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Effects of reduced dietary protein level and fat addition on heat production and nitrogen and energy balance in growing pigs

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Abstract — Two trials were conducted in order to quantify the effects of reduction of dietary crude protein (CP) level, with or without fat addition, on heat production and energy balance in growing pigs. In trial 1, extreme variations in diet composition were obtained by using purified ingredients; conventional ingredients were used in trial 2. In each trial, three diets were prepared. Diet 1 had a conventional CP level (18.9 and 17.4% in trials 1 and 2, respectively) while diet 2 had a reduced CP level (12.3% and 13.9% in trials 1 and 2, respectively); diet 3 also had a reduced CP level (13.6 and 14.9%, respectively) and 3.5% (trial 1) or 4% (trial 2) fat was added. In both trials, diets 2 and 3 were supplemented with industrial amino acids in order to ensure similar ratios between digestible essential amino acids and net energy (NE) between diets while exceeding requirements of animals. Each diet was measured in 6 (trial 1) or 5 (trial 2) individually caged 60-kg pigs for digestibility, components of heat production (indirect calorimetry) and energy, protein and fat balances. Energy supply was standardised between diets (1.9 MJ NE per kg $BW^{0.60}$). A reduction of dietary CP level (diets 2 and 3 vs. diet 1) significantly reduced urinary nitrogen loss without impairing nitrogen gain in pigs. A reduction of dietary CP alone (diet 2 vs. diet 1) contributed to a significant reduction of total heat production and, more specifically, its component related to feed utilisation. This effect was accentuated when fat was added (diet 3 vs. diet 2). Fasting heat production (770 kJ per kg $BW^{0.60}$) and activity heat production (8% of ME intake) were not affected by dietary treatment. These results emphasise the interest of using an NE concept for estimating the energy value of pig feeds.

pig / crude protein /crude fat / heat production / energy value

Résumé — **Effets de la réduction du taux de protéines et de l'addition de matières grasses dans l'aliment sur la production de chaleur et le bilan d'azote et d'énergie chez le porc en croissance.** Dans le but de quantifier les effets d'une diminution de la teneur en matières azotées totales (MAT) et de l'addition de matières grasses dans l'aliment chez le porc, deux essais ont été réalisés.

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Trois aliments ont été préparés pour chaque essai. L'aliment 1 a une teneur normale en MAT (18,9 et 17,4 % respectivement dans les essais 1 et 2) ; la teneur en MAT de l'aliment 2 est abaissée (12,3 et 13,9 % de MAT pour les essais 1 et 2) ; il en est de même pour l'aliment 3 (13,6 et 14,9 % de MAT) qui contient également 3,5 % (essai 1) ou 4 % (essai 2) de matières grasses ajoutées. Les aliments 2 et 3 sont supplémentés en acides aminés industriels de façon à conserver constants les ratios entre les teneurs en acides aminés essentiels digestibles et la teneur en énergie nette (EN) de tous les aliments. Chaque aliment a été distribué à 6 (essai 1) et 5 (essai 2) porcs de 60 kg de poids vif (PV) maintenus individuellement en cage afin de mesurer les coefficients de digestibilité, les composantes de la production de chaleur (calorimétrie indirecte) et les bilans d'énergie, de protéines et de lipides. Les niveaux alimentaires sont égalisés entre les traitements (1,9 MJ d'EN par kg $PV^{0.60}$). La diminution du taux de MAT réduit nettement l'excrétion d'azote urinaire sans affecter le niveau de rétention azotée. L'abaissement du taux de MAT (aliment 2 vs. aliment 1) entraîne une diminution significative de la production de chaleur et plus particulièrement la composante liée à l'utilisation de l'aliment. Cet effet est accentué lorsque l'aliment est enrichi en matières grasses (aliment 3 vs. aliment 2). La production de chaleur à jeun (770 kJ par kg $PV^{0.60}$) et les dépenses d'activité physique (8 % de l'EM ingérée) ne sont pas affectées par la nature de l'aliment. Ces résultats confirment l'intérêt d'utiliser le concept EN pour estimer la valeur énergétique des aliments pour le porc.

porc / matières azotées / matières grasses / production de chaleur / valeur énergétique

1. INTRODUCTION

Progress in the determination of amino acid (AA) requirements for growing pigs and the increasing availability of industrial AA allow to supply essential AA at levels that meet the requirements for optimal growth but at lower dietary crude protein (CP) contents. Such diets have no detrimental effect on animal performance and contribute to a marked reduction of nitrogen excretion [2, 4]. According to the results of Just [9] and Noblet et al. [14, 15], these low-protein diets should generate less heat due to the reduced energy expenditure for urea synthesis and turnover of body proteins [23]. A further reduction of heat production can be achieved by including fat in the diet [14]. However, such diets may produce fatter carcasses in ad libitum fed pigs [10].

