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Review

Fat deposition, fatty acid composition and meat quality: A review

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Abstract

This paper reviews the factors affecting the fatty acid composition of adipose tissue and muscle in pigs, sheep and cattle and shows that a major factor is the total amount of fat. The effects of fatty acid composition on meat quality are also reviewed. Pigs have high levels of polyunsaturated fatty acids (PUFA), including the long chain (C20-22) PUFA in adipose tissue and muscle. The full range of PUFA are also found in sheep adipose tissue and muscle whereas cattle 'conserve' long chain PUFA in muscle phospholipid. Linoleic acid (18:2$n-6$) is a major ingredient of feeds for all species. Its incorporation into adipose tissue and muscle in relation to the amount in the diet is greater than for other fatty acids. It is deposited in muscle phospholipid at a high level where it and its long chain products eg aracidonic acid (20:4$n-6$) compete well for insertion into phospholipid molecules. Its proportion in pig adipose tissue declines as fat deposition proceeds and is an index of fatness. The same inverse relationships are not seen in ruminant adipose tissue but in all species the proportion of 18:2$n-6$ declines in muscle as fat deposition increases. The main reason is that phospholipid, where 18:2$n-6$ is located, declines as a proportion of muscle lipid and the proportion of neutral lipid, with its higher content of saturated and monounsaturated fatty acids, increases. Oleic acid (18:1*cis* -9), formed from stearic acid (18:0) by the enzyme stearoyl Co-A desaturase, is a major component of neutral lipid and in ruminants the same enzyme forms conjugated linoleic acid (CLA), an important nutrient in human nutrition. Like 18:2$n-6$, α-linolenic acid (18:3$n-3$) is an essential fatty acid and is important to ruminants since it is the major fatty acid in grass. However it does not compete well for insertion into phospholipid compared with 18:2$n-6$ and its incorporation into adipose tissue and muscle is less efficient. Greater biohydrogenation of 18:3$n-3$ and a long rumen transit time for forage diets also limits the amount available for tissue uptake compared with 18:2$n-6$ from concentrate diets. A positive feature of grass feeding is that levels of the nutritionally important long chain $n-3$ PUFA are increased ie EPA (20:5$n-3$) and DHA (22:6$n-3$). Future research should focus on increasing $n-3$ PUFA proportions in lean carcasses and the use of biodiverse pastures and conservation processes which retain the benefits of fresh leafy grass offer opportunities to achieve this. The varying fatty acid compositions of adipose tissue and muscle have profound effects on meat quality. Fatty acid composition determines the firmness/oiliness of adipose tissue and the oxidative stability of muscle, which in turn affects flavour and muscle colour. Vitamin E is an essential nutrient, which stabilises PUFA and has a central role in meat quality, particularly in ruminants.

Keywords: Fatty acids; Meat quality; Pigs; Sheep; Cattle; Diets; Genetics; Lipid oxidation; Flavour

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1. Introduction

In many countries, fat is an unpopular constituent of meat for consumers, being considered unhealthy. Yet fat and fatty acids, whether in adipose tissue or muscle, contribute importantly to various aspects of meat quality and are central to the nutritional value of meat. This review considers the factors controlling fat deposition and fatty acid composition in adipose tissue and muscle of pigs, sheep and cattle and the roles of fat in meat quality in these different species.

2. Fatty acid composition of adipose tissue and muscle in meat animals

The fatty acid composition and total fatty acid content of subcutaneous adipose tissue and *longissimus* muscle from loin chops or steaks of pigs, sheep and cattle purchased at retail are shown in Table 1 (Enser, Hallett, Hewitt, Fursey, & Wood, 1996). The concentrations of total fatty acids in *longissimus* are higher than in other studies in which cores from the central part of the muscle, with no adhering subcutaneous or intermuscular adipose tissue, have been examined. The intention of the study of Enser et al. (1996) was to examine muscle and fat tissues as normally consumed, so only rough dissection was performed, as for someone separating muscle from fat on the dinner plate. Cores from the centre of *longissimus* typically contain 1% total lipid in pigs. The data show that adipose tissue has a much higher fatty acid content than muscle but the fatty acid composition of the two tissues is broadly similar. However, there are important species differences. Pigs have much higher proportions of the major polyunsaturated fatty acid (PUFA) linoleic acid (18:2$n-6$) in both tissues than cattle and sheep. In this study, the proportions were similar in the two tissues but most reports show higher proportions in pig adipose tissue than muscle (Teye et al., 2006a; Teye, Wood, Whittington, Stewart, & Sheard, 2006b). Linoleic acid is derived entirely from the diet. It passes through the pig's stomach unchanged and is then absorbed into the blood stream in the small intestine and incorporated from there into tissues. In ruminants, the fatty acid, which is at high levels in concentrate feedstuffs (grains and oilseeds), is degraded into monounsaturated and saturated fatty acids in the rumen by microbial biohydrogenation and only a small proportion, around 10% of dietary 18:2$n-6$, is available for incorporation into tissue lipids. In both sheep and cattle, the fatty acid is at higher levels in muscle than adipose tissue. The second most important PUFA is α-linolenic acid (18:3$n-3$), which is present in many concentrate feed ingredients but at lower levels than 18:2$n-6$. In pigs, the proportion is higher in adipose tissue than muscle. This is a major dietary fatty acid for ruminants since it constitutes over 50% of total fatty acids in grass and grass products. Again, a high proportion is biohydrogenated to saturated fatty acids in the rumen. In a review, Doreau and Ferlay (1994) found that a variable proportion of dietary 18:3$n-3$ is biohydrogenated (85–100%) but this is more than for 18:2$n-6$ (70–95%), so less is available for incorporation into tissues. As with 18:2$n-6$, proportions in ruminants are higher in muscle than adipose tissue.

Muscle contains significant proportions of long chain (C20-22) PUFAs which are formed from 18:2$n-6$ and 18:3$n-3$ by the action of Δ5 and Δ6 desaturase and elongase enzymes. Important products are arachidonic acid

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

	Adipose tissue			Muscle		
	Pigs	Sheep	Cattle	Pigs	Sheep	Cattle
14:0	1.6[a]	4.1[b]	3.7[b]	1.3[a]	3.3[c]	2.7[b]
16:0	23.9[b]	21.9[a]	26.1[c]	23.2[b]	22.2[a]	25.0[c]
16:1cis	2.4[a]	2.4[a]	6.2[b]	2.7[b]	2.2[a]	4.5[c]
18:0	12.8[a]	22.6[b]	12.2[a]	12.2[a]	18.1[c]	13.4[b]
18:1*cis* − 9	35.8[b]	28.7[a]	35.3[b]	32.8[a]	32.5[a]	36.1[b]
18:2$n-6$	14.3[b]	1.3[a]	1.1[a]	14.2[b]	2.7[a]	2.4[a]
18:3$n-3$	1.4[c]	1.0[b]	0.5[a]	0.95[b]	1.37[c]	0.70[a]
20:4$n-6$	0.2	ND	ND	2.21[b]	0.64[a]	0.63[a]
20:5$n-3$	ND	ND	ND	0.31[b]	0.45[c]	0.28[a]
$n-6$:$n-3$	7.6	1.4	2.3	7.2	1.3	2.1
P:S	0.61	0.09	0.05	0.58	0.15	0.11
Total	65.3	70.6	70.0	2.2	4.9	3.8

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

Table 2
Fatty acid composition (g/100 g fatty acids) of subcutaneous adipose tissue and *longissimus* muscle in pigs fed a control diet (Kouba et al., 2003 60 day feeding period) and Soay sheep fed a control diet (Wachira et al., 2002)

	Adipose tissue		Muscle	
	Pigs	Sheep	Pigs	Sheep
18:2$n-6$	13.20	2.03	9.69	5.60
18:3$n-3$	1.47	1.09	0.65	1.73

(20:4$n-6$) and eicosapentaenoic acid (EPA, 20:5$n-3$) which have various metabolic roles including eicosanoid production. Greater incorporation of 18:2$n-6$ into pig muscle fatty acids compared with ruminants produces higher levels of 20:4$n-6$ by synthesis and the net result is a higher ratio of $n-6$:$n-3$ PUFA compared with the ruminants (Table 1). Nutritional advice is for ratios <4.0 (Scollan et al., 2006a) so pig muscle is unbalanced relative to that of the ruminants. On the other hand, the ratio of all PUFA to saturated fatty acids (P:S), the target for which is 0.4 or above, is much higher, beneficially so, in pigs and other monogastrics compared with the ruminants.

Results in Table 2 (Kouba, Enser, Whittington, Nute, & Wood, 2003; Wachira et al., 2002) confirm those in other studies showing that ruminants have higher proportions of the two main PUFAs in muscle than adipose tissue whereas the opposite is true for pigs.

3. Fatty acid composition of triacylglycerol (neutral lipid) and phospholipid

The major lipid class in adipose tissue (>90%) is triacylglycerol or neutral lipid. In muscle, a significant proportion is phospholipid, which has a much higher PUFA content in order to perform its function as a constituent of cellular membranes. Values for the fatty acid composition of *longissimus* muscle neutral lipid and phospholipid from studies on pigs, sheep and cattle conducted with collaborators at Bristol are shown in Table 3 (Wood et al., 2004; Demirel et al., 2004; Warren et al., in press-a). The three studies are not directly comparable because different diets were fed but the trends within each species are typical. In all three species, oleic acid (18:1*cis* − 9), the major fatty acid in meat, was much more predominant in neutral lipid. This fatty acid is formed from stearic acid (18:0) by the enzyme stearoyl Co-A desaturase, a major lipogenic enzyme. On the other hand, 18:2$n-6$ was at much higher proportions in phospholipid than neutral lipid. The proportion of 18:3$n-3$ was slightly higher in neutral lipid than phospholipid in pigs but in sheep and cattle the proportions were higher in phospholipid. The differences between sheep and cattle for 18:2$n-6$, 18:3$n-3$ and the long chain $n-6$ and $n-3$ PUFA in Table 3 are partly due to the different concentrate diets fed. In the work with sheep, dried grass (high in 18:3$n-3$) formed 75% of the concentrate whereas in the cattle study the concentrate contained a high proportion of full fat soyabean meal, high in 18:2$n-6$. Nevertheless, we have often seen higher values for individual phospholipid PUFAs in sheep compared with cattle.

