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Effects of Dietary Energy Density on Growth, Carcass Quality and mRNA Expression of Fatty Acid Synthase and Hormone-sensitive Lipase in Finishing Pigs

Liu, Z. H.[1], F. Y. Yang[1], L. J. Kong[2], C. H. Lai[2,]*, X. S. Piao[2], Y. H. Gu[1] and X. Q. Ou[1]

[1]Chongqing Academy of Animal Science, Chongqing, 402460, China

ABSTRACT : A single factorial experiment was conducted to test the effects of three dietary levels of energy on mRNA expression of fatty acid synthase (FAS-mRNA) and hormone-sensitive lipase (HSL-mRNA) and their association with intramuscular fat in finishing pigs. 72 crossbred (Large White×Rongchang) barrows with an average initial body weight of 20.71 (s.e. 0.1) kg, were randomly allotted to three dietary treatments (11.75, 13.05 and 14.36 MJ DE/kg) and fed until slaughtered at 100 or 101 kg. The diets were iso-nitrogenous and iso-essential amino acids. The growth performances including the duration of finishing were changed linearly ($p<0.05$) or quadratically ($p<0.05$) with increased dietary energy levels. The effects of dietary energy content on the percentage of external fat, intramuscular backfat and the fat thickness were linear ($p<0.05$). The content of dietary energy increased FAS-mRNA linearly or quadratically, while HSL-mRNA decreased linearly or quadratically in backfat and *Longissmus dorsi* muscle. Meanwhile, significant positive correlations ($p<0.05$) were found between energy level and intramuscular fat, FAS-mRNA or the ratio of FAS-mRNA to HSL-mRNA, between the ratio of FAS-mRNA to HSL-mRNA and intramuscular fat. However, the correlations between HSL mRNA and dietary energy or intramuscular fat were negative ($p<0.05$). The results indicated that dietary energy level regulates lipid accumulation, especially intramuscular fat, possibly by modulating the mRNA of FAS and HSL together rather than individually. (**Key Words :** Energy, Fatty Acid Synthase, Hormone-sensitive Lipase, Carcass Quality, Finishing Pigs)

INTRODUCTION

Many researchers have investigated the effect of dietary energy density on growth performance and carcass characteristic (Smith et al., 1999), physical and/or chemical composition of total body at slaughter (Bikker et al., 1996a and b; Quiniou et al., 1996a and b; Quiniou and Noblet, 1997) in pigs. It is well established that the increase of energy supply can improve the growth rate, and increasing the level of DE also means an increase in the level of dietary fat/oil, consequently affecting the composition of fatty acids in the body no matter the difference of genotypes and sexes.

Body fat is mainly consisted of triglyceride, which is found in both adipose tissue and muscle tissue (Van der Vusse and Reneman, 1996; Holm et al., 2000). Adipose tissue triglyceride represent the main storage of fatty acids, which come from de novo fatty acid biosynthesis and dietary lipids and are catalyzed by two enzyme systems that function sequentially: acetyl CoA carboxylase and fatty acid synthase (FAS) (Smith et al., 2003). On the other hand, hydrolization of adipose is done mainly by hormone-sensitive lipase (HSL) that has a critical role in the control of energy homeostasis and catalyzes the rate-limiting step in the breakdown of adipocyte triglyceride (Belfrage et al., 1984). In a general way, the deposition of adipose is in a homeostasis and the content of body fat depends on the two contrary processes of adipose synthesis and breakdown. Regulation of the enzymatic activities of FAS and HSL is very important for the synthesis and mobilization of triglyceride. However, there is little information on the relationship between dietary energy levels and FAS-mRNA or HSL-mRNA.

The objective of the current study was to determine whether the changes of dietary energy would influence body fat content, FAS-mRNA or HSL-mRNA, and to investigate whether the effect of energy levels on lipid accumulation was related to the cooperative action of FAS and HSL.

* Corresponding Author: C. H. Lai. Tel: +86-10-62732723, Fax: +86-10-62734608, E-mail: laichh@mafic.ac.cn

[2] College of Animal Science and Technology, China Agricultural University, Beijing, 100094, China.

