FACTORS INFLUENCING FAT COMPOSITION IN MUSCLE AND ADIPOSE TISSUE OF FARM ANIMALS

Nürnberg, K., Wegner, J., Ender, K.

Division of Muscle Biology and Growth, Research Institute for Biology of Farm Animals; Wilhelm-Stahl-Allee 2; D-18196 Dummerstorf

Abstract

Fat deposition can be characterised chemically by continual accretion of lipids, primarily in the form of triacylglycerols, and morphologically by adipocyte differentiation and hypertrophy. The relative proportion of nutrients and the fatty acid composition are influenced by numerous factors including diet, fatness, age/body weight, gender, breed, environmental temperature, depot site, maintenance and hormones. Deposition of body fat can be modulated by nutritional and hormonal means. The level of food intake and the composition of food regulates the rate of fatty tissue growth and the composition of lipids. Exogenous endocrine substances have effects on adipose tissue metabolism. For example, porcine somatotropin reduces lipid deposition by decreasing lipogenesis. There is a correlation between the amount of fatty tissue and the fatty acid composition. The differences between animals of different gender are partially due to the amount of fat deposited. Finally, the potential for dietary variation of lipid composition in monogastric animals is much greater than in ruminants. In young sheep and cattle, there is a limited possibility to influence fatty acid content.

Keywords:
Fatty acid composition, muscle, backfat, pig, cattle, sheep

Introduction

Dietary fat is one of the three main energy providing macronutrient groups. Humans require a certain amount of polyunsaturated fatty acids (PUFA) which are essential for life and health, but which cannot be manufactured in the body. These are the essential fatty acids. There are also a few vitamins (A, D, E, F) which, being fat soluble, require a certain amount of fat in the diet to enable the supply and absorption of these substances. Current dietary guidelines recommend reducing fat consumption to 25-30 % of daily caloric intake and a contribution of one third of each of saturated, monounsaturated and PUFA in dietary fat. The requirement of n-3 fatty acids for young adults is 1.5 g/day and, for n-6 fatty acids, 10 g/day (Wolfram, 1997). The alteration of animal lipids has been the subject of numerous investigations, in large part because of the effect of dietary fat on human blood lipids and on cardiovascular health (Hartog et al., 1987; Madsen et al., 1992). The relative proportion of nutrients and the fatty acid composition of adipose and muscle tissues can be affected by different factors like diet, species, fatness, age/weight, depot site, gender, breed, maintenance and hormones (Enser, 1991; Bouchard et al., 1993; Flint and Vernon, 1993; Rule et al., 1995). Therefore, it is possible to produce meat and meat products that meet the human dietary guidelines (Lough et al., 1992). The objective of this review is to summarize our own results and results of other studies influencing the fatty acid composition in lipids of mammals.

1. Diet

The level and the chemical composition of feed affects deposited fat tissues in animals. The ratio of lipid to protein deposition increased in pigs given a high energy intake [16.3 MJ digestible energy (DE)/day] as compared with a lower intake (12.6 MJ DE/day)(Greef et al., 1994). In one study, Hereford cattle were reared under extensive methods of management and Black Pied (BP) cattle were kept in stables with intensive feeding. The growth of muscle fibres and adipocytes was nearly linear from 140 up to 500 days of age in Black Pied. However, the extensive feeding of the Hereford cattle caused a lower diameter of muscle fibres and adipocytes (Wegner and Matthes, 1994). The potential for dietary manipulation of the fatty acid composition of monogastric animal depots is much greater than for ruminants. In the former, saturated and unsaturated fatty acids from the diet pass through the digestive system without changing and are deposited in the different depots. Lipids in various tissues, including adipose tissue and skeletal muscle, strongly reflect the major dietary fatty acids. In pigs, consumption of different levels of oil seed rape feeds resulted in marked changes in backfat and muscle composition in growing-finishing pigs (Nürnberg et al., 1994a, 1994b; Kracht et al., 1996). The linolenic acid percentage (C18:3 n-3) in rape seed (RS) fat is about 10 %. The relative content of linoleic- (C18:2 n-6) and linolenic fatty acids in backfat and muscle was increased with enhanced rape cake (RC) content in feed mixtures (Tables 1and 2).

Table 1 Influence of feeding different dietary levels of oil seed rape cake (RC) on the polyunsaturated fatty acids (PUFA), saturated fatty acids (SFA) and unsaturated fatty acids (UFA) content of backfat in pigs (Nürnberg et al., 1994a)*

	Control	10 % RC	15 % RC	20 % RC	30 % RC
Daily gain (g)	845 ^{a}	819 ^{a}	826 ^{a}	787 ^{b}	743 ^{c}
Backfat PUFA (% of total FA)					
- castrate male	6.6 ^{a}	9.8 ^{b}	9.1 $^{a, b}$	11.2 ^{b}	14.6 ^{c}
- female	8.1 ^{a}	10.3 ^{b}	11.6 ^{b}	12.6 $^{b, c}$	20.0 $^{b, c, d}$
Backfat SFA (% of total FA)					
- castrate male	45.2 ^{a}	42.1 ^{a}	43.2 ^{a}	41.4 ^{a}	35.4 ^{b}
- female	44.2 ^{a}	39.7 ^{b}	41.3 $^{a, b}$	42.9 $^{a, b}$	30.0^{c}
Backfat UFA (% of total FA)					
- castrate male	54.8 ^{a}	57.9 ^{a}	56.8 ^{a}	58.6 ^{a}	64.6 ^{b}
- female	55.8 ^{a}	60.3	58.7 $^{a, b}$	57.1 $^{a, b}$	70.0 ^{c}

* The data were analysed by the least squares method using GLM procedures (SAS®). All subsequent tables and figures contain LSMeans (LSM) adjusted by covariate live weight.
a,b,c Within row, LSM with different letters differ between groups at $P < 0.05$.