Table 3
Fatty acid composition (%) of *longissimus* muscle triacylglycerol (neutral lipid) and phospholipid in pigs (Wood et al., 2004, Durocs), sheep (Demirel et al., 2004, megalac diet) and cattle (Warren et al., in press-a, Aberdeen Angus 14 months) fed concentrate-type diets

	Neutral lipid			Phospholipid		
	Pigs	Sheep	Cattle	Pigs	Sheep	Cattle
14:0	1.6	3.0	2.7	0.3	0.4	0.2
16:0	23.8	25.6	27.4	16.6	15.0	14.6
16:1cis	2.6	2.2	3.5	0.8	1.5	0.8
18:0	15.6	13.6	15.5	12.1	10.4	11.0
18:1*cis* − 9	36.2	43.8	35.2	9.4	22.1	15.8
18:2$n-6$	12.0	1.5	2.3	31.4	12.4	22.0
18:3$n-3$	1.0	1.2	0.3	0.6	4.6	0.7
20:4$n-6$	0.2	ND	ND	10.5	5.9	10.0
20:5$n-3$	ND	ND	ND	1.0	4.1	0.8

Long chain $n-3$ and $n-6$ PUFA are mainly found in phospholipid but are detected in pig and sheep muscle neutral lipid and adipose tissue (Enser, Richardson, Wood, Gill, & Sheard, 2000; Cooper et al., 2004). We have never seen these fatty acids in beef muscle neutral lipid or adipose tissue (Scollan et al., 2001; Warren et al., in press-a), confirming other studies showing 'conservation' of essential fatty acids in cattle muscle where they are less likely to be used for energy production (Crawford, Hare, & Whitehouse, 1984).

The double bonds in unsaturated fatty acids are usually of the cis type, i.e. the hydrogen atoms attached to the carbon atoms in the fatty acid chain point in the same direction. In ruminants, as a result of biohydrogenation in the rumen, a significant proportion of double bonds are of the trans type, i.e. the hydrogen atoms point in different directions. These fatty acids have particularly low melting points as a result of this structure. A major trans fatty acid is 18:1 trans vaccenic which is a biohydrogenation product of 18:2$n-6$. This fatty acid is converted to conjugated linoleic acid (CLA, 18:2*cis* − 9, *trans* − 11) in adipose tissue by the action of stearoyl Co-A desaturase, the same enzyme responsible for the production of 18:1*cis* − 9 from 18:0. Like 18:1*cis* − 9, both 18:1 trans vaccenic and CLA are at higher proportions in neutral lipid than phospholipid and higher in adipose tissue than muscle. CLA is also produced in the rumen but synthesis from 18:1 trans vaccenic in tissues is quantitatively the most important contributor to tissue levels (Scollan et al., 2006a). CLA has health benefits in the human diet although meat from ruminants makes only a small contribution towards nutritionally significant levels.

4. Effects of fat content on fatty acid composition

4.1. Adipose tissue

As the fat content of the animal and meat increases between early life and the time of slaughter, the propor-

tions of fatty acids change. In pig subcutaneous adipose tissue, Wood (1984) showed that the C18 fatty acids 18:0 and 18:1*cis* − 9 increased in proportion and 18:2*n* − 6 declined during this period. This was ascribed to an increasing role for *de novo* tissue synthesis of saturated and monounsaturated fatty acids and a relatively declining role for the direct incorporation of 18:2*n* − 6 from the diet. A similar result was found by Kouba et al. (2003). Pigs were fed a control diet from 40 kg live weight for 20, 60 or 100 days. During this time, the proportion of 18:0 increased from 10% to 13%, 18:1*cis* − 9 increased from 38% to 42% and the proportion of 18:2*n* − 6 fell from 19% to 11% of total fatty acids.

The inverse relationship between the proportion of 18:2*n* − 6 in subcutaneous adipose tissue and the amount of fat or an index of it such as backfat thickness has been observed in several studies in pigs. Wood et al. (1978) observed correlations of about 0.3 between the proportion of 18:2*n* − 6 in the inner layer of subcutaneous adipose tissue and loin fat thickness in Large White pigs from a line selected for fast growth and low fat thickness and a control line. The values for 18:2*n* − 6 were 9.3% in the control line and 10.7% in the selection line. Similarly, in 300 pigs with 8 mm, 12 mm and 16 mm P_2 backfat thickness, average values for 18:2*n* − 6 in subcutaneous adipose tissue fell from 14.9% to 12.4% to 10.6% (Wood, Enser, Whittington, Moncrieff, & Kempster, 1989) (Table 4). This study also compared entire male and female pigs. Proportions of PUFA tend to be high in subcutaneous adipose tissue from entire males and this study showed this was mainly due to their thinner backfat. However, even at the same backfat thickness, there was a higher proportion of 18:2*n* − 6 and a lower proportion of 18:1*cis* − 9 in subcutaneous adipose tissue from entires as the results in Fig. 1 show. At the same fat thickness as females, subcutaneous adipose tissue from entires contained a higher proportion of water and a lower proportion of lipid, signifying a less mature tissue. These results help explain why fat quality tends to be lower in entire male pigs than castrates and females.

The changes in adipose tissue fatty acid composition with age and fatness are different between pigs and cattle. Leat (1975) examined fatty acid composition in subcutaneous fat of Jersey cattle of different sexes using biopsies at different ages. Both 16:0 and 18:0 fell in proportion as age increased from 3 to 30 months, whereas 18:1*cis* − 9 increased, similar to the observation in pigs. In a comparison of extremes, Wood (1984) found proportions of 14.7% and 2.7% for 18:0 and 41.5% and 56.4% for 18:1*cis* − 9 in a young heifer and an old fat steer respectively. We have recently observed an increase in the proportion of 18:1*cis* − 9 in subcutaneous adipose tissue of Aberdeen Angus crossbred steers fed a concentrate diet between 14 and 24 months of age (Table 5). Carcass fat greatly increased during the period as shown by the carcass fat score (values are approximately the percentage of subcutaneous fat in the carcass ×10). The proportion of 18:0 fell during the same period (as in the study of Leat) and this allowed the proportion of 18:2*n* − 6 to remain constant (Table 5). This study also showed that the proportion of CLA increased with fatness, as did that of 18:1 trans vaccenic acid.

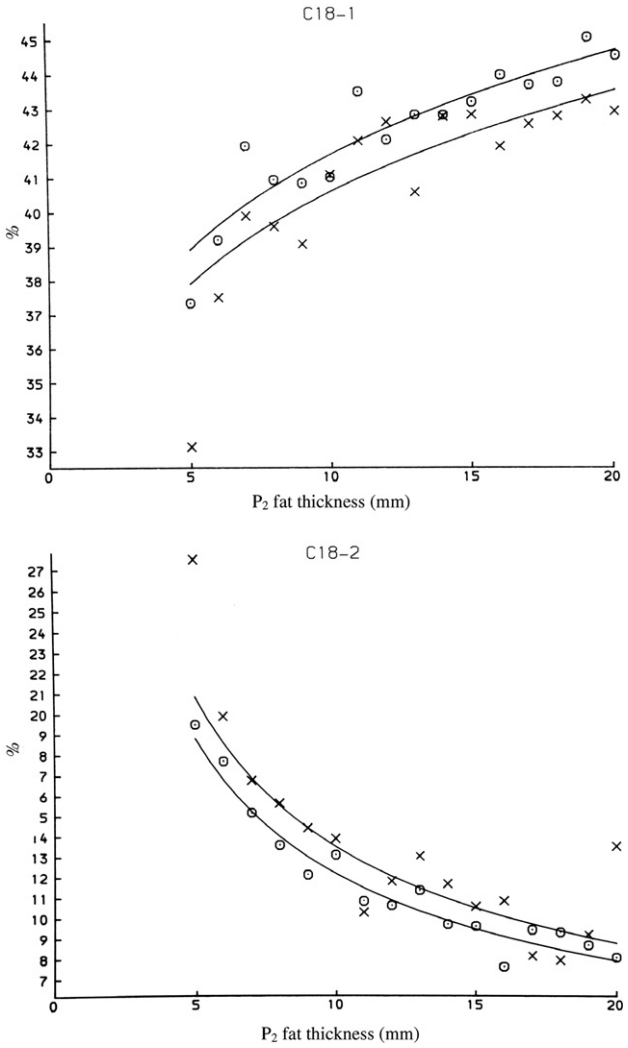

Fig. 1. Proportions (g/100 g fatty acids) of 18:1*cis* − 9 and 18:2*n* − 6 in subcutaneous adipose tissue lipid of pigs plotted against P_2 fat thickness (x–x entire males; o–o females) (Wood et al., 1989).

Table 4
Water and lipid content and fatty acid composition of subcutaneous adipose tissue from the loin (both layers combined) in 300 entire male and female pigs with different backfat thickness (Wood et al., 1989)

	P_2 fat thickness (mm)			
	8	12	16	
Water[a]	22.4	17.1	14.1	***
Lipid[a]	69.2	77.0	81.6	***
18:0[b]	13.1	13.8	13.9	***
18:1*cis* − 9[b]	40.3	41.8	43.1	***
18:2*n* − 6[b]	14.9	12.4	10.6	***
18:3*n* − 3[b]	1.1	0.9	0.8	***

[a] g/100 g fresh adipose tissue.
[b] g/100 g total fatty acids.