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Table 1. Composition and nutrient levels of diets (as fed basis)

Energy density (MJ/kg)	20 to 50 kg			50 to 80 kg			80 to 100 kg		
	11.75	13.05	14.36	11.75	13.05	14.36	11.75	13.05	14.36
Ingredients (%)									
Corn	39.34	61.0	71.3	44.86	66.8	77.15	48.95	70.0	83.4
Wheat bran (milled)	44.0	17.1	0	44.4	17.0	0	44.0	17.5	0
Soybean meal	14.0	19.0	23.5	8.0	13.2	17.4	4.4	10.0	11.7
Soybean oil	0	0	2.1	0	0	2.2	0	0	2.1
Salt	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
L-lysline	0.06	0	0	0.14	0.1	0.05	0.05	0	0
Calcium carbonate	1.3	1.1	0.7	1.3	1.1	0.7	1.3	1.1	0.8
Dicalcium phosphate	0	0.5	1.1	0	0.5	1.2	0	0.1	0.7
Premixture[1]	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Total	100	100	100	100	100	100	100	100	100
Nutrient levels[2]									
DE (MJ/kg)	11.76	13.05	14.35	11.72	13.01	14.35	11.72	13.05	14.35
Crude protein (%)	16.28	16.04	16.17	14.22	14.02	14.04	12.96	13.00	12.82
Calcium (%)	0.59	0.62	0.61	0.57	0.6	0.61	0.56	0.50	0.52
Total phosphorus (%)	0.58	0.51	0.51	0.57	0.49	0.51	0.56	0.42	0.41
Lysline (%)	0.61	0.61	0.62	0.56	0.56	0.56	0.41	0.41	0.41
Methionine (%)	0.21	0.23	0.25	0.17	0.20	0.23	0.15	0.19	0.21
Threonine (%)	0.58	0.51	0.55	0.38	0.44	0.48	0.34	0.40	0.40
CF (%)	4.22	3.21	2.43	4.08	2.95	2.26	3.9	2.85	2.02
NDF (%)	20.7	13.7	8.8	20.2	13.4	8.5	20.7	13.4	8.2
ADF (%)	8.1	5.6	4.1	7.7	5.2	3.7	7.4	5.1	3.3

[1] Provided per kilogram of complete feed: vitamin A, 9,000 IU; vitamin D_3, 1,700 IU; vitamin E, 16 IU; vitamin K_3, 2 mg; vitamin B_1, 1.6 mg; vitamin B_2, 4 mg; vitamin B_6, 1.6 mg; vitamin B_{12}, 0.02 mg; niacin, 20 mg; pantothemic acid, 10 mg; folic acid, 0.9 mg; biotin, 0.08 mg; choline chloride, 640 mg; Fe, 192 mg; Cu, 120 mg; Zn, 140 mg; Mn, 23 mg; I, 0.6 mg; Se, 0.32 mg.

[2] Crude protein, calcium and total phosphorus are analyzed and others are calculated values.

MATERIALS AND METHODS

Experimental animals and diets

Seventy-two crossbred (Large White×Rongchang) barrows were randomly allotted to three dietary treatments, with six pens per treatment and four pigs per pen. The initial average body weight of pigs was 20.71 (s.e. 0.10) kg, and end body weight was 100 to 101 kg. Pigs were housed during the whole experimental period in pens on a concrete floor (temperature 20 to 28°C), equipped with a feeder and a water nipple. Feed and water were available *ad libitum*.

The control diet was formulated according to Feeding Standard of Swine (Ministry of Agriculture of Chinese People's Republic, 2004) with 13.05 MJ DE/kg. The experimental diets with high (14.36 MJ DE/kg) or low (11.75 MJ DE/kg) digestible energy level were formulated by increasing or decreasing dietary DE with 10% on the base of control diet, and the dietary crude protein or lysine levels were in consistent with the control diet (Table 1).

Performance recording

Individual body weight at the beginning and end of the trial was measured. Daily feed intake and feed conversion ratio were calculated on a per pen basis.

When pig body weight was about 100 kg, two pigs per pen were transported to the research slaughterhouse for slaughter by electrical stunning and bled then scalded, dehaired and eviscerated.

