increase and decrease, respectively). The decrease in 18:2n-6 is due to a declining contribution of dietary fat and a greater importance of de novo synthesis of SFA and MUFA to total fat deposition as it accelerates. In cattle, the percentage of 18:1 *cis*-9 also increases as total fat increases but the percentage of 18:2n-6 remains low and does not change much (Wood et al., 2007).

Effects of Breed on Muscle Fatty Acid Composition

It follows from the results in Figures 1 to 3 that the main factor determining muscle fatty acid composition is the total amount of fat. In the study of 4 breeds by Wood et al. (2004), high percentages of 18:1 *cis*-9 and low percentages of 18:2n-6 in Berkshire and Duroc were due to them having higher concentrations of total fatty acids in muscle than Large White and Tamworth. The concentration of muscle fatty acids was not predicted from the amount of subcutaneous fat in these 4 breeds, Durocs having high values of muscle fatty acids at low subcutaneous fat, whereas Berkshire, with a similar value for muscle fat, had much fatter carcasses (Figure 4). It therefore appears that the genetic difference in fat partition between depots is more significant than that in fatty acid composition.

The underlying importance of total fat in explaining breed differences in muscle fatty acid composition was shown by Fisher et al. (2000) in Soay sheep and Raes et al. (2001) in the double-muscled Belgian Blue cattle breed. Both had high values of 18:2n-6 because the concentration of total fatty acids was very low, producing a high ratio of phospholipid to neutral lipid.

Effects of Diet on Muscle Fatty Acid Composition

When diet effects the concentration of total fatty acids in muscle, an effect on fatty acid composition is also expected. This was shown in a recent comparison of a low-protein diet and a standard diet by Teye et al. (2006). The low-protein diet increased the concentration of muscle fatty acids, which explained the higher percentage of 18:1 *cis*-9 and the lower percentage of 18:2n-6 (Table 3). A companion paper by Doran et al. (2006) provided a biochemical explanation for the effect on 18:1 *cis*-9. In muscle of pigs fed the low-protein diet, the expression of the enzyme stearoyl coenzyme A desaturase, which converts 18:0 to 18:1 *cis*-9, was increased.

There are many examples of diet effects that override these effects of fat content. For example, feeding a high level of 18:2n-6 in the pig's diet can greatly increase the concentration of this fatty acid in muscle. Of all the fatty acids, 18:2n-6 shows the greatest tissue response to dietary levels (Nguyen et al., 2003). Feeding linseed can