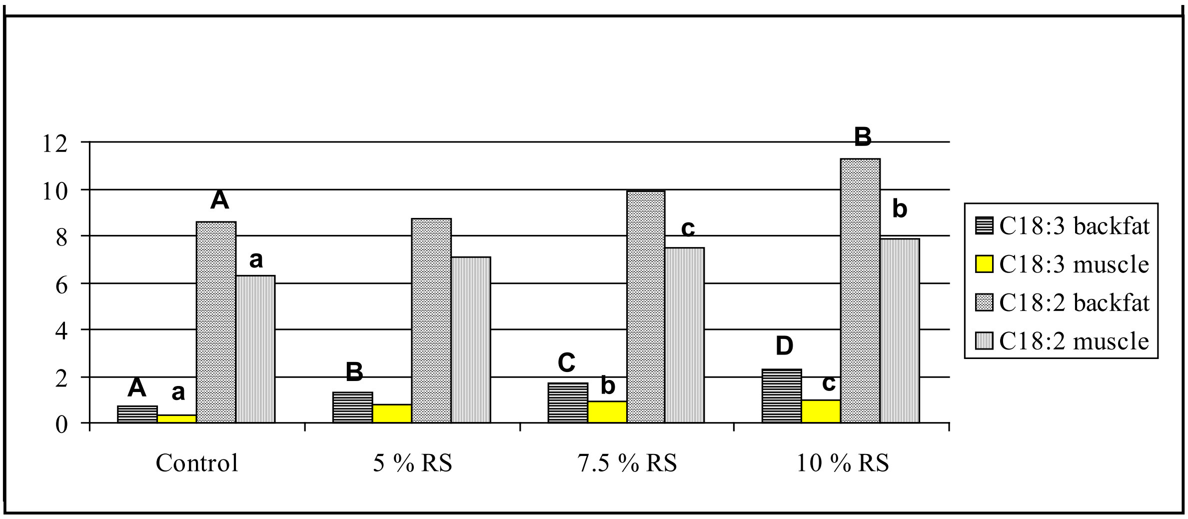
A decrease in feed intake [2.58 kg/animal/day (control) down to 2.23 (at 30% inclusion)] and a significant decrease in daily gain occurred. The meat quality did not differ between control and RC groups (Nürnberg et al., 1994a). Influences on off-flavour development can be expected by increasing C18:3 content (Wood and Enser, 1997). The feeding of 15 % RC is recommended to avoid loss of carcass quality and performance.

Table 2 Influence of feeding different dietary levels of oil seed rape cake (RC) on linoleic and linolenic acid contents of longissimus muscle in pigs (Nürnberg et al., 1994b)

	Male		Female	
	LSM	SE	LSM	SE
C18:2 n-6 (% of total FA)				
Control	3.5 [ac]	0.9	5.4 [a]	0.7
10 % RC	5.9 [a, c]	0.8	8.2 [b]	0.9
20 % RC	8.0 [b, c]	1.0	9.7 [b, c]	0.8
30 % RC	10.5 [b]	1.0	12.3 [c]	0.9
C18:3 n-3 (% of total FA)				
Control	0.3 [a]	0.2	0.3 [a]	0.2
10 % RC	0.8 [a]	0.1	1.1 [b, c]	0.2
20 % RC	1.2 [a]	0.2	1.3 [b]	0.1
30 % RC	2.0 [b]	0.2	2.4 [b, c]	0.2

a,b,c LSM with different letters within the same gender differ at $P < 0.05$.

Figure 1 Influence of feeding different dietary levels of rape seed (RS) on backfat and longissimus muscle fat (% of total fatty acids) of male pigs (Kracht et al., 1996)



a,b,c LSM with different letters differ at $P < 0.05$ in longissimus muscle.
A,B,C LSM with different letters differ at $P < 0.05$ in backfat.

The application of full-fat rape seed at three levels (5 %, 7.5 %, 10 %) during growing and finishing periods in pigs caused an accumulation of PUFA in subcutaneous and longissimus muscle fat. The PUFA content of backfat increased from 9.5 % (control) to 13.8 % (10 % RS) in castrated males and from 9.9 % to 16.0 % in females, respectively (Kracht et al., 1996). Linoleic and linolenic acid percentages were increased ($P < 0.05$) in both tissues (Figure 1). The increase of C18:3 is considered beneficial to consumer health, but it caused a reduced lipid melting point and firmness of backfat, and an increase in iodine value and an increased risk for PUFA peroxidation (Gill et al., 1995; Warnants et al., 1996).
The withdrawal of 15 and 20 % RS/kg to the control diet in the finishing period (from 70 days to slaughter at 126 days) caused reduced PUFA percentages in backfat and longissimus muscle (Table 3). There was also a dilution of the incorporated polyenoic fatty acids. Gill et al. (1995) also reported a decrease in linolenic acid content of subcutaneous fat by withdrawal of full-fat rape seed. Rape seed supplementation in fattening bulls did not change the fatty acid composition in depot and muscle fat (Flachowsky et al., 1994).

Table 3 Influence of feeding different dietary levels of rape seed (RS) for different durations on polyunsaturated fatty acids (PUFA) and saturated fatty acids (SFA) contents (% of total fatty acids) of longissimus muscle and backfat in pigs (Kracht et al., 1996; unpublished data, 1995)

Feeding (days)	Control 126	15 % RS 126	15 % RS 70	20 % RS 126	20 % RS 70	Significant influence
Muscle PUFA (%)						Feed, Gender, Gender x feed
- male	-	8.0	5.5	8.2	6.2	
- female	-	8.9	5.7	12.2	6.5	
Backfat PUFA (%)						Feed, Gender, Gender x feed
- male	7.3	16.5	11.7	19.7	12.7	
- female	10.2	17.5	11.4	19.5	12.5	
Muscle SFA (%)						Feed, Gender
- male	-	36.3	39.5	36.0	40.5	
- female	-	35.8	39.1	32.4	37.2	
Backfat SFA (%)						Feed, Gender
- male	42.8	29.0	35.9	26.1	35.7	
- female	39.5	28.5	36.0	25.1	33.8	

In many studies, n-3 fatty acid- enriched diets were given to raise the total content of n-3 fatty acids in adipose tissue, to change the membrane properties or to use the pig as an animal model (Irie and Sakimoto, 1992; Morgan et al., 1992; Nürnberg et al., 1996a; Van Oeckel et al., 1996; Warnants et al., 1996; Mandell et al., 1997). Feeding a n-3 fatty acid-enriched diet to pigs did not influence the carcass composition and meat quality aspects measured (Morgan et al., 1992; Otten et al., 1993; Nürnberg et al., 1996b; ∅verland et al., 1996; Van Oeckel et al., 1996). Daily intake of 14 g of n-3 fatty acids caused an incorporation of these fatty acids in all adipose tissues and in longissimus muscle membranes in pigs (Nürnberg et al. 1996a; Table 4).

Table 4 Fatty acid composition (% of total fatty acids) of polar and neutral fractions of longissimus muscle lipids of pigs (Nürnberg et al., 1996a)

	Polar fractions			**Neutral fractions**		
	Control (n = 10)	n-3 diet (n = 10)	Significant effect	Control (n = 10)	n-3 diet (n = 10)	Significant effect
C16:0	7.5	6.8	-	22.7	22.7	-
C18:0	16.3	11.0	+	13.4	13.1	-
C18:1 cis 9	17.7	17.0	-	49.9	46.8	+
C18:2	26.0	15.6	+	2.5	3.7	+
C18:3	0.5	0.5	-	0.1	0.3	+
C20:4	18.5	6.0	+	0.2	0.1	-
C20:5	1.8	20.3	+	0.01	0.5	+
C22:6	1.6	10.0	+	0	0.8	+
n-3 fatty acids	3.9	30.7	+	0.1	1.7	+
n-6 fatty acids	46.6	23.0	+	2.7	3.8	+

In ruminants, all PUFA were extensively biohydrogenated (86.6 - 95.3 %) by rumen micro-organisms to more saturated fatty acids (Jenkins, 1993; Doreau and Ferlay, 1994; Choi et al., 1997). Contrary to those studies, Ashes et al. (1992) demonstrated that ruminal micro-organisms did not hydrogenate eicosapentaenoic acid and docosahexaenoic acid to any significant extent. Despite the hydrogenation in the rumen, the fatty acid composition of meat can be modulated by the diet. Feeding of different sources of n-3 fatty acids (linseed; fish oil) to steers did not influence animal performance (Mandell et al., 1997; Scollan et al., 1997). In addition, compared with the control, linseed and fish oil increased ($P<0.05$) the quantity of n-3 fatty acids in longissimus muscle. Permanent fattening indoors (group I), maintenance on pasture and finishing indoors (group II) and permanent maintenance on pasture (group III) of steers and lambs caused differences in growth performance, meat and fat quality (Nürnberg et al., 1996; Ender et al., 1997; Table 5).