Backfat (dorsal adipose tissues) and *longissimus dorsi* muscle were removed and immediately frozen in liquid nitrogen, then stored at -80°C until analyses.

Carcass evaluation and meat quality

Carcass weight was the hot weight of both sides of the carcass. Carcass is the body that blood, hair, hoofs, and viscera are excluded. Backfat thickness was a mean value of the depths of subcutaneous layer including the skin thickness from three points (the shoulder, the joint of chest and middle, and the joint of middle and haunch and between the sixth and seventh ribs) measured using a ruler with a precision of 0.1 mm. The pH of meat at 45 min after slaughter (pH_{45min}) was taken by using a meat probe connected to a pH meter (CRISON 507, Crison Instruments SA, Barcelona, Spain) and inserted into the *longissimus doris* muscle at the level of the last rib of each carcass. Also, a chop of 100±15 g *longissimus doris* muscle was taken from the left side loin of each carcass at the last rib level and recorded before and after chilling to estimate dripping losses. At the same time, carcasses were boned and muscles were separated from skin and fat to calculate the percentage of lean and external fat (subcutaneous and kidney fat). Intramuscular (IM) fat in *longissimus dorsi* muscle was

Table 2. Effect of dietary energy density on growth performance and duration of fattening over the whole experiment

Items	Energy density (MJ/kg)			SEM[a]	p value	
	11.75	13.05	14.36		Linear	Quadratic
Initial body weight (kg)	20.82	20.73	20.58	0.18	-	-
Final body weight (kg)	100	101	101	0.32	0.25	0.41
Average daily gain (g)	595	656	640	14.5	0.09	0.03
Average daily feed intake (g)	2,332	2,420	2,124	36.6	0.05	0.01
Feed: gain	3.92	3.69	3.32	0.05	0.01	0.05
Duration of fattening (days)	135	122	125	0.37	0.02	0.01

[a] Standard error of the mean, n = 12.

chemically determined using the method of direct soxhlet extraction of fat by a solvent (hexane) and expressed as the weight percentage of wet muscle tissue (AOAC, 1990).

Extraction of RNA and cDNA production

Total RNA was extracted from the dorsal adipose tissues and *longissimus dorsi* muscle by using TRIzol reagent (Invitrogen. Life Technologies. USA) according to the manufacturer's instructions. RNA was treated with DNase I to remove any contaminating DNA. RNA integrity was verified electrophoretically by ethidium bromide staining. RNA purity was determined by OD_{260} and OD_{280} using a TECAN GENios Microplate reader (TECAN. Austria).

Total RNA was reverse transcribed as following way. Briefly. 2 μg RNA isolated from each sample was added to a 40 μl reaction system containing 1.0 μl of Oligo-dT_{18} (Promega, Madison. WI), 1.0 μl of dNTPs (Sigma, Chemical). 1.0 μl of RNasin inhibitor (Promega. Madison, WI). 2.0 μl of M-MLV transcriptase (Promega, Madison, WI). 8.0 μl of M-MLV RT reaction buffer (Promega, Madison. WI) and 25 μl of RNase-free water. Cycle parameters for the reverse-transcription procedure were 1 cycle of 75°C. 5 min; 1 cycle of 37°C 2 h; 1 cycle of 75°C. 15 min; and 1 cycle of 4°C, 5 min. The RT products (cDNA) were stored -20°C for relative quantification PCR.

Real-time fluorescence PCR for quantification of FAS and HSL mRNA

Quantitative analysis of gene expression was carried out in the DNA Engine Opticon 2 Fluorescence Detection System (MJ Research, USA) according to an optimized PCR protocol. which was described as Lai et al. (2005).

Complementary DNA was initially amplified by polymerase chain reaction using primer pairs for FAS. HSL and β-actin (as an internal control) with the following sequences: sense 5'- AGC CTA ACT CCT CGC TGC AAT -3', and anti-sense 5'- TCC TTG GAA CCG TCT GTG TTC -3' for FAS (196 bp. Genbank accession no. AY183428). sense 5'- GTC ACG CAC AGC ATG GAC CT -3' and anti-sense 5'- AAG CGG CCA CTG GTG AAG AG -3' for HSL (656 bp. Genbank accession no. AJ000482) as well as sense 5'- TGC GGG ACA TCA AGG AGA AG -3', and anti-sense 5'- AGT TGA AGG TGG TCT CGT GG -3' for β-actin (216 bp. Genbank accession no. AY550069).