Table 5
Changes in proportions of some adipose tissue fatty acids between 14 and 24 months of age in Aberdeen Angus cross steers fed a concentrate diet (Whittington, unpublished)

	Age (months)	
	14	24
Carcass fat score	55	86
18:0	17.7	10.9
18:1*cis* − 9	28.6	35.2
18:2*n* − 6	1.8	1.9
CLA	0.71	1.17

4.2. Muscle

Early work on meat fatty acid composition concentrated on adipose tissue, since that is where the bulk of the body's fatty acids are located. Recently, there has been more emphasis on muscle because of its greater significance as food and an increasing aversion to visible fat at retail. Muscle also contains higher concentrations of the long chain *n* − 6 and *n* − 3 fatty acids, the importance of which in human nutrition has been recognised relatively recently. Separation and identification procedures for low levels of unsaturated fatty acids in muscle have also greatly improved in recent years.

The overall fat content of the animal and muscle have an important impact on proportionate fatty acid composition because of the different fatty acid compositions of neutral lipid and phospholipid (Table 3). Phospholipid is an essential component of cell membranes and its amount remains fairly constant, or increases little, as the animal increases in fatness. In young lean animals, genetically lean animals or animals fed a low energy diet, the lower 18:1*cis* − 9 and higher 18:2*n* − 6 content of phospholipid has a major influence on total muscle fatty acid composition. But as body fat increases, neutral lipid predominates in overall fatty acid composition. Results from the study of Kouba et al. (2003) of pigs fed a control diet from 40 kg live weight for 20, 60 or 100 days are shown in Table 6. Phospholipid declined from 46% of total lipid at 20 days to 28% at 100 days. This was associated with an increase in the proportion of 18:1*cis* − 9 and a decrease in the proportion of 18:2*n* − 6.

Warren et al. (in press-a) examined the fatty acid content and composition of neutral lipid and phospholipid in cattle of three ages, 14, 19 and 24 months. There were two breeds, Aberdeen Angus cross and Holstein–Friesian, and two diets, concentrate and grass silage, fed from 6 months of age. A plot of the concentrations of total neutral lipid and phospholipid fatty acids in muscle in relation to total lipid fatty acids for all 96 steers in the trial is in Fig. 2. This illustrates the increasing importance of neutral lipid in total lipid as fattening proceeds and the fairly constant level of phospholipid. Results for Aberdeen Angus steers fed the concentrate diet are in Table 7. The proportion of phospholipid in total lipid fell from 30% at 14 months to 12% at 24 months and this was accompanied by an increase in the proportion of 18:1*cis* − 9 and a decrease in the proportion of 18:2*n* − 6 in total lipid. Data were statistically analysed within age group in this trial so age groups themselves were not directly compared.

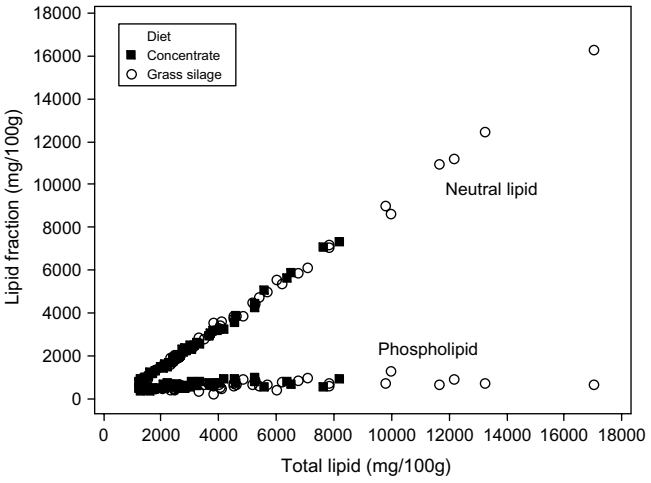

Fig. 2. Concentrations of neutral lipid and phospholipid (mg/100 g muscle) plotted against total lipid (mg/100 g muscle) in *longissimus* muscle of steers given a concentrate or grass silage diet and slaughtered at 14, 19 or 24 months of age (Warren et al., in press-a).

Table 6
Composition of carcass, *longissimus* muscle and muscle total fatty acids in pigs fed a control diet from 40 kg live weight for 20, 60 or 100 days (Kouba et al., 2003)

	Days of feeding			
	20	60	100	
Subcutaneous fat[a]	11	19	25	***
Phospholipid[b]	0.45	0.45	0.36	*
Neutral lipid[b]	0.53	0.80	0.92	***
Total lipid[b]	0.98	1.25	1.28	***
18:1*cis* − 9[c]	37.5	42.7	43.6	***
18:2*n* − 6[c]	14.7	9.7	8.0	***

[a] g/100 g carcass.
[b] g/100 g muscle.
[c] g/100 g total fatty acids.

Table 7
Composition of carcass, *longissimus* muscle and muscle total fatty acids in Aberdeen Angus cross steers fed a concentrate diet (Warren et al., in press-a)

	Months of age		
	14	19	24
Carcass fat score[a]	55	70	86
Phospholipid[b]	0.55	0.68	0.67
Neutral lipid[b]	1.28	2.45	4.80
Total lipid[b]	1.82	3.13	5.48
18:1*cis* − 9[c]	29.6	31.5	35.9
18:2*n* − 6[c]	8.1	6.7	3.8

[a] Visual score, range 20–145.
[b] g/100 g muscle.
[c] g/100 g total fatty acids.

However, comparison with other results in the trial suggests that the age effects on neutral lipid, total lipid and fatty acid proportions were statistically significant. The trends in Table 7 are similar to those in the pig study in Table 6. In both studies, there was an increase in the proportion of 18:1*cis* − 9 and a decrease in the proportion of 18:2*n* − 6 in neutral lipid during the periods under investigation, evidence of the increasingly important role of stearoyl Co-A desaturase and the declining importance of dietary fat as a source of muscle fatty acids as fat deposition accelerates, in muscle triacylglycerol as in adipose tissue.

5. Genetic effects on fatty acid composition

Breeds or genetic types with a low concentration of total lipid in muscle, in which phospholipid is a high proportion of the total, will have higher proportions of PUFA in total lipid, for the reasons given in Section 4. This was illustrated in sheep by Fisher et al. (2000) (Table 8). Welsh Mountain and Soay sheep were reared on grass diets and slaughtered at the same body weight. Soays had much leaner carcasses and less lipid in muscle. They had lower proportions of 18:1*cis* − 9 and higher proportions of all PUFA in *semimembranosus* muscle.

Raes, De Smet, and Demeyer (2001) have shown that the double muscling genotype (mh/mh) within the Belgian Blue Breed has low proportions of 18:1 *cis* − 9 and high proportions of 18:2*n* − 6 in muscle lipid compared with the normal genotype (+/+). This is due to a low concentration of total lipid in muscle and a higher ratio of phospholipid to total lipid. Average values for the total lipid content of five muscles in young bulls were 0.9 g/100 g and 2.6 g/100 g in mh/mh and +/+ respectively. The proportions of 18:1*cis* − 9 were 23.1 and 37.8 and the proportions of 18:2*n* − 6 were 16.3 and 6.5 in mh/mh and +/+ respectively. The mh/mh animals had a P:S ratio of 0.55, above the minimum recommended for the diet as a whole and much higher than reported elsewhere for beef (Table 1). This study, in common with others, showed only small differences between muscles in fatty acid composition.

Table 8
Fat content and fatty acid composition of total lipid in *semimembranosus* muscle of Welsh Mountain and Soay sheep fed grass diets (Fisher et al., 2000)

	Welsh Mountain	Soay	
Carcass fat[a]	12.8	6.8	***
Total lipid[b]	2.51	1.67	***
18:1*cis* − 9[c]	33.8	28.0	***
18:2*n* − 6[c]	4.4	12.9	***
20:4*n* − 6[c]	1.9	4.0	***
18:3*n* − 3[c]	1.6	3.3	***
20:5*n* − 3[c]	1.0	1.8	***

[a] g/100 g carcass.
[b] g/100 g muscle.
[c] g/100 g total fatty acids.

Table 9
Composition of carcass, *longissimus* muscle and muscle neutral lipid and phospholipid in Aberdeen Angus cross (AA) and Holstein–Friesian (HF) steers fed a concentrate diet and slaughtered at 14 or 24 months of age (Warren et al., in press-a)

	AA		HF	
	14	24	14	24
Carcass fat score[a]	55	86	24	42
Phospholipid[b]	0.55	0.67	0.49	0.70
18:1*cis* − 9[c]	15.8	19.4	12.9	15.8
18:2*n* − 6[c]	22.0	23.8	18.6	21.7
Neutral lipid[b]	1.28	4.80	1.10	3.35
18:1*cis* − 9[c]	35.2	38.2	35.3	37.9
18:2*n* − 6[c]	2.30	1.71	2.85	2.38

[a] Visual score, range 20–145.
[b] g/100 g muscle.
[c] g/100 g neutral lipid or phospholipid fatty acids.

In the study by Warren et al. (in press-a) of beef fatty acid composition involving two diets and slaughter at three ages (Table 7), Aberdeen Angus cross and Holstein–Friesian breeds were compared. Results for proportions of 18:1*cis* − 9 and 18:2*n* − 6 in phospholipid and neutral lipid in the 14 and 24 month groups fed concentrate are in Table 9. Aberdeen Angus had much fatter carcasses than Holstein–Friesian, but amounts of neutral lipid and phospholipid in *longissimus* muscle were not very different and consequently proportions of 18:1*cis* − 9 and 18:2*n* − 6 in both lipid fractions were also quite similar. Bigger differences would have been expected if muscle lipid concentration had mirrored subcutaneous fat. These results show that the dairy breed Holstein–Friesian had a higher ratio of muscle lipid to carcass fat than the beef breed Aberdeen Angus. This is consistent with other work showing differences in the partitioning of body fat between dairy and beef breeds, with dairy breeds having more "internal" and less "external" (subcutaneous) fat (Truscott, Wood, & MacFie, 1983).