Voluntary feed intake (and thus performance) in growing pigs is highly dependent on ambient temperature. A marked reduction in feed intake is observed at temperatures above 25 °C in order to reduce heat production and maintain homeothermy [19]. Such temperatures frequently occur in Europe during Summer and can be permanent in areas where pig production has been recently and rapidly developing (Brazil, Asia, ...). It can therefore be hypothesised that using diets that produce less heat should attenuate the reduction of feed intake and growth associated with heat stress.

The objective of this study is to measure heat production of diets that differ in CP and fat content in order to test the abovementioned hypothesis and confirm the underlying assumptions of NE systems [14]. Furthermore, it will serve to characterise diets that will be used in field trials conducted in both growing pigs [11] and lactating sows [22] exposed to either thermoneutral or warm climatic conditions. Other results from the same study have been published by Le Bellego et al. [12].

2. MATERIALS AND METHODS

2.1. Experimental design

The study consisted of two trials in which three diets were used. Diet 1 was a control diet where almost all AA were provided by

protein. The two other diets (diets 2 and 3) had reduced CP levels and were supplemented with L-lysine, DL-methionine, L-threonine, L-tryptophan, L-isoleucine and L-valine. Diet 3 contained additional fat. In trial 1, differences in CP content between treatments were amplified by using purified ingredients (corn starch and soybean proteins). In trial 2, conventional ingredients were used resulting in smaller differences between treatments. Ingredients and chemical composition of diets are given in Tables I and II. The AA levels were formulated in order to maintain a constant ratio between standardised digestible lysine and net energy (NE) (0.76 g per MJ) and to achieve standardised methionine + cystine, threonine, tryptophan, isoleucine and valine digestible supplies equivalent to at least 60, 65, 20, 60 and 70% of standardised digestible lysine supply, respectively [7, 8] (Tab. II).

In trial 1, six animals per treatment were selected from the experimental herd so that body weights (BW) and ages between the three diets were relatively balanced. In trial 2, five blocks of three littermates were chosen where each littermate was assigned to a diet. Pigs were Piétrain × (Landrace × Large White) barrows weighing about 60 kg at the beginning of the measurement period; their age then averaged 109 days in both trials. As described below, two respiration chambers were used and animals were measured successively (two per week); trial 1 was conducted first.

2.2. Housing and feeding

All animals were adapted to experimental conditions, diets and digestibility cages for two weeks. Feeding level was progressively increased in order to achieve about 1.90 MJ of NE per kg of $BW^{0.60}$ at the end of the adaptation period. This feeding level was maintained subsequently but the daily amount was adjusted each day according to

Table I. Composition of experimental diets.

	Trial 1			Trial 2		
Diet	1	2	3	1	2	3
Composition (%)						
Wheat	40.52	40.52	40.52	36.85	42.44	38.68
Corn	40.53	40.53	40.51	36.84	42.43	38.66
Soybean meal	7.00	7.00	7.00	23.00	11.00	14.50
Isolated soybean protein	8.70	–	0.70	–	–	–
Corn starch	–	7.28	3.00	–	–	–
Corn oil	–	–	3.50	–	–	4.00
L-lysine	–	0.58	0.61	0.06	0.43	0.42
D/L-methionine	–	0.18	0.20	–	0.11	0.13
L-threonine	–	0.25	0.27	–	0.16	0.17
L-tryptophan	–	0.08	0.09	–	0.05	0.05
L-isoleucine	–	0.14	0.15	–	0.04	0.04
L-valine	–	0.19	0.20	–	0.09	0.10
Dicalcium phosphate	1.20	1.20	1.20	1.20	1.20	1.20
Calcium carbonate	0.60	0.60	0.60	0.60	0.60	0.60
Salt	0.45	0.45	0.45	0.45	0.45	0.45
Minerals and vitamins	1.00	1.00	1.00	1.00	1.00	1.00

Table II. Chemical composition and nutritional value of experimental diets.