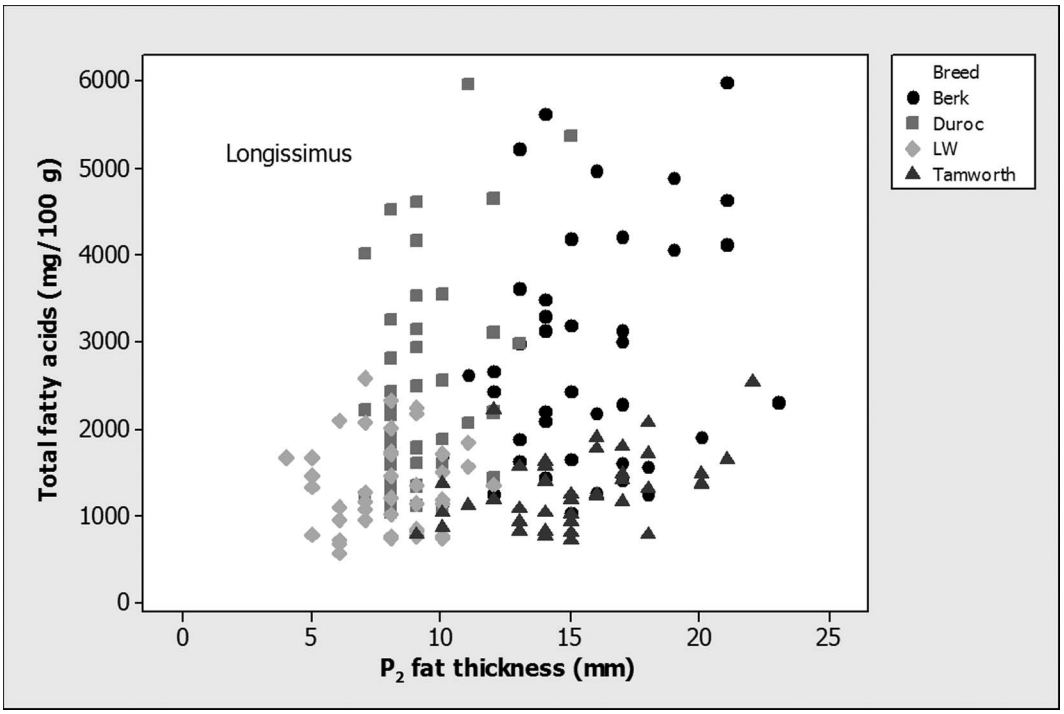

Figure 4. Total muscle fatty acids (marbling fat) in longissimus (mg/100 g) plotted against P2 backfat thickness in 4 pig breeds (Wood et al., 2004). Berk = Berkshire; LW = Large White.

increase the concentration of 18:3n-3 in meat, although the tissue response is less dramatic than with 18:2n-6, presumably because it competes less successfully than 18:2n-6 for incorporation into phospholipid molecules. However, it is easily possible to reduce the ratio of n-6:n-3 PUFA to below 4.0, the recommended value for the diet as a whole, by including linseed in the diet (Wood et al., 2007). When 18:3n-3 is present in muscle, it is then converted by elongase and desaturase enzymes into the long-chain n-3 PUFA 20:5n-3 (EPA) and 22:5n-3. Conversion to 22:6n-3 (DHA) is not always observed. The results in Table 4 are from a study in which a control diet containing 1.5 g of 18:3n-3 and 16 g of 18:2n-6/kg (ratio of 10:1 18:2n-6 to 18:3n-3) was compared with a linseed-enriched diet containing 4.5 g of 18:3n-3 and 10 g of 18:2n-6/kg (ratio of 2:1; Enser et al., 2000). The diets were fed between 25 and 95 kg of live weight. The ratios of 18:2n-6 to 18:3n-3 in longissimus total fatty acids and phospholipid were reduced in the pigs fed the linseed diet but not to the level in the diet itself. This illustrates the preferential deposition of 18:2n-6 and the difficulty of displacing it from neutral and phospholipid molecules.

Feeding grass, both fresh and conserved to ruminants, increases the concentration of 18:3n-3 in muscle, whereas feeding grain increases the concentration of 18:2n-6, despite the biohydrogenation of over 90% of these fatty acids in the rumen. Both can then be converted to long-chain n-3 and n-6 PUFA in muscle. In a study conducted by Warren et al. (2008b), approximately equal amounts of 18:2n-6 and 18:3n-3 were fed in grain and grass silage-based diets respectively between 6 and 24 mo of age.

Table 3. Fatty acid composition (%) and total fatty acid content (mg/100 g of muscle) of longissimus muscle in 60 pigs given a low-protein (LP) or a high-protein (HP) diet (Teye et al., 2006).

Item	HP	LP	Significance
18:1 *cis*-9	32.1	39.0	***
18:2n-6	14.0	8.9	***
Total	1,739	2,865	***

***$P < 0.001$.

Table 4. Fatty acid composition (%) of longissimus muscle total fatty acids and phospholipid in pigs given a control diet (C) or a linseed-enriched diet (L) with ratios of 18:2n-6:18:3n-3 of 10 and 2, respectively (Enser et al., 2000).