The protocol of PCR used in these amplified reactions included enzyme incubation at 50°C for 2 min. followed by the denaturation program at 95°C for 5 min. and finally the amplification and quantification program repeated 35 times at 94°C for 40 s. Different annealing temperatures were subjected to the different target genes for 40 s at 72°C to allow the DNA strand to extend for 40 s with a single second to detect fluorescence density. The melting curve program (65-95°C) was run with a heating rate of 0.1°C per second and a continuous fluorescence measurement and was finally extended for 8 min at 72°C. The annealing temperatures for FAS. HSL and β-actin were 59°C. 58.5°C. and 64°C. respectively. All samples were measured in triplicate.

Statistical analysis

Statistical analyses were performed with the SAS software package (SAS Inst. Inc., Cary. NC. 1996) and the general linear model (GLM) procedure was used. Polynomial contrasts (linear or quadratic) were used to determine the effect of energy levels on the various parameters. The results are given as means with standard error of the mean. At the same time. the correlation coefficients among energy density. intramuscular fat. FAS mRNA. HSL mRNA and mRNA ratio of FAS to HSL were computed. A level of $p \leq 0.05$ was set as the criterion for statistical significance. For growth data. pens were used as the experimental unit while the individual pig was used as the experimental unit for carcass composition, meat quality. FAS-mRNA and HSL-mRNA.

RESULTS

Growth performance and slaughter characteristics

The average daily gain was improved quadratically ($p < 0.05$). and average daily feed intake. feed conversion ratio and the fattening days were changed linearly ($p<0.05$) or quadratically ($p<0.05$) with the dietary digestible energy levels increased.

According to experiment plan the animals in different treatment groups were slaughtered at a similar finishing weight (Table 2). Carcass weights. dressing percentage.

Table 3. Effect of dietary energy density on carcass and meat quality of pigs at the end of the study

Item	Energy density (MJ/kg)			SEM[a]	p value	
	11.75	13.05	14.36		Linear	Quadratic
Carcass weight (kg)	71.6	74.5	72.6	1.66	0.51	0.17
Dressing proportion (%)	71.2	73.9	71.7	0.74	0.71	0.11
Lean (%)	46.0	45.1	43.0	6.04	0.72	0.94
External fat (%)	42.7	44.9	46.4	4.35	0.02	0.06
Backfat thickness (cm)	3.85	4.12	4.25	0.01	0.02	0.05
Intramuscular fat (%)	2.92	3.06	3.25	0.01	0.05	0.17
Drip loss (%)	15.8	15.7	15.4	1.72	0.92	0.97
pH_{45min}	6.31	6.32	6.52	0.09	0.15	0.26

[a] Standard error of the mean, n = 12.

Table 4. Effect of dietary energy density on mRNA expressions of fatty acid synthase and hormone-sensitive lipase in backfat and *longissmus dorsi* muscle of pigs at the end of study[a]

Items	Energy density (MJ/kg)			SEM[b]	P-value	
	11.75	13.05	14.36		Linear	Quadratic
Backfat						
FAS mRNA	3.97	4.52	5.65	0.28	0.05	0.01
HSL mRNA	19.87	16.76	15.14	0.91	0.04	0.01
FAS/HSL	0.20	0.26	0.37	0.01	0.05	0.01
Longissmus dorsi muscle						
FAS mRNA	0.65	0.80	0.94	0.06	0.01	0.02
HSL mRNA	2.43	2.10	1.88	0.10	0.03	0.01
FAS/HSL	0.26	0.38	0.49	0.03	0.01	0.01

[a] The values are expressed as a relative ratio of the amount of target gene copies to the amount of β-actin (housekeeping gene) copies.
[b] Standard error of the mean, n = 12.