The lowest internal fat (6.1 %), intramuscular fat of longissimus muscle (2.5 %) and daily gain (753 g/day) were measured in group III. Forage diets have a low energy density and restrict the rate of animal growth (Enser, 1991). The meat quality was very favourable in group II steers. The intramuscular fat was optimal at 3.8 %. Colour of meat and pH were not influenced by group.

The fatty acid profiles of the indoors and pasture diets were quite different. According to the composition of the feed, the percentage of n-3 fatty acids of semitendinosus muscle was increased ($P< 0.05$) in group II and III (Table 6). The total amount of saturated and unsaturated fatty acids was unaffected in intramuscular fat. The n-3 fatty acids were included at the expense of oleic acid and n-6 fatty acids.

Experiments with lambs indicated the same results (Nürnberg et al., 1996a; Table 7). The intramuscular fat quality of longissimus muscle in lambs and steers fed on pasture was better for human nutrition because of the high proportion of n-3 fatty acids.

Table 5 Carcass composition and meat quality of Black Pied steers reared differently (Ender et al., 1997)

Group	Permanent indoors (I) (n = 9)	Pasture and in-doors finished (II) (n = 9)	Permanent on pasture (III) (n = 9)	Significant effect
Carcass weight, kg	343	325	298	+
Daily gain, g/day	829	788	753	+
Internal fat, % of carcass weight	8.7	7.5	6.1	+
Intramuscular fat, % of longissimus muscle	6.9	3.8	2.5	+
pH at 17 h	5.7	5.8	5.9	-
Reflectance L	32.2	30.3	29.3	-

Table 6 Influence of feeding regime on fatty acid composition (% of total fatty acids) of semitendinosus muscle in Black Pied steers (Ender et al., 1997)

Group	Permanent indoors (I) (n=9)	Pasture and indoors finished (II) (n=9)	Permanent on pasture (III) (n=9)	Significant effect
C 18:1 cis 9	42.9	38.1	38.0	+
C 18:2	4.0	5.4	5.5	-
C 18:3	0.5	1.0	1.2	+
C 18:4	0.6	0.8	0.8	+
C 20:4	1.8	2.8	2.8	-
C 20:5	0.2	0.6	0.7	+
C 22:5	0.5	1.1	0.9	+
n-3 fatty acids	1.8	3.5	3.8	+

2. Fatness

Energy balance and the deposition of adipose tissue result from the maintenance of a fine balance between energy intake and energy expenditure, energy storage and energy mobilization. These processes are related to each other. The regulation of the pathways of lipogenesis and lipolysis is well documented (Mersman, 1991; Jenkins, 1993), but the precise mechanisms which control energy intake and expenditure are rather obscure. Patterns of deposition of adipose tissue in mammals are different in various species. Selection for increased lean meat content in pig carcasses has been associated, to some extent, with lower meat and fat quality. The backfat thickness declined in German Landrace pigs from 3.1 cm in 1984 to 2.4 cm in 1996,

Table 7 Influence of feeding regime on fatty acid composition (% of total fatty acids) of longissimus muscle in Black Head lambs (Nürnberg et al., 1996a)

	Permanent on pasture (n = 20)	Pasture and indoors finished (n = 20)	Significant effect
Live weight, kg	38.2	43.7	+
C 18:2	5.8	8.0	+
C 18:3	2.0	1.2	+
C 20:4	2.7	2.4	-
C 20:5	1.7	0.7	+
C 22:6	1.2	0.9	-
n-3 fatty acids	4.9	2.8	+
n-6 fatty acids	8.5	10.4	+

while the total carcass fat content declined from 35.4 to 25.2 %, respectively (Kuhn et al., 1997). The decrease of carcass fat and the increase of lean meat resulted in a marked reduction in fat content in the depot fat and an increase in PUFA (Wood and Enser, 1997). There are relationships between the lipid content, the proportion of lean meat and the relative proportion of linoleic acid in backfat (Table 8). Pigs with higher leanness have more linoleic acid content in fat. These changes, whilst good nutritionally, result in softening of the fat and a higher oxidative instability. All fat parameters were negatively correlated to linoleic acid concentration.

Table 8 Correlation coefficients between carcass composition and relative content of linoleic acid in pig backfat (Nürnberg and Ender, 1989)

	C18:2 (%) of backfat	
	Castrate males (n = 58)	Intact males (n = 88)
Lean meat (%)	+ 0.52	+ 0.47
Backfat thickness (cm)	- 0.40	- 0.33
Lipid in backfat (%)	- 0.57	- 0.42
Backfat (kg)	- 0.48	- 0.42

The selection of mice (Rehfeldt and Bünger, 1990) by protein accretion (Du-6P), body weight (Du-6) and based on an index combining high body weight and high treadmill performance (Du-6LB) caused a high differentiation in body composition, growth performance and fatty acid profile of depot fatty tissue. A control line (Du-Ks) was created from the same base population. Animals selected for body weight (Du-6) accumulated the highest total body fat content (Table 9). The epididymal fat of these mice had the lowest relative concentration of linoleic acid whilst α-linolenic acid was unchanged. Wood and Enser (1997) reported that the inverse correlation between unsaturated fatty acid quantity and the lipid content was absent for α-linolenic acid. They suggested different control factors for the concentration of linoleic and linolenic acids. Both fatty acids are derived entirely from the diet and compete for incorporation into the tissue lipids.