	Total fatty acids		Phospholipid	
Item	C	L	C	L
18:2n-6	17.5[b]	14.1[a]	30.2[b]	27.0[a]
20:4n-6	4.1[b]	3.1[a]	9.7[b]	8.1[a]
18:3n-3	0.8[a]	1.3[b]	0.9[a]	1.8[b]
20:5n-3	0.42[a]	0.73[b]	1.0[a]	2.0[b]
22:5n-3	0.95[a]	1.06[a]	2.0[a]	2.5[b]
22:6n-3	0.43[a]	0.47[a]	1.0[a]	1.2[b]
18:2n-6/ 18:3n-3	20.5[b]	10.5[a]	33.3[b]	14.8[a]

[a,b]Means within a lipid class with different superscripts are significantly different ($P < 0.05$).

Table 5. Fatty acid composition of longissimus neutral lipid and phospholipid (%) in Aberdeen Angus cross steers fed a concentrate (C) or grass silage (GS) diet from 6 to 24 mo of age (Warren et al., 2008b).

	Neutral lipid		Phospholipid	
Item	C	GS	C	GS
18:2n-6	1.7b	0.6a	18.6b	5.9a
20:4n-6	ND	ND	10.4b	3.7a
18:3n-3	0.1a	0.4b	0.5a	3.3b
20:5n-3	ND	ND	0.5a	2.8b
22:5n-3	ND	ND	1.1a	4.0b
22:6n-3	ND	ND	0.07a	0.5b

[a,b]Means within a lipid class with different superscripts are significantly different ($P < 0.05$).

However, the concentration of 18:2n-6 and its proportion in neutral lipid and phospholipid reached much higher values than 18:3n-3 (Table 5). These results again show the preferential incorporation of 18:2n-6 into tissue lipids.

Effects of Fatty Acid Composition on Meat Quality

In pigs, the importance of fatty acid composition for the quality of adipose tissue has been recognized for many years. For example, Ellis and Isbell (1926) showed that backfat became soft and oily as the concentration of 18:2n-6 increased in pigs fed high levels of soybeans. This is due to the low melting point of PUFA relative to SFA and MUFA. Palm kernel oil with high concentrations of SFA produces firm fat with a high melting point. In pigs with different backfat thickness, Wood et al. (1986) showed that high concentrations of 18:2n-6 present in thin, undeveloped fat, coupled with low concentrations of SFA and MUFA, were responsible for the greater softness and lower cohesiveness of the fat (i.e., thin subcutaneous fat is less well attached to muscle and fat separation occurs). Thin fat is said to appear gray and floppy.

In muscle, fatty acid composition is a major factor in oxidative stability, the characteristic that limits the shelf life of meat. The double bonds of PUFA are susceptible to oxidation, which results in the production of lipid oxidation products having undesirable odors and flavors. These compounds can also accelerate the color change, which occurs as meat is displayed (i.e., it becomes less bright more quickly). An extreme example of the effect of muscle PUFA on lipid oxidation and eating quality was reported for lamb meat by Nute et al. (2007). Lambs were fed dietary supplements to increase levels of n-3 PUFA in muscle (e.g., fish oil, marine algae, and linseed protected from rumen breakdown). After slaughter, leg steaks were conditioned for 6 d then displayed in modified atmosphere packs (O_2:CO_2 75:25) under simulated retail display conditions. Lipid oxidation was measured by the thiobarbiturate reactive substances (TBARS) test at 7 d of display and increased to high levels in some treatments, well above the guideline figure of 0.5 mg of malondialdehyde/kg taken to indicate the likely detection of off-odors and flavors. The trained taste panel scored various abnormal odors and flavors in the grilled lamb (e.g., rancid and fishy) higher in the treatments producing high levels of long-chain PUFA. Sensory scores were strongly correlated with PUFA concentrations [e.g., fishy with EPA percentage (0.36)].