The Duroc pig breed is notable in having a high muscle lipid (marbling fat) content relative to subcutaneous fat compared with other breeds. Wood et al. (2004) examined purebred Berkshire, Duroc, Large White and Tamworth breeds fed for 12 weeks on a standard concentrate diet. The two traditional breeds (Berkshire and Tamworth) grew slowly and were lighter and fatter than the two modern breeds at slaughter (Table 11). The amount of phospholipid in *longissimus* was similar between the breeds but the amounts of neutral lipid and total lipid were higher in Berkshire and Duroc than in Large White and Tamworth. Durocs had the highest ratio of muscle lipid to subcutaneous fat thickness. The proportion of phospholipid in total lipid was 18.8, 23.8, 38.9 and 31.7 in Berkshire, Duroc, Large White and Tamworth, respectively. Values for the proportions of 18:1*cis* − 9 and 18:2*n* − 6 in total lipid were as expected based on these figures except for Duroc, the proportion of 18:1*cis* − 9 being lower and the proportion of 18:2*n* − 6 being higher than expected. A

Table 10
Proportions of $n-3$ PUFA (g/100 g fatty acids) in *longissimus* phospholipid of Aberdeen Angus cross (AA) and Holstein–Friesian (HF) steers fed grass silage and slaughtered at 14 or 24 months of age (Warren et al., in press-a)

	AA		HF	
	14	24	14	24
18:3$n-3$	3.70	3.30	3.60	4.00
20:5$n-3$	3.37	2.77	3.42	4.15
22:5$n-3$	4.60	4.00	4.50	4.40
22:6$n-3$	0.85	0.47	1.00	1.02
DHA/18:3	0.23	0.14	0.28	0.25

possible explanation for these results is the slightly higher proportion of phospholipid in Duroc *longissimus* muscle (Table 11) associated with their 'redder' muscle fibre type profile compared with the other breeds reported in a companion paper by Chang et al. (2003). Their fatty acid profile would be expected to be closer to *psoas* than *longissimus*, with higher 18:2$n-6$ and lower 18:1*cis* -9 proportions.

Analysis of long chain $n-3$ PUFA proportions in the steers fed grass silage in the study of Warren et al. (in press-a) and referred to in Tables 7 and 9, suggested that Holstein–Friesians formed more docosahexaenoic acid (DHA, 22:6$n-3$) than Aberdeen Angus from its precursor 18:3$n-3$ in phospholipid. Values for these phospholipid fatty acids and the index DHA/18:3$n-3$ for the 14 and 24 month silage-fed groups are in Table 10. Most fatty acid proportions were significantly different between the breeds at 24 months ($P<0.05$) but not at 14 months. The DHA/18:3$n-3$ ratio was significantly different between the breeds at both ages ($P<0.05$). These results suggest that Holstein–Friesians have a greater activity or a greater expression of Δ5 and Δ6 desaturase enzymes. Evidence that the double muscled (mh/mh) Belgian Blue genotype converts a higher proportion of 18:3$n-3$ to 20:5$n-3$ and 22:5$n-3$ but not 22:6$n-3$ was presented by Raes et al. (2001).

6. Diet effects on fatty acid composition

6.1. Pigs

The pig, being a monogastric species, is amenable to changes in the fatty acid composition of adipose tissue and muscle using diets containing different oils. Spectacular results can be achieved using diets with high levels of 18:2$n-6$, which is a common fatty acid in grains and oilseeds. In general, the proportion of this fatty acid in tissues increases linearly as the dietary intake increases (Wood, 1984). In early studies of Ellis and Isbell (1926) the proportion of 18:2$n-6$ in subcutaneous adipose tissue increased from 1.9% on a low fat diet to over 30% on diets containing a high level of soyabeans.

Other dietary lipid sources containing particular fatty acids can be used to influence meat fatty acid composition.

Table 11
Neutral lipid, phospholipid and total lipid content of *longissimus* muscle and fatty acid composition of total lipid in four pig breeds (Wood et al., 2004)

	Berkshire	Duroc	Large white	Tamworth
P_2 fat thickness (mm)	15[b]	9[a]	8[a]	15[b]
Phospholipid[d]	0.39	0.42[a]	0.38[a]	0.38[a]
Neutral lipid[d]	1.67[b]	1.35[b]	0.60[a]	0.82[a]
Total lipid[d]	2.05[b]	1.77[b]	0.97[a]	1.20[a]
18:1*cis* -9[e]	33.5[c]	29.8[b]	27.9[a]	29.4[b]
18:2$n-6$[e]	11.8[a]	16.6[b]	19.4[c]	15.9[b]

[a–c] Within a row, means with different superscripts are significantly different ($P<0.05$).
[d] g/100 g muscle.
[e] g/100 g total fatty acids.

Teye et al. (2006a, 2006b) fed concentrate diets containing 2.8% added oil coming from palm kernel oil high in lauric acid (12:0), myristic acid (14:0) and 18:0; palm oil high in palmitic (16:0) and palmitoleic (16:1) acids; and soyabean oil high in 18:2$n-6$. The greatest dietary impact in adipose tissue and muscle was on proportions of 12:0, 14:0 (these had very low proportions) and 18:2$n-6$, with the C16 and C18 saturated and monounsaturated fatty acids hardly affected by dietary concentrations. These results are explained by the fact that 12:0 and 14:0 are mainly derived from the diet and 18:2$n-6$ is entirely derived from the diet. Conversely, the C16 and C18 saturated and monounsaturated fatty acids are mainly the products of synthesis in the animal and interconversions between them limit the impact of dietary additions. The clearest effect was that of soyabean oil on 18:2$n-6$ in adipose tissue. Proportions in muscle were lower than in adipose tissue and the dietary effect was smaller.

Several studies have examined the effect of 18:3$n-3$ in linseed/flaxseed on its concentration in pork. The motivation for this research is the high $n-6$:$n-3$ fatty acid ratio in pork and the need to reduce this for human nutritional reasons. An example is the work of Enser et al. (2000). Two diets were fed, differing in the ratio of 18:2$n-6$:18:3$n-3$, to 80 entire male and female pigs between 25 kg and 95 kg live weight,. The aim was to favour deposition of 18:3$n-3$ and its long chain products in triacylglycerol and phospholipid. The $n-6$ and $n-3$ PUFA compete for access to desaturase enzymes and for incorporation into lipids. A control diet contained 1.5 g 18:3$n-3$ and 16 g 18:2$n-6$ kg^{-1} and a linseed-rich diet contained 4.5 g 18:3$n-3$ and 10 g 18:2$n-6$ kg^{-1}. This gave 18:2$n-6$:18:3$n-3$ ratios of 11.0 and 2.0 respectively. The results (Table 12) show that the linseed diet increased the deposition of 18:3$n-3$ in adipose tissue and muscle, particularly muscle phospholipid. Conversion of this extra 18:3$n-3$ into the C20-22$n-3$ PUFA 20:5$n-3$, docosapentaenoic (DPA, 22:5$n-3$) and 22:6$n-3$ occurred and these were deposited in muscle phospholipid but not in muscle neutral lipid (results not shown). Only 20:5$n-3$ of the long chain $n-3$ PUFA was significantly higher in muscle total lipid

Table 12
Fatty acid composition of adipose tissue, *longissimus* muscle total lipid and muscle phospholipid (%) in female pigs given a control or linseed-rich diet (Enser et al., 2000)

	Adipose tissue		Muscle		Phospholipid	
	C	L	C	L	C	L
18:*cis* − 9	33.3[a]	34.6[a]	29.6[a]	32.2[a]	12.1[a]	13.6[b]
18:2*n* − 6	18.4[b]	13.8[a]	17.5[b]	14.1[a]	30.2[b]	27.0[a]
20:4*n* − 6	0.23[b]	0.16[a]	4.1[b]	3.1[a]	9.7[b]	8.1[a]
18:3*n* − 3	1.74[a]	2.43[b]	0.84[a]	1.32[b]	0.9[a]	1.84[b]
20:5*n* − 3	0.05[a]	0.05[a]	0.42[a]	0.73[b]	1.0[a]	2.0[b]
22:5*n* − 3	0.19[a]	0.24[b]	0.95[a]	1.06[a]	2.0[a]	2.5[b]
22:6*n* − 3	0.08[a]	0.12[b]	0.43[a]	0.47[a]	1.0[a]	1.2[b]
18:2*n* − 6:18:3*n* − 3	10.5[b]	5.7[a]	20.5[b]	10.5[a]	33.3[b]	14.8[a]

Within tissue/lipid class category and within a row, means with different superscripts are significantly different ($P < 0.05$).

of pigs fed the linseed diet. However, there was evidence of extra long chain $n-3$ PUFA deposition (except for 20:5$n-3$) in adipose tissue, albeit the levels of these fatty acids were very low.

Nguyen, Nuijens, Everts, Salden, and Beynen (2003) studied the uptake of dietary $n-6$ and $n-3$ PUFA into pig adipose tissue and muscle in their own and in published work and concluded that the efficiency of uptake, defined as the slope of the line relating tissue level to dietary intake, was greater for 18:2$n-6$ than 18:3$n-3$ in both adipose tissue and muscle. They found that in the case of 18:2$n-6$, the slope was higher for adipose tissue than muscle but for 18:3$n-3$, efficiency of uptake into the two tissues was similar. The results of Enser et al. (2000) are consistent with these conclusions.