Table 9 Influence of genetic selection on total body fat and fatty acid (FA) composition (% of total FA) in epididymal fat of mice (68th generation, age 60 days, male mice; Nürnberg, 1995a) *

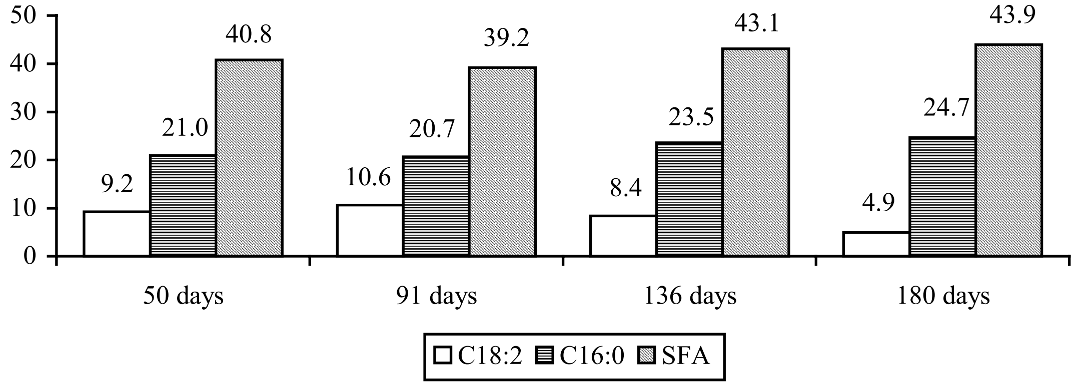
	Du-6P (n = 12)	Du-6 (n = 11)	Du-6LB (n = 10)	Du-Ks (n=11)
Total body fat (%)	6.26 $^{a, b}$	11.21 ^{c}	5.70 ^{b}	7.73 ^{a}
C18:2	38.0 ^{a}	34.9 ^{c}	42.3 ^{b}	41.2 ^{b}
C18:3	4.1	4.3	4.1	4.2
Polyunsaturated FA	42.7 ^{a}	39.7 ^{c}	46.6 ^{b}	45.7 ^{b}

* see text for details on selection groups.
a,b,c LSM with different letters differ at $P < 0.05$.

3. Age and body weight

In market weight animals, the energy stored in adipose tissue represents about 80 to 90 % of total body energy (Etherton and Walton, 1986). The adipose tissue contains 70 - 90 % fat, 5 - 20 % water and approximately 5 % connective tissue. The subcutaneous depot of pigs is the most important site of deposition, with about 62 % of total fatty tissue at slaughter (German Landrace); the internal fat content is 13 % and intermuscular fat about 24 % (Kuhn et al., 1997). However, the body fat content of new-born pigs is only about 2 % (Le Dividich et al., 1991). In cattle, the intermuscular fat is the most important site of fat deposition at slaughter (Black Pied, 24 months), with 45 % of total carcass fat; the internal fat content is 38 % and the subcutaneous fat content is 17 %.
The amount of adipose tissue increases with age. In cattle, the fat cell diameter of subcutaneous fat tissue grows rapidly up to 12 months. After this period, there is a further but reduced increase up to 2 years of age (Wegner et al., 1998). The effect of age on fatty acid profiles is also related to body fatness (Robelin, 1986; Huerta-Leidenz et al., 1996). During growth, the proportion of energy available for fat deposition in pigs increases so that the rate of *de novo* fatty acid synthesis is increased (Enser, 1991). The result of synthesis is mainly palmitic and stearic acid. The accumulation of saturated acids in adipose tissues increases also with age and growth of animals. In lambs, the percentage of saturated fatty acids of muscle increased with age whilst PUFA decreased (Nürnberg et al., 1996a; Figure 2).

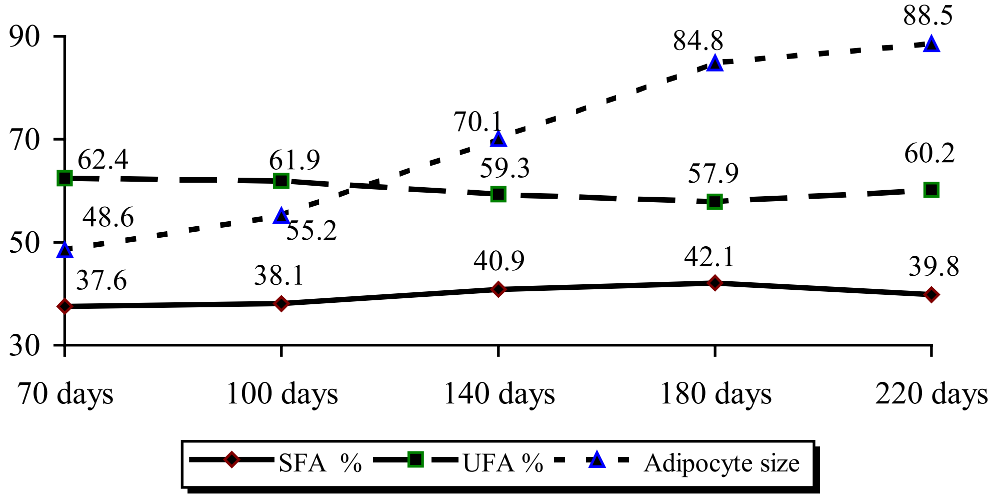
Figure 2 Influence of age on fatty acid composition (% of total fatty acids) in longissimus muscle of lambs (Nürnberg et al., 1996a; unpublished data, 1995) *



* Age effect was P < 0.05 for C18:2 (%) and C16:0 (%); SFA = saturated fatty acids.

The chemical fat content of backfat increased with growth of pigs. This deposition of fat in the period from 70 days of life up to 220 days, caused an increase in adipocyte diameter of the two backfat layers (Nürnberg and Wegner, 1990; Figure 3). The rapid adipose tissue growth in pigs (100-180 days of age) is followed by a phase when adipocyte growth is minimal (180-220 days of age). The relative percentage of unsaturated fatty acids decreased with growth up to 180 days of age. There are no changes in fatty acid composition after 180 days of age.

Figure 3 Influence of age on fatty acid profile (% of total fatty acids) and adipocyte diameter (µm) in pig backfat (Nürnberg and Wegner, 1990) *