In cattle, the relatively high concentration of 18:3n-3 and its long-chain products resulting from grass and forage consumption might be expected to result in greater production of lipid oxidation products during processing and cooking and reduce eating quality. However, in our studies, 18:3n-3 has been found to be a positive contributor to sensory quality. In a study by Warren et al. (2008a), steers were fed a grain-based or a grass-silage-based diet from 6 to 14, 19, or 24 mo of age. At each age, values for n-6 PUFA percentages were high in muscle of the groups fed grain, and n-3 percentages were high in muscle of the groups fed grass silage (Table 5). Eating quality scores were similar in the 2 groups at all ages. Lipid oxidation measured by the TBARS test was higher in the concentrate-fed animals. This was explained by lower levels of vitamin E in muscle. Vitamin E is an effective tissue antioxidant, which limits fatty acid oxidation. It was pres-

Table 6. Effects of a standard control diet (C) or a linseed-enriched diet (L) and sex (male, M or female, F) on eating quality of grilled bacon (Sheard et al., 2000).

	Diet			Gender		
Item	C	L	Significance	M	F	Significance
Fat assessment						
Bacon odor	3.4	3.3	NS	3.1	3.6	NS
Abnormal odor	3.3	3.3	NS	3.5	3.1	**
Lean assessment						
Bacon flavor	3.9	3.9	NS	3.9	4.0	NS
Abnormal flavor	2.9	2.9	NS	3.0	2.7	**
Hedonic						
Flavor liking	3.7	3.8	NS	3.6	3.9	**

**$P < 0.1$.

ent at a low level in the concentrate diet (25 mg/kg), and levels in muscle were significantly lower than in the steers fed grass silage (approximately 1.5 mg/kg compared with 3.5 mg/kg). Vitamin E is present at high concentrations in leafy grass and was apparently incorporated into the muscle of the grass-fed group from the grass silage consumed. In subsequent research, we have seen very high values of vitamin E in muscles of grass-fed cattle reared on certain pastures.

In comparison with lamb and beef, levels of lipid oxidation seen in our studies on pigs have generally been low. Values for TBARS have usually been much lower than the threshold value of 0.5, even when diets high in PUFA have been fed to increase tissue levels. Other workers have generally found no adverse effects on pork flavor when 18:2n-6 concentrations are increased to high levels. Excessive oxidation and off-flavors have been reported after feeding fish oils at high levels and also linseed (flaxseed). With linseed, these occur at concentrations above about 3% 18:3n-3 in total lipid, which is higher than that required to reduce the n-6:n-3 PUFA ratio in pork to acceptable levels. In the study reported in Table 4, in which the concentration of 18:3n-3 in total lipid reached 1.3%, there was no adverse effect on sensory quality, even for sausages and bacon, which are less oxidatively stable products than fresh pork due to comminution and exposure to air, release of prooxidants such as iron, and (in the case of bacon) salt injection followed by freezing and thawing (Sheard et al., 2000). In this study, the taste panel detected differences in abnormal flavor between entire males and females but not between the control and linseed diets (Table 6). In a study by Kouba et al. (2003), a diet containing 60 g of whole crushed linseed/kg was fed for 60 d. At this time, values of 3% fatty acids were recorded in total lipid, neutral lipid, and phospholipid, compared with about 0.7% in controls. Muscle TBARS values in displayed pork were slightly higher in the linseed group and the taste panel gave higher scores for abnormal odor to griddled pork from these pigs, showing that 3% 18:3n-3 is around the upper limit in pork. Although vitamin E was included at a high level in both diets (150 mg/kg), the concentration in muscle was lower in the pigs fed linseed after 60 d (2.1 vs 2.9 μg/g), indicating utilization of the antioxidant as tissue n-3 PUFA levels increased. Usually muscle vitamin E is around 3.0 μg/g in pig longissimus, protecting PUFA and maintaining meat quality.

Acknowledgments

We thank the Department for Environment, Food and Rural Affairs (Defra), British Pig Executive (BPEX), and English Beef and Lamb Executive (EBLEX) for funding the research at Bristol described in this paper

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