The study of Kouba et al. (2003) showed that incorporation of 18:3$n-3$ from a 6% crushed linseed diet into muscle neutral lipid and phospholipid reached a maximum in terms of proportions after 60 days of feeding. However, 91% and 87% of the effect had occurred in neutral lipid and phospholipid respectively at 20 days. For 20:5$n-3$ incorporation into neutral lipid and phospholipid, the maximum proportions were also reached at 60 days, with 85% and 71% of the effect having occurred at 20 days in neutral lipid and phospholipids respectively. These results confirm the rapid uptake of $n-3$ PUFA into pork found by Warnants, Van Oeckel, and Boucque (1999) and show that incorporation of chain elongation products is more rapid in neutral lipid than phospholipid.

In a recent study, Teye et al. (2006a) used low protein diets (18% versus 20% crude protein) with the same energy content to increase the concentration of total lipid in *longissimus* muscle. Low protein limits muscle deposition and the energy which would have been used for muscle synthesis is diverted to fat synthesis. In the later stages of growth, intramuscular fat is particularly affected. This strategy increased total lipid from 1.7% to 2.8% and had a marked effect on the proportion of 18:1*cis* − 9 which increased from 32.1% to 39.0% of total muscle lipid. Proportions of all $n-6$ and $n-3$ PUFA were reduced when this diet was fed. A companion paper by Doran et al. (2006) showed that low protein diets increased the expression of stearoyl Co-A desaturase in *longissimus* muscle and there was a linear relationship between the expression of stearoyl Co-A desaturase and the amount of 18:1*cis* − 9 in muscle. These data also show that *de novo* synthesis of fatty acids can dominate fatty acid profiles in some circumstances.

6.2. Cattle and sheep

Several studies have shown that dietary $n-6$ and $n-3$ PUFA can be incorporated into adipose tissue and muscle of ruminants despite the biohydrogenation of dietary fatty acids in the rumen. The study of Warren et al. (in press-a) of steers of two breeds fed a concentrate or grass silage diet from 6 months of age to 14, 19 and 24 months contrasts the incorporation of 18:2$n-6$ from a grain-based concentrate diet with 18:3$n-3$ from a grass silage diet. Results in Tables 5 and 7 show that 18:2$n-6$ in steers fed the concentrate diet was at higher proportions in muscle than adipose tissue at 14 and 24 months of age. The same was true for 18:3$n-3$ from the grass silage diet. For example, the proportions of 18:3$n-3$ in adipose tissue lipid and total muscle lipid at 14 months were 0.52 and 1.17 g/100 g respectively. At 24 months, the figures were 0.45 and 0.62 g/100 g respectively. These results show that ruminants preferentially incorporate essential fatty acids, with their important metabolic roles, into muscle rather than storing them in adipose tissue.

In the study of Warren et al. (in press-a), the proportion of 18:2$n-6$ in total muscle lipid varied from 1% to 12%. As total lipid increased, the proportion fell steeply (Fig. 3a) before plateauing at about 6 g/100 g total lipid. This curvilinear pattern was explained by the high proportion of 18:2$n-6$ in phospholipid and a declining

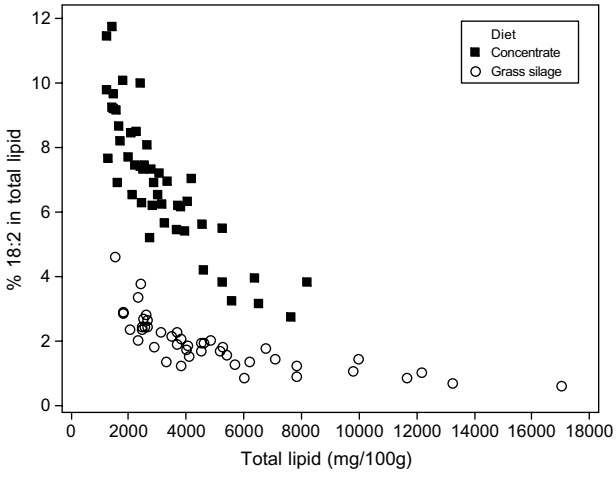

Fig. 3a. Proportion of 18:2$n-6$ in total lipid against total lipid (mg/100 g muscle) in *longissimus* muscle of steers given a concentrate or grass silage diet and slaughtered at 14, 19 or 24 months of age (Warren et al., in press-a).

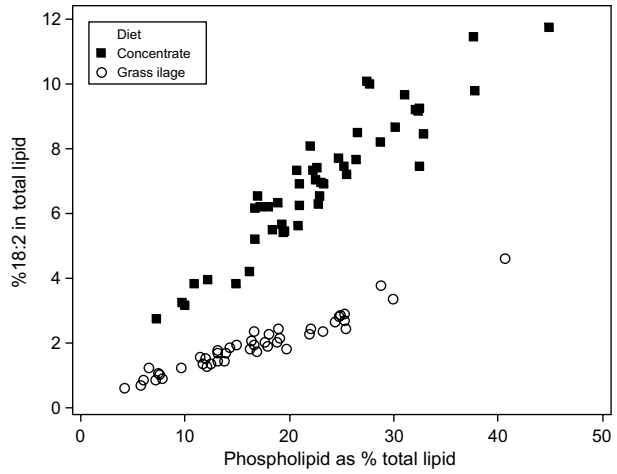

Fig. 3b. Proportion of 18:2$n-6$ in total lipid plotted against phospholipid expressed as a % of total lipid in *longissimus* muscle of steers given a concentrate or grass silage diet and slaughtered at 14, 19 or 24 months of age (Warren et al., in press-a).

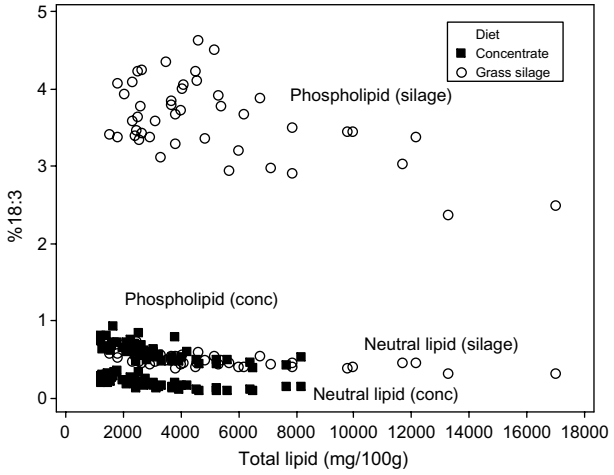

Fig. 4b. Proportions of 18:3$n-3$ in neutral lipid and phospholipid in *longissimus* muscle of steers given a concentrate or grass silage diet and slaughtered at 14, 19 or 24 months of age (Warren et al., in press-a).

proportion of phospholipid in total lipid as total lipid increased. Proportions of 18:2$n-6$ in muscle from steers given the two diets were closely related to the percentage of phospholipid in total lipid (Fig. 3b). The proportions of 18:2$n-6$ and 18:3$n-3$ in phospholipid and neutral lipid plotted against total muscle lipid for all steers fed the concentrate and grass silage diets are shown in Figs. 4a and 4b. These graphs emphasise the much greater incorporation of 18:2$n-6$ than 18:3$n-3$ into muscle lipids, especially phospholipid, and the declining proportions of these PUFA as muscle lipid increased. The content of phospholipid fatty acids remained fairly constant but neutral lipid, with its high proportions of saturated and monounsaturated fatty acids, increased markedly as total lipid increased (Fig. 2). These differences in tissue levels of the two essential fatty acids are the more surprising considering that intakes of the fatty acids were similar. For example in the 14 month groups, the approximate daily intakes were

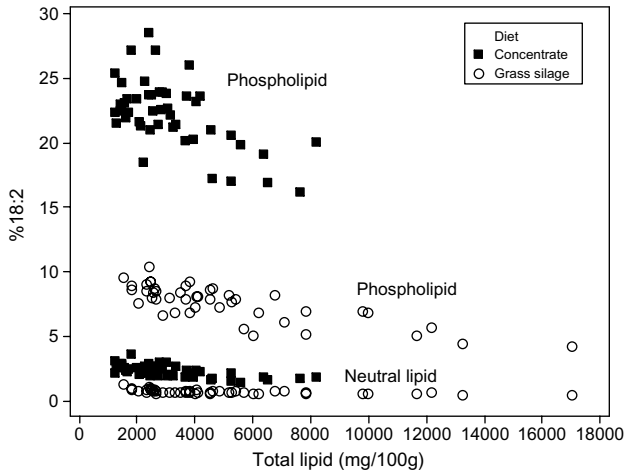

Fig. 4a. Proportions of 18:2$n-6$ in neutral lipid and phospholipid in *longissimus* muscle of steers given a concentrate or grass silage diet and slaughtered at 14, 19 or 24 months of age (Warren et al., in press-a).

74 g 18:2$n-6$ and 73.5 g 18:3$n-3$ from the concentrate and grass silage diets respectively.

Higher levels of 18:2$n-6$ than 18:3$n-3$ in tissues are not only due to a higher affinity for incorporation into phospholipid molecules as illustrated in Figs. 4a and 4b but also reduced biohydrogenation in the rumen. This occurs when the form of the diet is similar (Doreau & Ferlay, 1994) and particularly in typical 18:2$n-6$-rich concentrate diets. These have a small particle size and a shorter rumen transit time than fibrous forage diets, limiting the opportunities for microbial biohydrogenation. Our studies with sheep have mainly used concentrate-based diets and this may be one reason why concentrations and proportions of PUFA in muscle are higher than in the studies on beef which have mainly used diets containing 60% forage and 40% concentrate (Demirel et al., 2004; Scollan et al., 2001).