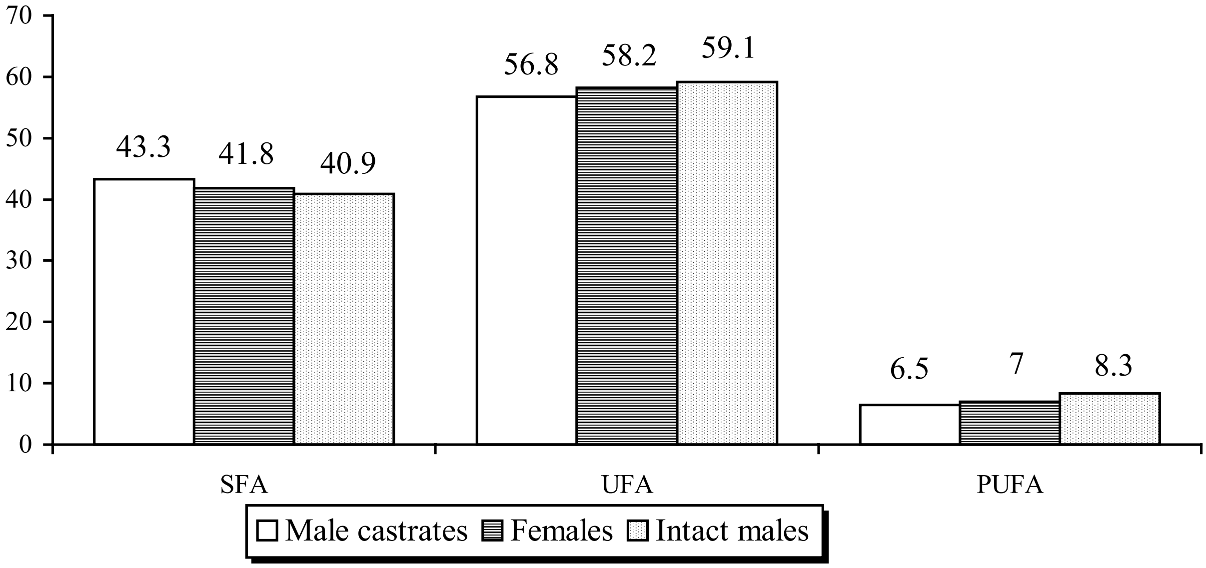


- Age effect was P < 0.05 for saturated fatty acids (SFA), unsaturated fatty acids (UFA) and adipocyte diameter.

4. Gender / gonadal status

The gender of animals is also an important factor for fatty acid composition because of its effect on carcass fatness. At equal slaughter weights, males are leaner than gilts which in turn are leaner than male castrates (Enser, 1991). Relative concentration of linoleic acid and PUFA in backfat decreases in the order of males > females > male castrates whilst the saturated fatty acid percentage increases (Nürnberg and Ender, 1989; Figure 4). These differences are seen in lambs (Nürnberg et al., 1996a), pigs (Cameron and Enser, 1991; Nürnberg and Ender, 1992; Tables 1 and 3) and cattle (Enser, 1991; Malau-Aduli et al., 1998) and are caused by the negative relationship between concentrations of fat and PUFA in the carcass (Table 8). In contrast, performance test traits, lipid content of subcutaneous fat and lipoprotein lipase activity were positively correlated with the unsaturated fatty acids in sheep divergently selected for carcass lean (Cameron et al., 1994).

Figure 4 Influence of gender on backfat fatty acid composition (% of total fatty acids) in pigs (Nürnberg and Ender, 1989) *



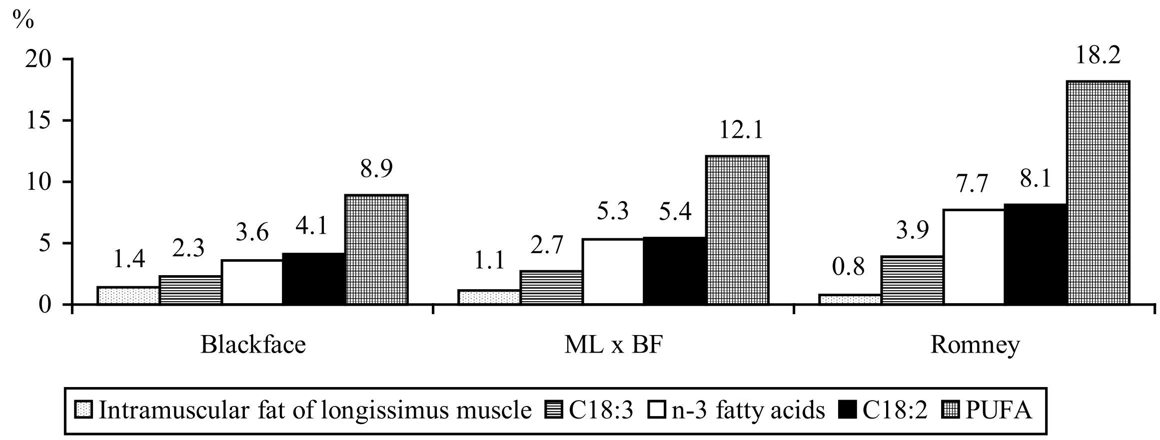
* Gender effect was $P < 0.05$ for saturated fatty acids (SFA), unsaturated fatty acids (UFA) and polyunsaturated fatty acids (PUFA).

Malau-Aduli et al. (1998) reported differences in phospholipid composition of shoulder muscle between heifers and steers. They suggest that hormonal differences between steers and heifers caused these gender differences.

5. Breed

The differences in fat composition between breeds of lambs depends on carcass fatness (Enser, 1991; Nürnberg et al., 1996a; Demise, 1997). The intramuscular fat content in Romney lambs was very low at 0.76 %, but the relative proportion of linoleic acid (C18:2) was the highest (8.1 %) compared with Blackface and Merino x Blackface (ML x BF) crossbred (Figure 5). In contrast, the fatty acid composition of subcutaneous fat in Texel x Oxford and Scottish Blackface sheep, both divergently selected for carcass lean content, did not differ in PUFA (Cameron et al., 1994).

Figure 5 Influence of sheep breed on fatty acid composition (% of total fatty acids) of longissimus muscle (unpublished data, 1994) *

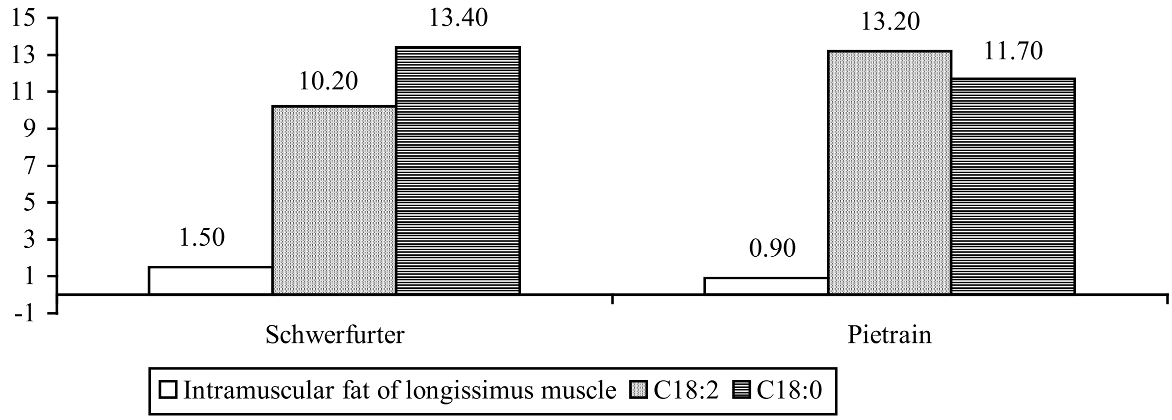


* Breed effect was $P < 0.05$ for intramuscular fat of longissimus muscle, C18:2, C18:3, sum of n-3 fatty acids and polyunsaturated fatty acids (PUFA).