Table 5. Correlations between dietary energy density and intramuscular fat, mRNA expression of fatty acid synthase and hormone-sensitive lipase and the mRNA ratio of FAS to HSL in *longissmus dorsi* muscle of pigs at the end of study (no. = 12)[a]

	Energy density	Intramuscular fat	FAS mRNA	HSL mRNA
Intramuscular fat	0.723*	1.00		
FAS mRNA	0.743*	0.677	1.00	
HSL mRNA	-0.832**	-0.694*	0.199	1.00
mRNA ratio of FAS to HSL	0.766*	0.755*	0.830*	-0.537

[a] Superscript * and ** mean significance of correlation coefficients at 0.05 and 0.01 levels, respectively.

leans, drip loss and pH_{45min} were not influenced by dietary energy content (Table 3). However, the percentage of external fat and intramuscular backfat, and the thickness fat were increased linearly ($p<0.05$) as the increasing of the dietary energy content.

FAS-mRNA and HSL-mRNA in backfat and longissmus dorsi muscle

The FAS-mRNA in backfat and *longissmus dorsi* muscle were increased in linear or quadratic ($p<0.05$), while the HSL-mRNA in backfat and *longissmus dorsi* muscle were decreased linearly or quadratically ($p<0.05$) with dietary energy content increasing. Moreover, compared with the low energy group, the high energy group had a greater ($p<0.05$) ratio of FAS-mRNA to HSL-mRNA (Table 4). In addition, both FAS-mRNA and HSL-mRNA in backfat were greater than those in *longissmus dorsi* muscle ($p<0.01$).

Correlations between energy and intramuscular fat, FAS-mRNA or HSL-mRNA

The correlations between energy and intramuscular fat, FAS-mRNA or HSL-mRNA were showed in Table 5. The positive correlations ($p<0.05$) were observed between energy and intramuscular fat, FAS-mRNA or the ratio of FAS-mRNA to HSL-mRNA, between the ratio of FAS-mRNA to HSL-mRNA and intramuscular fat, respectively. However, the dietary energy and mRNA of HSL, the intramuscular fat and mRNA of HSL were negatively correlated ($p<0.05$), respectively.

DISCUSSION

The present experimental results showed that there was a quadratic increase in average daily gain, while a linear or quadratic decrease in average daily feed intake, feed conversion ratio and the fattening days as the density of energy in the diets increased. The lower average daily gain on low energy density diet has been previously noticed in

the studies of Quiniou et al. (1995, 1996a and 1997). However, Smith et al. (1999) reported that increasing energy density did not affect overall average daily gain; while average daily feed intake and feed efficiency (feed:gain ratio) were decreased linearly. Except for the type of pigs, the inconsistency might be associated with the composition of diets. In this present study, the proportion of corn was substituted with different level of milled wheat bran to obtain different contents of digestible energy with isonitrogen and isolysine, which resulted in the lower energy with the higher fibre level. Thus the result that the lowest average daily gain was observed in lowest energy group may be related to the higher level of fibre in this group. O'Doherty et al. (2002) also reported that pigs fed the 5% crude fibre diets had a higher average daily gain during the finisher and combined grower and finisher phases than pigs fed the 7% crude fibre diets. Meanwhile, Eggum (1995) reported that the utilization of energy and absorption of other nutrients were not only influenced, but also improved to some extent when the content of fibre was appropriate in pig diets. Moreover, Galassi et al. (2004) reported that diet (4.7% CF) containing higher milled wheat bran was not associated with decreased in net energy content. Therefore, the effect of crude fibre on the net energy content was ignored because the levels of crude fibre were less than 4.3% in this present study.

In the present study, we found energy levels trended to decrease the lean and increased the external fat proportion, backfat thickness and intramuscular fat content, which was in agreement with the results of Quiniou et al. (1995) who reported that as ME intake increased lean proportion continuously decreased from 604 to 569 g/kg of eBW (empty body weight), while fat content increased from 67 to 105 g/kg eBW with energy level increased. As a chemical composition, intramuscular fat is similar to others adipose tissue, which is consisted of triglyceride. Therefore, we mainly investigated that the relationship between dietary energy and intramuscular fat in *longissmus dorsi* muscle in this study.