Incorporation of 18:2$n-6$ from the concentrate diet and 18:3$n-3$ from the grass silage diet into muscle in the study of Warren et al. (in press-a) led to synthesis of the long chain $n-6$ and $n-3$ PUFA in phospholipid. Results for the 14 month Aberdeen Angus steers are in Table 13. These data are concentrations in muscle

Table 13
Concentrations (mg/100 g muscle) of $n-6$ and $n-3$ PUFA in *longissimus* phospholipid of Aberdeen Angus steers fed concentrate or grass silage and slaughtered at 14 months of age (Warren et al., in press-a)

	Concentrate	Grass silage	
18:2$n-6$	119.0	46.6	***
20:3$n-6$	14.3	6.1	***
20:4$n-6$	54.2	33.2	***
22:4$n-6$	6.3	2.2	***
18:3$n-3$	4.0	20.6	***
20:4$n-3$	0.8	4.4	***
20:5$n-3$	4.8	18.6	***
22:5$n-3$	11.2	25.7	***
22:6$n-3$	1.2	4.7	***

(mg/100 g) rather than proportions in phospholipid. The concentrate diet produced relatively high levels of 18:2$n-6$ and all its long chain products and the grass silage diet produced high levels of 18:3$n-3$ and its long chain products, including 22:6$n-3$. Feeding linseed in previous research had not led to synthesis of 22:6$n-3$ (DHA) and a block on DHA synthesis or a failure to compete for incorporation has been noted in other studies (Scollan et al., 2001). It seems that grass feeding has a special ability to raise DHA levels.

In the 19 and 24 month age groups in the study of Warren et al. (in press-a), there was evidence of extra incorporation of 18:2$n-6$ and synthesis of 20:4$n-6$ in phospholipid beyond 14 months (Fig. 5a). However, the amounts of 18:3$n-3$ and its products remained constant, despite continued consumption of the grass silage diet. These results suggest that the capacity for incorporation of PUFA into phospholipid is limited and that 18:2$n-6$ competes for incorporation much more effectively than 18:3$n-3$. Evidence suggests that the $n-3$ PUFA are the preferred substrates for the Δ5 and Δ6 desaturase enzymes (Williams & Burdge, 2006) so limited access to the enzyme systems cannot explain low values for long chain $n-3$ PUFA.

In contrast to these results for phospholipid, extra incorporation of 18:2$n-6$ and 18:3$n-3$ into muscle triacylglycerol (neutral lipid) occurred beyond 14 months of age (Fig. 5b). The level and rate of incorporation was greater for 18:2$n-6$ than for 18:3$n-3$.

Levels of $n-3$ PUFA in ruminant tissues can be increased by feeding dietary lipid which is 'protected' from biohydrogenation in the rumen using formaldehyde treatment of linseed. In a study by Scollan, Enser, Gulati, Richardson, and Wood (2003), in which a protected lipid supplement comprised of soyabean, linseed and sunflower seeds was fed, the concentration of 18:3$n-3$ in muscle phospholipid increased from 12.7 to 16.0 mg/100 g, a small increase and no chain elongation and desaturation to long chain $n-3$ PUFA occurred. However, the supplement

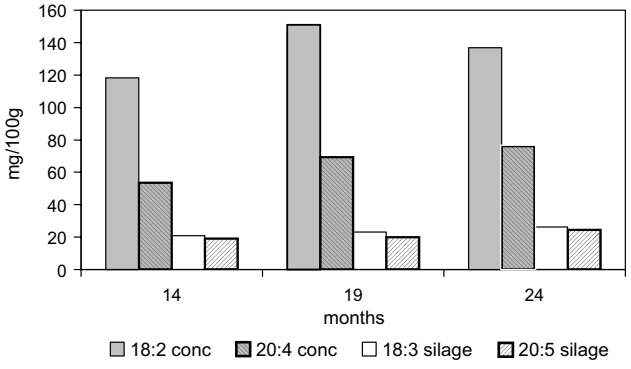

Fig. 5a. Amounts (mg/100 g muscle) of 18:2$n-6$ and 20:4$n-6$ in *longissimus* phospholipid of steers given concentrate and 18:3$n-3$ and 20:5$n-3$ in *longissimus* phospholipid of steers given grass silage (Warren et al., in press-a).

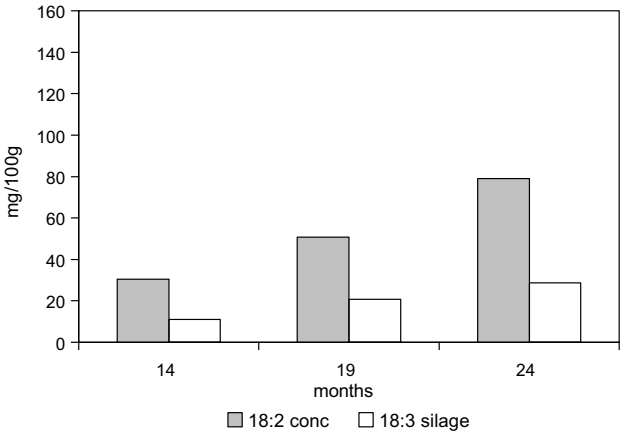

Fig. 5b. Amounts (mg/100 g muscle) of 18:2$n-6$ and 18:3$n-3$ in *longissimus* neutral lipid of steers given concentrate or grass silage respectively (Warren et al., in press-a).

doubled the concentration of 18:2$n-6$ in phospholipid and substantially increased the concentration of this fatty acid in neutral lipid compared with 18:3$n-3$. Because of the high incorporation of 18:2$n-6$, the P:S ratio in muscle was increased from 0.1 in controls to 0.4 in animals given a high level of the supplement. These results again demonstrate the higher efficiency of incorporation of 18:2$n-6$ into muscle compared with 18:3$n-3$. In Australian research, Cook, Scott, Faichney, and Davies (1972) observed that the proportion of 18:2$n-6$ increased to 35 g/100 g fatty acids in perirenal fat of steers given a protected sunflower supplement for 8 weeks. A value of 20 g/100 g was achieved after 2 weeks.

In the work of Warren et al. (in press-a), a group of steers was fed fresh grazed grass rather than grass silage between 14 and 19 months of age. The results in subcutaneous adipose tissue (Table 14) showed that the proportion of 18:3$n-3$ was slightly higher in the steers fed grazed grass. This group also had higher proportions of 18:1 trans vaccenic acid and CLA than those fed grass silage, showing that the process of rumen biohydrogenation is different between fresh and conserved grass. A similar result was found by French et al. (2000). The CLA values were similar in the groups fed grazed grass and concentrate in our work (Table 14).

Table 14
Fatty acid composition (g/100 g fatty acids) of subcutaneous adipose tissue of steers given concentrate, grass silage or fresh grazed grass between 14 and 19 months of age Whittington et al. (in preparation)

	Concentrate	Grass silage	Grazed grass	
18:0	14.00	10.09	15.20	***
18:1*cis* − 9	31.17	32.83	32.06	NS
18:1trans	4.07	1.48	4.32	***
CLA	0.95	0.43	0.93	***
18:2$n-6$	2.39	0.90	0.97	***
18:3$n-3$	0.22	0.59	0.68	***

Changes in grassland management, such as harvesting at different times of the grass growing season or allowing the grass to wilt before harvesting and conservation have an effect on fatty acid proportions in grasses and also in the meat of cattle and sheep (Wood et al., 2007). Different grasses and pasture plants also produce different concentrations of PUFA in meat due to higher levels of certain PUFA or because of differences in the way the feed is processed in the rumen. Scollan et al. (2006b) showed that the proportions of both 18:2$n-6$ and 18:3$n-3$ in muscle were significantly increased when steers were fed silage comprised of red clover rather than perennial ryegrass. Other research (Lee et al., 2004) suggests that the pattern of rumen fermentation and biohydrogenation for red clover is different from that of perennial ryegrass due to the inhibition of lipolysis in clover by the plant enzyme polyphenol oxidase.

7. Effects of fat and fatty acids on meat quality

7.1. Adipose tissue

Work with pigs and ruminants has shown that the fatty acid composition of adipose tissue affects its firmness, because the different fatty acids have different melting points. The composite fatty acids of meat melt between about 25 °C and 50 °C, with saturated fatty acids melting at higher and polyunsaturated fatty acids at lower temperatures e.g. 18:0 melts at 69 °C and 18:2$n-6$ at −5 °C (Wood, 1984).

In pigs, the differences in fatty acid composition of subcutaneous fat between carcasses of different P_2 fat thickness have an important effect on fat quality defined in terms of firmness and the degree of cohesiveness between lean and fat tissues (fat separation). In a study of carcasses with 8 mm, 12 mm and 16 mm P_2 fat thickness, the proportion of 18:0 increased and that of 18:2$n-6$ decreased as fat thickness increased (Table 4). The backfat of pigs with 16 mm P_2 was firmer and there was less separation between fat and underlying muscle than in backfat from the 8 mm P_2 group (Wood, Jones, Francombe, & Whelehan, 1986). Firmness, measured both objectively and subjectively in the shoulder and loin regions, was correlated with fatty acid proportions, the highest correlations being with 18:0 (positive) and 18:2$n-6$ (negative). The proportion of 18:2$n-6$ provided the best prediction of fat firmness (Table 15). In an earlier study of Large White pigs from two genetic selection lines, 18:0 and 18:2$n-6$ proportions were correlated with the melting point of extracted lipid from subcutaneous fat and in this case the proportion of 18:0 provided the best prediction of melting point (Wood et al., 1978).