In pig, intramuscular fat content appears to be highly heritable (h^2 estimates generally of 0.4-0.6; Sellier and Monin, 1994). The fatty acid composition of muscle lipid is moderately to highly heritable (Cameron and Enser, 1991). Intramuscular fat of Duroc pigs had higher concentrations of saturated and monounsaturated fatty acids, and lower PUFA content than Landrace pigs (Cameron and Enser, 1991). The adipocyte diameter of backfat, intermuscular fat and intramuscular fat in Pietrain pigs is lower than in obese phenotypes (Hauser et al., 1997). Compared with Schwerfurter pigs, the lower fat concentration of backfat in Pietrain pigs (66.9 vs. 71.5 % in Schwerfurter pigs) caused a higher PUFA and a lower saturated fatty acid percentage in depot adipose tissue (Nürnberg et al., 1995b; Figure 6).
In cattle, there are genetic-based differences in intramuscular fatty acid composition of longissimus muscle (Robelin, 1986; Enser, 1991; Ender et al., 1997). White-blue Belgian bulls (WBB) produced more lean meat and a very small amount of fat compared with Black Pied (BP) bulls (Table 10).
The relative content of linoleic acid was 18.3 % in total muscle fat. The percentage of phospholipids in longissimus muscles of genetically different bulls was similar. About 66 % of the intramuscular fat was phospholipids in WBB; therefore, the PUFA concentration was very high (Ender et al., 1997). Huerta-Leidenz et al. (1993) reported differences in fatty acid composition of subcutaneous adipose tissue of Hereford and Brahman cows. The average fat thickness was 1.7 and 1.3 cm, respectively. Hereford cows had a higher percentage of saturated fatty acids and a lower percentage of mono- and polyunsaturated fatty acids in subcutaneous adipose tissue compared with Brahman. In contrast, Zembayashi and Nishimura (1996)

suggest from their investigation with different Japanese Black breed types that leaner steers had more saturated fatty acids in subcutaneous and intramuscular fat.

Figure 6 Influence of breed on backfat composition (% of total fatty acids) in pigs (Nürnberg et al., 1995b) *



* Breed effect was $P < 0.05$ for intramuscular fat of longissimus muscle, C18:2 and C18:0.

Table 10 Influence of breed on meat and fat quality in cattle (Ender et al., 1997)

	WBB Bulls (n = 5)	BP Bulls (n = 5)	Significant effect
Meat (% of carcass weight)	85.4	81.1	+
Subcutaneous fat (% of carcass weight)	1.4	4.5	+
Longissimus muscle:			
Intramuscular fat (% of muscle weight)	0.6	2.1	+
Phospholipid (% of muscle weight)	0.4	0.4	-
Saturated fatty acid (% of total fatty acids)	40.2	48.7	+
Linoleic acid (% of total fatty acids)	18.3	3.2	+

6. Application of hormones

The net increase in the quantity of triacylglycerols stored in adipose tissue is the result of *de novo* fatty acid synthesis, the uptake of exogenous fatty acids and lipolysis. The hydrolysis of adipose tissue triacylglycerols is controlled mainly by a variety of hormonal and neural influences allowing release of this energy. The key enzymes for lipolysis are two lipases: lipoprotein lipase (degradation of circulating lipoprotein triacylglycerols and the regulation of the uptake of their fatty acids into adipose tissue) and hormone-sensitive lipase (degradation of stored triacylglycerols promoting the release of free fatty acids into the blood). Porcine somatotropin (pST) caused an increase in protein accretion and a dramatic decrease in fat deposition (Ender et al., 1993; Etherton et al., 1993). The ability of pST to reduce adipose tissue accretion in growing pigs is the result of a decrease in insulin sensitivity of the adipocytes resulting in a marked decrease in insulin-regulated events such as glucose transport and lipogenesis. The decline of lipogenesis occurs because of the reduction in glucose transport and the activity of several key lipogenic enzymes like fatty acid synthase, NADPH-generating enzymes and acetyl-coenzyme A carboxylase (Dunshea et al., 1992b; Harris et al., 1993; Etherton et al., 1995; Donkin et al., 1996). This inhibitory effect of pST reduced body fat content and altered the chemical composition of backfat. In pST-treated pigs, the backfat thickness was reduced, and the size and number of fat cells, the chemical fat content and the PUFA concentration were higher than in controls (Rehfeldt et al., 1994; Nürnberg et al., 1995b; Table 11).

Table 11 Effect of pST on backfat composition in pigs (Nürnberg et al., 1995b)

	Control (n = 37)	pST (n = 35)	Significant effect
Backfat thickness (cm)	1.8	1.37	+
Fat cell diameter (μm)	70.2	58.5	+
Lipid content of backfat (%)	75.7	62.8	+
C18:2 (%) of backfat	11.7	13.2	+
Polyunsaturated fatty acids (% of total) of backfat	12.9	14.6	+

Dunshea et al. (1992a) demonstrated in an in vivo kinetic study that pST modestly increased plasma free fatty acids concentrations but did not cause an increase in glycerol concentration, or FFA or glycerol entry rates. The PUFA content of longissimus muscle was also higher ($P<0.05$) in pST-treated pigs (Mourot et al., 1992). Meat quality parameters were slightly affected by pST (Mourot et al., 1992; Nürnberg et al., 1995b).

Conclusion

Alterations in the fatty acid composition of animal lipids, both in adipose tissue and intramuscular fat, are caused by different factors. In nonruminant species, dietary fat can greatly modify the fatty acid composition of fat deposited. The addition of 15 % rape cake and 7.5-10 % rape seed in feed mixtures is recommended in growing-finishing pigs to avoid loss of carcass quality and performance. In ruminants, small changes in fat composition can be induced by feeding unsaturated fatty acids. Fattening on pasture increased the n-3 fatty acid content of muscle in lambs by up to 175 % and of muscle of steers by up to 210 % compared with indoors- finished animals. The increase of n-3 fatty acids in meat by feeding grass or fish oil to farm animals improves their value for human nutrition, but careful attention must be paid to the potential for an increase in rancidity. The differences between animals of different gender are partially due to the amount of fat deposited. The relationship between PUFA and consistency of adipose tissue is important for producing meat with high quality. Porcine somatotropin improves the carcass composition of pigs by reducing fat deposition. The unsaturated fatty acids in backfat are increased by pST.

References

Ashes, J.R., Siebert, B.D., Gulati, S.K., Cuthbertson, A.Z., Scott, T.W., 1992. Incorporation of n-3 fatty acids of fish oil into tissue and serum lipids of ruminants. Lipids 27, 629-631.

Bouchard, C., Despres, J-P., Mauriege, P., 1993. Genetic and nongenetic determinants of regional fat distribution. Endocrine Reviews 14, 72-93.

Cameron, N.D. and Enser, M.B., 1991. Fatty acid composition of lipids in longissimus dorsi muscle of Duroc and British Landrace pigs and its relationship with eating quality. Meat Sci. 29, 295-307.