The quantity of triglyceride in adipose and muscle tissue is the net outcome of synthesis and degradation. Therefore, the state and rate of synthesis and breakdown of triglyceride influence the deposition of adipose tissue. The FAS catalyzes the last step in the fatty acid biosynthetic pathway, which is regarded as a rate-limiting enzyme in fatty acid synthesis. HSL is the sole enzyme responsible for the removal of the first fatty acid chain from intracellular triglyceride (Langin et al., 1996; Holm et al., 2000) that is rate-limiting in triglyceride degradation in all situations (Kazala et al., 2003). The results of this study showed that the lower the content of intramuscular fat was, the lower the mRNA expression of FAS was, while the higher the mRNA expression of HSL was. These results suggested that the content of intramuscular fat had an increased trend with the increasing of FAS-mRNA or with the decreasing of HSL-mRNA, which were in agreement with the lipogenesis of FAS and the lipolysis of HSL. There was no significant correlation between FAS-mRNA and intramuscular fat while a significant negative correlation was observed between HSL-mRNA and intramuscular fat. The latter was consistent with the result of Kazala et al. (2003) in study of cattle. The significant correlations between HSL-mRNA in muscle and intramuscular fat content suggested that HSL mRNA or activity might be useful in predicting the extent of intramuscular fat deposition.

Because of the contrary roles of FAS and HSL in the deposition of adipose, it was investigated that the relationship between the ratio of FAS-mRNA to HSL-mRNA and intramuscular fat in the present study. The result showed that the correlation coefficient between the ratio of FAS-mRNA to HSL-mRNA and intramuscular fat was significant, which is in agreement with the result of Chen et al. (2004). In their studies, they divided 100 finishing obese crossbred (Suzhou×Taihu) pigs to three groups according to the fat content to investigate their particular fat metabolism. The results indicated that the pigs with high intramuscular fat content exhibited significantly higher the ratio of FAS-mRNA to HSL-mRNA, and they speculated that FAS and HSL were involved in the deposition of intramuscular fat in *longissimus dorsi* muscle. The results of present study supported the speculation of Chen's (2004) and indicated that the processes of synthesis and mobilization of triglyceride together influenced the adipose deposition, in which the mobilization of triglyceride plays a crucial role. The FAS accelerates the adipose deposition, but the lipolysis by HSL reduces the accumulation of adipose in muscle. The antagonistic effects of FAS and HSL result in the net deposition of adipose in muscle.

There are many factors that influence expression or activities of FAS and HSL, in which nutrients play an important role. Carbohydrate (Clarke et al., 1990; Cheng et al., 2006), protein (Mildner and Clarke, 1991) and trace element (Wilson et al., 1997) affected the mRNA expression or enzymatic activity of FAS. The mRNA expression or enzymatic activity of FAS was also modulated by the saturation degree (Toussant et al., 1981; Clarke et al., 1990) and content (Wicker and Puigserver, 1990) of fatty acids, position of double bond (Yin et al., 2001) and length of carbon chain (MacDougald et al., 1992) of fatty acid also influence. Similarly, energy content (Stich et al., 1997), fatty type (Awad and Chattopadhyay, 1986) and fasting (Sztalryd and Kraemer, 1994; Lee et al., 2006) influence expression or activity of HSL. In this study, it was found that the mRNA expression of FAS in backfat was increased, while the HSL-mRNA in backfat and muscle was decreased and the ratio of FAS-mRNA to HSL-mRNA was improved

significantly with dietary energy content increasing. Thus, considering the effect of dietary energy on the deposition of intramuscular fat and the mRNA expression of FAS and HSL, as well as the correlations among them, it could be speculated that dietary energy levels influenced the fat deposition, at least in part, through the pathway of regulating the expression of FAS and HSL together. However, the confirmed mechanism should be further investigated in the future.

IMPLICATIONS

The significant correlation coefficients between energy density and intramuscular fat, mRNA expression of FAS and HSL suggested that dietary energy might regulate the adipose accumulation by affecting the mRNA expression of FAS and HSL. Moreover, the significantly negative coefficient between HSL mRNA and intramuscular fat indicated that the expression of the enzyme might serve as potential indicator of the fat content of muscle, which also provided us an idea on improving meat quality by nutrition regulation.

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