Table 15
Correlations between fatty acid proportions and firmness of subcutaneous fat in the shoulder region of pig carcasses having a wide range of P_2 fat thickness (5–20 mm) (Wood et al., 1989)

	18:0	18:2$n-6$
Firmness objective	0.35	−0.75
Firmness subjective	0.40	−0.78

Changing the fatty acid composition of subcutaneous adipose tissue using different dietary oils also changes lipid melting point and fat firmness. For example, palm kernel oil produced firmer fat than soyabean oil in the study of Teye et al. (2006b). When all the data were pooled, the proportions of 12:0 and 14:0 (high in pigs given palm kernel oil) were strongly correlated with fat quality parameters, as also were 18:0 and 18:2$n-6$.

In lamb subcutaneous fat sampled throughout the year in four abattoirs, Enser and Wood (1993) found that melting point varied with the time of year, being lowest in the Spring and Summer and highest later in the year. Melting (slip) point ranged from 30 °C to 49 °C and 18:0, which ranged from 7.0% to 32.9% of fatty acids (mean 18.8%) was the fatty acid most highly correlated with melting point (r 0.89). Linoleic acid was 1.3% of fatty acids overall and its correlation with melting point was −0.3.

Lamb subcutaneous fat is unusual in having significant concentrations of methyl branched fatty acids of medium to long chain length (C8-17) with low melting points. Their concentration reached 4% of the total in the study of Enser and Wood (1993). These fatty acids are responsible for the soft, oily fat found in sheep that have consumed high grain diets which produce high levels of propionic acid in the rumen.

7.2. Muscle

The total lipid content of muscle (intramuscular fat, often termed marbling fat, although this is strictly the flecks of adipose tissue composed mainly of neutral lipid) has a role in the tenderness and juiciness of cooked meat although the strength of the correlation varies considerably between studies, with some showing an important role for marbling fat and others showing only a weak relationship with sensory traits. The role of marbling fat is of particular interest in pigs because genetic selection for lean pigs has reduced the level of marbling fat to below 1% of muscle weight in modern pigs (e.g. Large Whites in Table 11) compared with 2–4% in US studies in the 1960s (Wood, 1990). In the study of four breeds of Wood et al., 2004, the highest correlation between marbling fat concentration and sensory traits across all four breeds was 0.17, for tenderness. The correlation in Berkshires was 0.34.

The study of Wood et al. (1986) showed that total lipid (marbling fat) in *longissimus* muscle was 0.55, 0.66 and 0.96 g/100 g in pig carcasses having 8 mm, 12 mm and 16 mm P_2 fat thickness respectively. These were very light carcasses, weighing 58 kg on average. Correlations across all pigs between marbling fat and sensory traits were 0.13 for tenderness and 0.31 for juiciness. Juiciness was significantly lower in the 8 mm than the 16 mm P_2 fat thickness

group. In a recent comparison of lamb chops produced in organic and conventional production systems, Angold et al. (in press) showed that the correlations between the total fatty acid content of *longissimus* (marbling fat) and eating quality scores given by the taste panel were 0.36 and −0.06 for juiciness and toughness respectively. It seems from these results that juiciness is the trait most affected by increasing levels of marbling fat, associated with greater retention of water in meat during cooking. The location of marbling fat in the perimysial connective tissue between muscle fibre bundles may also be important in 'opening up' the structure of muscle, allowing it to be more easily broken down in the mouth (Wood, 1990). There are therefore good reasons to expect a positive role for marbling fat in meat quality.

The use of low protein diets to increase marbling fat in pigs has sometimes produced a higher score for tenderness and juiciness in cooked pork. In the study of Teye et al. (2006a), total lipid was increased to 2.8% of *longissimus* using an 18% protein diet compared with 1.7% in a standard diet containing 20% protein. The scores for tenderness and juiciness (1–8 range) were increased from 4.2 and 3.9 in the 20% protein diet to 4.8 and 4.4 in the 18% protein diet (both $P < 0.01$).

Despite contradictory results between studies for the role of marbling fat in the tenderness and juiciness of fresh pork, beef and lamb, incorporation of adipose tissue at different levels into burgers or patties has been linked positively to tenderness and juiciness in several studies (e.g. Kregel, Prusa, & Hughes, 1986). In these cases, positive effects on tenderness and juiciness are observed at between 10% and 20% lipid rather than at the lower levels seen for marbling fat.

The fatty acid composition of muscle affects its oxidative stability during processing and retail display, the polyunsaturated fatty acids in phospholipid being liable to oxidative breakdown at this stage. A standard test for lipid oxidative stability in foods is the thiobarbituric acid reacting substances (TBARS) test of Tarladgis, Watts, Younathan, and Dugan (1960) which measures the oxidation product malondialdehyde. Values above about 0.5 are considered critical since they indicate a level of lipid oxidation products which produce a rancid odour and taste which can be detected by consumers.

Values of TBARS in our studies with pork have usually been well below 0.5, even when PUFA proportions have been increased to high levels using soyabean oil or linseed (Riley, Enser, Nute, & Wood, 2000; Kouba et al., 2003; Sheard et al., 2000). In the studies of Riley et al. (2000) and Sheard et al. (2000), minced and comminuted products were produced which develop higher levels of oxidation because the fatty acids are exposed to pro-oxidants such as iron released from muscle cells. Even here, TBARS values remained below 0.5 except in the case of bacon in the work of Sheard et al. (2000). In this study, several factors contributed to high levels of oxidation. The loin joint was conditioned at 1 °C for 10 days, after which it was injected with brine to a target level of 10%. The loin was immersed in brine for 3 days after which the bacon was sliced, blast frozen, stored at −18 °C for 8 weeks, thawed, packed in overwrapped trays and kept under retail display conditions for up to 9 days. Injection of salt followed by freezing and thawing were probably the most important contributors to lipid oxidation. Even after this treatment, TBARS values were below 0.5 at 5 days of retail display, increasing to about 1.5 after 9 days. The bacon with a high level of 18:3$n-3$ (1.3%) had a similar TBARS value to the controls (18:3$n-3$ 0.85%). The bacon was assessed by the trained taste panel after the freezing stage and no differences n flavour characteristics between feeding treatments were detected.

It is possible that in the study of Sheard et al. (2000), 18:3$n-3$ proportions in muscle of treated pigs were below those likely to produce oxidation products having adverse effects on pork flavour. In the work of Kouba et al. (2003), in which the proportion of 18:3$n-3$ was increased to 3.0% of muscle fatty acids compared with 0.65% in controls, an increase in TBARS after 7 days of retail display was observed, although only to 0.15 mg malondialdehyde/kg compared with 0.10 in controls. A slightly higher level of abnormal odour was detected by the taste panel in subcutaneous adipose tissue compared with the controls, and the 'flavour liking' score of *longissimus* muscle was significantly reduced. It is at levels of around 3% 18:3$n-3$ in muscle fatty acids that other workers have detected off flavours as a result of feeding linseed (Shackelford, Miller, Haydon, & Reagan, 1990).

Feeding fish oils to pigs increases levels of long chain $n-3$ PUFA in adipose tissue and particularly in muscle and fishy odours and flavours are detected when critical tissue levels are exceeded. In the work of Overland, Taugbol, Haug, and Sundstol (1996), feeding a 1% fish oil diet between 10 and 100 kg live weight increased the proportions of 20:5$n-3$ and 22:6$n-3$ from 0.6 and 0.9% of muscle fatty acids in controls to 1.5% and 1.8% respectively. This caused significantly higher 'off odour' and 'off flavour' scores in cooked subcutaneous adipose tissue sampled both fresh and after 6 months frozen storage. A 3% fish oil diet increased these scores even more.

Several studies with pigs have shown that high levels of vitamin E in the diet are incorporated into tissues where they are effective in reducing lipid oxidation in stored and displayed pork (Buckley, Morrissey, & Gray, 1995). However, a level of 150 mg/kg diet did not prevent the deterioration in flavour when linseed feeding raised the level of 18:3$n-3$ to 3% of muscle fatty acids in the study of Kouba et al. (2003) and extra vitamin E did not increase storage stability in pigs given diets containing 0.5% fish oil in a study by Hertzman, Goransson, and Ruderus (1988). In some studies, 'supranutritional' vitamin E has reduced drip loss and improved colour stability in pork, probably by preventing oxidation of muscle pigments by lipid oxidation products but in others, limited effects on drip loss and colour stability have been seen (Jensen et al., 1997).

In ruminants, we have frequently seen higher values of TBARS than in our studies on pork. In a recent study, Nute et al. (in press) examined oxidative stability and eating quality in lambs which had been fed different levels of $n-3$ PUFA from linseed oil, fish oil, a protected lipid supplement (PLS) made from linseed, sunflower seed and soyabean meal, marine algae (contains long chain $n-3$ PUFA) and combinations of these different oil sources. Leg steaks were conditioned for 6 days at 0 °C then packed in modified atmosphere packs (O_2:$CO_2$75:25) and displayed under retail conditions. Lipid oxidation was measured on the *semimembranosus* muscle at 7 days of display. The lowest TBARS value was in muscles from the group given linseed oil (0.6 mg/kg) and all other groups had values above 2.0 mg/kg, the highest value being 6.2 in the group given a combination of algae and fish oil. All the groups, except those given linseed, had low taste panel scores for lamb flavour and high scores for abnormal lamb flavour. These scores were correlated with fatty acid proportions in phospholipid, negative correlations being found between long chain $n-3$ PUFA and lamb flavour (Table 16). The fatty acid composition of *semimembranosus* phospholipid was greatly affected by diet in this study. For example, 18:2$n-6$ varied from 11.5 (fish oil) to 33.7% (PLS), 18:3$n-3$ from 1.4 (combination of fish oil and marine algae) to 6.9% (linseed) and 22:6$n-3$ from 0.6% (PLS) to 5.35% (combination of PLS and marine algae). Significant proportions of long chain $n-3$ PUFA were also detected in adipose tissue. A companion paper by Elmore et al. (2005) showed that very high levels of lipid oxidation products were produced during the cooking of these samples to affect the flavour scores. Muscle samples from the fish oil/marine algae treatments had the highest lipid oxidation and the lowest concentration of vitamin E. Other work has shown low vitamin E levels in pig tissues containing high PUFA proportions, suggesting utilization of the vitamin to control oxidation (Kouba et al., 2003).