Cameron, N.D., Bishop, S.C., Speake, B.K., Bracken, J., Noble, R.C., 1994. Lipid composition and metabolism of subcutaneous fat in sheep divergently selected for carcass lean content. Anim. Prod. 58, 327-242.

Choi, N.J., Kim, E.J., Maeng, W.J., Neville, M.A., Enser, M., Wood, J.D., Scollan, N.D., 1997. Rumen biohydrogenation of fatty acids from different sources of fat. Proc. Brit. Soc. Anim. Sci., 19.

Demise, S., 1997. [Fattening and carcass performance of sheep breed and ecological performances of sheep and goats on extensive pastures]. Thesis, University of Rostock.

Doerau, M. and Ferlay, A., 1994. Digestion and utilisation of fatty acids by ruminants. Anim. Feed Sci. Technol. 45, 379-396.

Donkin, S.S., Chiu, P.Y., Yin, D., Louveau, I., Swencki, B., Vockroth, J., Evock-Clover, C.M., Peters, J.L., Etherton, T.D., 1996. Porcine somatotropin differentially down-regulates expression of the GLUT4 and fatty acid synthase genes in pig adipose tissue. J. Nutr. 126, 2568-2577.

Dunshea, F.R., Harris, D.M., Bauman, D.E., Boyd, R.D., Bell, A.W., 1992a. Effect of somatotropin on nonesterified fatty acid and glycerol metabolism in growing pigs. J. Anim. Sci. 70, 132-140.

Dunshea, F.R., Harris, D.M., Bauman, D.E., Boyd, R.D., Bell, A.W., 1992b. Effect of porcine somatotropin on in vivo glucose kinetics and lipogenesis in growing pigs. J. Anim. Sci. 70, 141-151.

Ender, K., Nürnberg, K., Kuhn, G., Rehfeldt, Ch., 1993. Effect of porcine somatotropin on carcass , meat and fat quality of growing-finishing pigs. Proc. 39th Intern. Congr. Meat Sci. & Technol.; Calgary, Canada, 22.

Ender, K., Papstein, H-J., Nürnberg, K., Wegner, J., 1997. Muscle and fat related characteristics of grazing steers and lambs in extensive systems. Proc. EU-workshop on "Effect of extensification on animal performance and product quality". 14-16 May, Melle-Gontrode, Belgium.

Enser, M., 1991. Animal carcass fats and fish oils. In: J.B. Rossel and J.L.R. Pritchard (Eds.), Analysis of oilseeds, fats and fatty foods. Elsevier Appl. Sci., London, 329-394.

Etherton, T.D. and Walton, P.E., 1986. Hormonal and metabolic regulation of lipid metabolism in domestic livestock. J. Anim. Sci. 63, Suppl. 2, 76-88.

Etherton, T.D., Donkin, S.S., Bauman, D.E., 1995. Mechanisms by which porcine somatotropin (pST) decreases adipose tissue growth in growing pigs. In: S.B. Smith and D.R. Smith (Eds.), The biology of fat in meat animals. Champaign, Illinois, 53-69.

Etherton, T.D., Louveau, I., Soerensen, M.T., Chaudhuri, S., 1993. Mechanism by which somatotropin decreases adipose tissue growth. Amer. J. Clin. Nutr. 58 , 287S-295S.
Flachowsky, G., Richter, G.H., Wendemuth, M., Möckel, P., Graf, H., Jahreis, G., Lübbe, F., 1994. [Influence of rape seed in beef cattle feeding on fatty acid composition, vitamin E concentration and oxidative stability of body fat]. Z. Ernährungswiss. 33, 277-285.
Flint, D.J. and Vernon, R.G., 1993. Hormones and adipose growth. In: M.P. Schreibman, C.G. Scanes and P.K. Pang (Eds.), The endocrinology of growth, development, and metabolism in vertebrates. Academic Press, San Diego, 469-494.
Gill, B.P., McCone, S., Onibi, G.E., Peatfield, S., Gall, K., 1995. Effect of inclusion rate and withdrawal of full-fat rapeseed on the performance and carcass fatty acid profile of finishing pigs. Anim. Sci. 60, 520.
Greef, K. H. de, Verstegen, M. W. A., Kemp, B., Togt, P. L. van der, 1994. The effect of body weight and energy intake on the composition of deposited tissue in pigs. Anim. Prod. 58, 263-270.
Harris, D.M., Dunshea, F.R., Bauman, D.E., Boyd, R.D., Wang, S.-Y., Johnson, P.A., Clarke, S.D., 1993. Effect of in vivo somatotropin treatment of growing pigs on adipose tissue lipogenesis. J. Anim. Sci. 71, 3293-3300.
Hartog, J.M., Verdouw, P.D., Klompe, M., Lamers, J.M.J., 1987. Dietary mackerel oil in pigs: effect on plasma lipids, cardiac sarcolemmal phospholipids and cardiovascular parameters. J. Nutr. 117, 1371-1378.
Hauser, N., Mourot, J., De Clercq, L., Genart, C., Remacle, C., 1997. The cellularity of developing adipose tissues in Pietrain and Meishan pigs. Reprod. Nutr. Dev. 37, 617-625.
Huerta-Leidenz, N.O., Cross, H.R., Savell, J.W., Lunt, D.K., Baker, J.F., Pelton, L.S., Smith, S.B., 1993. Comparison of the fatty acid composition of subcutaneous adipose tissue from mature Brahman and Hereford cows. J. Anim. Sci. 71, 625-630.
Huerta-Leidenz, N.O., Cross, H.R., Savell, J.W., Lunt, D.K., Baker, J.F., Smith, S.B., 1996. Fatty acid composition of subcutaneous adipose tissue from male calves at different stages of growth. J. Anim. Sci. 74, 1256-1264.
Irie, M. and Sakimoto, M., 1992. Fat characteristics of pigs fed fish oil containing eicosapentaenoic and docosahexaenoic acids. J. Anim. Sci. 70, 470-477.
Jenkins, T. C., 1993. Lipid metabolism in the rumen. J. Dairy Sci. 76, 3851-3863.
Kracht, W., Jeroch, H., Matzke, W., Nürnberg, K., Ender, K., Schumann, W., 1996. The influence of feeding rapeseed on growth and carcass fat quality of pigs. Fett/Lipid 98, 343-351.
Kuhn, G., Hartung, M., Nürnberg, G., Falkenberg, H., Langhammer, M., Schwerin, M., Ender, K., 1997. [Growth, carcass composition and meat quality in pigs with different capacity for lipid deposition]. Arch. Tierz. 40, 345-355.
Le Dividich, J., Esnault, T., Lynch, B., Hoo-Paris, R., Castex, C., Peiniau, J., 1991. Effect of colostral fat on fat deposition and plasma metabolites in the new born pig. J. Anim. Sci. 69, 2480-2488.
Lough, D.S., Solomon, M.B., Rumsey, T.S., Elsasser, T.H., Slyter, L.L., Kahl, S., Lynch, G.P., 1992. Effects of dietary canola seed and soy lecithin in high-forage diets on cholesterol content and fatty acid composition of carcass tissues of growing ram lambs. J. Anim. Sci. 70, 1153-1158.
Madsen, A., Jakobsen, K., Mortensen, H.P., 1992. Influence of dietary fat on carcass fat quality. A review. Acta Agric. Scand., Sec. A, Anim. Sci. 42, 220-225.
Mandell, I.B., Buchanan-Smith, J.G., Holub, B.J., Campbell, C.P., 1997. Effects of fish meal in beef cattle diets on growth performance, carcass characteristics, and fatty acid composition of longissimus muscle. J. Anim. Sci. 75, 910-919.