In cattle, consumption of concentrate produced higher TBARS values in steaks than consumption of grass silage in a study of Warren et al. (in press-b). This is a companion study to that of Warren et al. (in press-a). Aberdeen Angus cross and Holstein–Friesian steers were fed the diets from 6 to 14 months of age. After slaughter, loin joints were conditioned at 1 °C for 10 days. Steaks were then placed in modified atmosphere packs (O_2:$CO_2$75:25) and displayed under retail-type conditions. Lipid oxidation measurements were made at 4 and 7 days of display. The results (Table 17) show that the concentrate diet increased lipid oxidation in the steaks, values increasing to over 2.0 after 7 days of display in both breeds. On the other hand, TBARS values remained at low levels in the grass silage-fed groups, albeit these were higher than we normally see in pork. These TBARS values were apparently inversely related to the vitamin E concentration in muscle and plasma. Steers fed grass silage had higher values for muscle and plasma vitamin E than those fed concentrate. Muscle values for the grass silage groups were around the 3.3–3.5 mg/kg level found by Arnold, Scheller, Arp, Williams, and Schaefer (1993) to give optimum lipid stability in *longissimus* while values in the concentrate group were considerably lower. The high vitamin E values in the steers fed grass silage are partly the result of lower PUFA levels in muscle but mainly due to greater uptake of vitamin E from the diet. When the data from all animals slaughtered at 14, 19 and 24 months was combined, TBARS were higher in the concentrate-fed animals than in those fed grass silage

Table 16
Correlations between lamb flavour scores and proportions of phospholipid fatty acids in lambs given different dietary oil sources (Nute et al., in press)

	Lamb flavour	Abnormal flavour
18:2$n-6$	−0.25	0.11
18:3$n-3$	0.51	−0.49
20:4$n-6$	0.11	−0.20
20:5$n-3$	−0.13	0.24
22:6$n-3$	−0.28	0.32

Table 17
Lipid oxidation (TBARS) and vitamin E content of *longissimus* muscle and vitamin E content of plasma in Aberdeen Angus cross (AA) or Hostein–Friesian (HF) beef steers given concentrate or grass silage diets between 6 and 14 months of age (Warren et al., in press-b)

	AA		HF		Significance	
	Concentrate	Grass silage	Concentrate	Grass silage	Breed	Diet
TBARS[a]						
day 4	1.2	0.3	1.4	0.3	NS	***
day 7	2.1	0.4	2.7	0.4	NS	***
Vitamin E						
muscle[b]	1.3	3.6	1.3	3.2	NS	***
plasma[c]	2.2	5.8	2.1	4.5	*	***

[a] mg malondialdehyde/kg.
[b] mg/kg.
[c] mg/l.

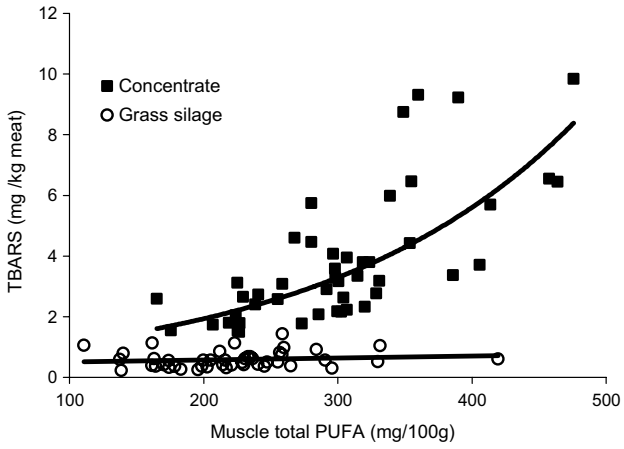

Fig. 6. Relationships between lipid oxidation (TBARS) and *longissimus* total PUFA (mg/100 g) in steers given concentrate or grass silage diets (Warren et al., in press-b).

at all levels of PUFA in muscle (Fig. 6). TBARS increased with PUFA level only in those fed concentrate. For the steers fed grass silage it appears that vitamin E was sufficiently high to protect the PUFA from oxidation, at least for the 7 days during which the beef was displayed.

In the study of Warren et al. (in press-b), the concentrate diet contained a standard level of vitamin E (25 mg/kg). In work with sheep, Demirel et al. (2004) fed concentrate diets containing different oil sources (5%) and either 100 or 500 mg/kg vitamin E. Despite these 'supranutritional' levels, concentrations of the vitamin in muscle were 0.27 and 0.52 mg/kg for the 100 and 500 mg/kg diets respectively. Values around 5 mg/kg would be expected. The reason for these very low levels is unclear but these results, together with those of Warren et al. (in press-b) point to excessive utilisation of antioxidants in concentrate-type diets.

A change in muscle colour seen during retail display in the study of Warren et al. (in press-b) suggested a link between lipid oxidation, vitamin E concentration and colour. The intensity of the red colour, termed saturation or chroma, declined gradually as the display period progressed but the decline was more rapid in the muscles from the groups fed concentrate than the groups fed grass silage. A value of 18 for colour saturation, which has been used as an index of the end of shelf life, was reached 2–3 days sooner in the concentrate groups.

Elmore et al. (2004) examined the flavour volatile compounds produced when beef samples from the study of Warren et al. (in press-b) were grilled. Products of 18:2$n-6$ oxidation such as pentanal and hexanal were detected in steaks produced using concentrate and the alcohols 1-penten-3-ol and *cis* − 2-penten-1-ol, products of 18:3$n-3$ oxidation, were detected in steaks from the grass-silage-fed group. A compound formed from chlorophyll, 2-phytene, was higher in samples from the grass-fed groups. Despite these differences in lipid oxidation, the trained taste panel at Bristol could detect few clear differences in sensory (eating) quality between the concentrate and grass silage groups. On balance, the panel preferred loin steaks from steers fed grass silage. This result is consistent with papers which have shown that when grain- and grass-fed cattle grow at similar rates, sensory scores are similar (Bidner et al., 1986). Comparisons of well finished grain-fed with poorly finished grass-fed steers have often found results in favour of those fed grain (Medeiros, Field, Menkhaus, & Russell, 1987).

Campo et al. (2006) examined eating quality in 73 beef loins produced using different feeding treatments and containing different concentrations of $n-6$ and $n-3$ PUFA. Lipid oxidation was promoted by conditioning for 10 days, freezing, thawing and storing steaks in modified atmosphere packs (O_2:CO_2 75:25) before sensory analysis. This series of procedures promoted high levels of lipid oxidation, TBARS values up to 12.0 being recorded. As the TBARS value increased, the scores for beef flavour, bloody, metallic and livery declined, and scores for abnormal flavour, rancid and greasy increased (Table 18). This study identified a TBARS value of 2.3 as the point where rancid and other abnormal flavours overpower beef flavour to produce an unacceptable flavour profile in beef. Below this, rancidity was detected but beef flavour remained high. These results suggest that the upper limit for TBARS of 0.5 suggested by Tarladgis et al. (1960) based on pork may not be appropriate for beef (or lamb) where the natural level of lipid oxidation is higher.

Table 18
Correlations (Spearmans rho) between lipid oxidation (TBARS) and beef flavour terms in samples in which oxidation was promoted (Campo et al., 2006)

Beef flavour	-0.80^{***}
Abnormal flavour	$+0.82^{***}$
Rancid	$+0.84^{***}$
Greasy	$+0.70^{***}$
Bloody	-0.60^{***}
Metallic	-0.36^{***}
Livery	-0.60^{***}

*** $P < 0.001$, $n = 216$.

8. Conclusions

This review has shown that the fatty acid composition of adipose tissue and muscle in pigs, sheep and cattle depends on the amount of fat in the carcass and in muscle. Effects of diet and breed have to be judged against the amount of fat. Also, there are important differences between the species which are only partly explained by differences in the digestive process. These include: ruminants conserve PUFA in muscle whereas in pigs, concentrations are higher in adipose tissue; long chain (C20-22) PUFA are found in adipose tissue and muscle neutral lipid in pigs and sheep but not in cattle; and the ratio of 18:0/18:2$n-6$ in adipose tissue increases as fattening proceeds in pigs but declines in ruminants.

In muscle, the high proportion of 18:2$n-6$ in phospholipid compared with neutral lipid in all species means that muscle from lean animals has high proportions of this major PUFA. As the animal is fattened for meat, the decline in PUFA proportions is more dramatic in the ruminants because PUFA levels in neutral lipid are so low. Since desirable sensory characteristics tend to increase with fatness, there is potentially an inverse relationship between nutritional value and eating quality in ruminants.

Of the 2 major PUFA, 18:2$n-6$ is more rapidly taken up into meat tissues than 18:3$n-3$ and reaches much higher levels. Synthesis of long chain PUFA from these precursors occurs in phospholipid but the available sites for incorporation are soon filled and long term feeding of linseed to pigs or grass to cattle does not increase levels and so proportions decline.

Oxidation of fatty acids proceeds at a naturally higher level in ruminants than pigs after slaughter despite the lower PUFA proportions. Vitamin E is a vital meat quality

enhancing nutrient, particularly in ruminants where high concentrations resulting from grass feeding prevent fatty acid oxidation and extend colour shelf life. Low concentrations, often seen after the feeding of concentrate diets, lead to a shorter colour shelf life and unfavourable beef flavour notes.

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