Malau-Aduli, A.E.O., Siebert, B.D., Bottema, C.D.K., Pitchford, W.S., 1998. Breed comparison of the fatty acid composition of muscle phospholipids in Jersey and Limousin cattle. J. Anim. Sci. 76, 766-773.
Mersman, H.J., 1991. Regulation of adipose tissue metabolism and accretion in mammals raised for meat quality. In: Growth regulation in farm animals. A.M. Pearson and T.R. Dutson (Eds.), Vol. 7. Elsevier Appl. Sci., London, 135-168.
Morgan, C.A., Noble, R.C., Cocchi, M., McCartney, R., 1992. Manipulation of the fatty acid composition of pig meat lipids by dietary means. J. Sci. Food Agric. 58, 357-368.
Mourot, J.; Bonneau, M., Charlotin, P., Lefaucheur, L., 1992. Effects of exogenous porcine somatotropin (pST) administration on pork quality. Meat Sci. 31, 219-227.
Nürnberg, K. and Ender, K., 1989. [Fatty acid composition of backfat in castrated males, females and young boars]. Arch. Tierz. 32, 455-464.
Nürnberg, K. and Wegner, J., 1990. [Fatty acid composition and adipocyte diameter of backfat in boars during growth]. Arch. Tierz. 34, 51-56.
Nürnberg, K. and Ender, K., 1992. [Influence of porcine somatotropin (pST) on the fat quality in pigs of different sex]. Fat Sci. Technol. 94, 349-354.
Nürnberg, K., Kracht, W., Nürnberg, G., 1994a. [Influence of feeding rapecake on carcass composition and meat quality in pigs]. Züchtungskunde 66, 230-241.
Nürnberg, K., Kracht, W., Ender, K., 1994b. [Dietary influence on the intramuscular fat composition in pigs]. Fleisch 48, 391-394.
Nürnberg, K., 1995a. Modification of polyunsaturated fatty acids in different fatty tissue. Proc. 2nd Dummerstorfer Muscle-Workshop "Muscle growth and meat quality", 17-19 May, Rostock, 149-157.
Nürnberg, K., Kuhn, G., Nürnberg, G., Rehfeldt, Ch., Ender, K., 1995b. Effect of porcine somatotropin (pST) on body composition, meat quality and characteristics of backfat in genetically different pigs. Fat Sci. Technol. 97, 153-158.
Nürnberg, K., Grumbach, S., Papstein, H-J., Matthes, H-D., Ender, K., Nürnberg, G., 1996a. [Fatty acid composition of lamb meat]. Fett/Lipid 98, 77-80.
Nürnberg, K., Küchenmeister, U., Ender, K., Hackl, W., 1996b. Influence of exogenous application of n-3 fatty acids upon the membrane properties of muscle and heart in pigs. Proc. 47th Annual Meeting of the EAAP, 25-29 August 1996, Lillehammer, Norway, 243.
Otten, W., Wirth, Ch., Iaizzo, P. A., Eichinger, H. M., 1993. A high omega 3 fatty acid diet alters fatty acid composition of heart, liver, kidney, adipose tissue and skeletal muscle in swine. Ann. Nutr. Metab. 37, 134-141.
∅verland, M., Taugb∅l, O., Haug, A. and Sundst∅l, E.,1996. Effect of fish oil on growth performance, carcass characteristics, sensory parameters, and fatty acid composition in pigs. Acta Agri. Scand., Sect. A, Anim. Sci. 46, 11-17.
Rehfeldt, Ch. and Bünger, L., 1990. [Effect of long-term selection of mice on parameter of muscle growth]. Arch. Tierz. 33, 507-516.
Rehfeldt, Ch., Nürnberg, K., Ender, K., 1994. Effects of exogenous porcine somatotropin on the development of fat cells and fatty acid composition in backfat of live finishing pigs. Meat Sci. 36, 321-331.
Robelin, J., 1986. Growth of adipose tissues in cattle; partitioning between depots, chemical composition and cellularity. A review. Livest. Prod. Sci. 14, 349-364.
Rule, D.C., Smith, S.B., Romans, J.R., 1995. Fatty acid composition of muscle and adipose tissue of meat animals. In: S.B. Smith and D.R. Smith (Eds.), The biology of fat in meat animals. Champaign, Illinois, 144-165.

Scollan, N.D., Fisher, W.J., Davies, D.W.R., Enser, M., Wood, J.D., 1997. Manipulating the fatty acid composition of muscle in beef cattle. Proc. Brit. Soc. Anim. Sci., 20.
Sellier, P. and Monin, G., 1994. Genetics of pig meat quality: a review. J. Muscle Foods 5, 187-219.
Van Oeckel, M.J., Casteels, M., Warnants, N., Van Damme, L., Boucque, Ch.V., 1996. Omega-3 fatty acids in pig nutrition: implications for the intrinsic and sensory quality of the meat. Meat Sci. 44, 55-63.
Warnants, N., Van Oeckel, M.J., Boucque, Ch.V., 1996. Incorporation of dietary polyunsaturated fatty acids in pork tissue and its implications for the quality of the end products. Meat Sci. 44, 125-144.
Wegner, J. and Matthes, H.-D., 1994. [Cellular growth of muscle fibres and adipocytes, and meat quality of Hereford steers under extensive maintenance]. Arch. Tierz., 37, 599-604.
Wegner, J., Albrecht, E., Ender, K., 1998. [Morphological aspects of intramuscular fat deposition in cattle]. Arch. Tierz. 41, 313-320.
Wolfram, G., 1997. [Fat as source of energy, essential fatty acids and fat soluble substances: recommendation for fat intake of healthy people]. In: C. Wenk, R. Amado and M. Dupius (Eds.), Fat in diet and nutrition. Wiss. Verlagsgesellschaft Stuttgart, 153-159.
Wood, J. D. and Enser, M., 1997. Factors influencing fatty acids in meat and the role of antioxidants in improving meat quality. Brit. J. Nutr. 78, Suppl. 1, S49-S60.
Zembayashi, M. and Nishimura, K., 1996. Genetic and nutritional effects on the fatty acid composition of subcutaneous and intramuscular lipids of steers. Meat Sci. 43, 83-92.