	Trial 1			Trial 2		
Diet	1	2	3	1	2	3
Chemical composition[1] (%)						
Ash	4.5	4.1	4.3	5.0	4.3	4.4
Crude protein	18.9	12.3	13.6	17.4	13.9	14.9
Starch	48.1	54.5	50.7	45.0	52.2	47.3
Ether extract	2.1	2.1	5.6	2.4	2.4	6.0
Crude fibre	1.7	1.8	1.6	2.4	1.9	2.4
NDF	8.2	8.6	8.5	10.5	8.5	9.4
ADF	2.3	2.4	2.4	3.4	2.7	3.1
ADL	0.3	0.4	0.3	0.5	0.3	0.4
Total amino acids[1] (%)						
Lysine	0.91	0.89	0.94	0.89	0.87	0.91
Threonine	0.65	0.61	0.64	0.61	0.59	0.63
Tryptophan	0.22	0.18	0.21	0.21	0.19	0.20
Methionine	0.29	0.37	0.41	0.27	0.30	0.30
Methionine + cysteine	0.58	0.58	0.62	0.57	0.55	0.56
Isoleucine	0.75	0.52	0.58	0.70	0.51	0.55
Leucine	1.51	0.96	1.01	1.42	1.08	1.13
Valine	0.86	0.67	0.72	0.82	0.67	0.72
Histidine	0.42	0.27	0.27	0.40	0.30	0.31
Phenylalanine	0.87	0.52	0.54	0.84	0.61	0.65
Nutritional values[2]						
Gross energy[1] ($MJ \cdot kg^{-1}$)	16.21	15.84	16.56	15.90	15.84	16.67
DE ($MJ \cdot kg^{-1}$)	14.24	13.97	14.74	14.00	13.93	14.77
ME ($MJ \cdot kg^{-1}$)	13.70	13.61	14.36	13.45	13.50	14.32
NE ($MJ \cdot kg^{-1}$)	10.25	10.51	11.19	9.96	10.29	11.00
Digestible lysine ($g \cdot MJ^{-1}$ NE)	0.76	0.76	0.76	0.76	0.76	0.76

[1] Measured values adjusted for 87.3% dry matter.
[2] DE and ME for digestible and metabolisable energy, respectively; values are calculated according to INRA (1989); NE for net energy; NE calculated according to Noblet et al. (1994); standardised digestible lysine content according to Eurolysine – ITCF tables (1995); values adjusted for 87.3% dry matter.

expected increases in BW. The diets were fed as pellets and pigs had free access to water. Feed was given to the animals in three approximately equal meals when they were not in the respiration chamber and in four equal meals (distributed at 09.00 h, 13.00 h, 17.00 h and 21.00 h using automatic feeders) while in the respiration chamber.

Following adaptation, faeces and urine were collected daily during an 8-d period. During the last five days of the collection period, animals were placed in respiration chambers. Two 12 m^3 open-circuit respiration chambers similar to those described by Vermorel et al. [30] were used. In the respiration chamber, the animal was housed in an individual metabolism cage, which was mounted on force sensors (Kistler, type 9104A, Winterthur, Switzerland) that produced an electrical signal proportional to the physical activity of the animal. The trough was placed on a load cell in order to measure the time, size and duration of each meal. Respiration chambers were

air-conditioned to maintain a temperature of 24 °C whereas relative humidity was controlled at 70%. A 13 h lighting schedule (8:00 a.m. to 9:00 p.m.) was used. After the collection period, animals remained for two additional days in the respiration chamber for measurement of the fasting heat production. During this period, no feed was available until 20.30 h on the second day.

2.3. Measurements

Animals were weighed at the beginning and at the end of the collection period. During the total period, feed intake was measured and feed refusals or spillage were collected daily and analysed for DM content. For each diet and each pig, a feed sample was taken for DM determination. Samples were pooled per diet and trial for further chemical analysis.

Faeces were collected daily, stored at 2 °C, pooled over successive days and, at the end of the period, weighed, mixed, subsampled and freeze-dried for chemical analysis. A second sample of faeces was dried for 48 h to determine faecal DM excretion. Similarly, urine was collected daily in a H_2SO_4 solution, pooled over successive days, weighed and sub-sampled for chemical analysis at the end of the period. The nitrogen losses to the air, recovered in condensed water and outgoing air from the respiration chamber, were measured according to methods described by Noblet et al. [15].

During the 7-d period in the respiration chamber, gas concentrations (CO_2, O_2, and CH_4) of outgoing air and ventilation rate were continuously measured as described by van Milgen et al. [27]. The O_2 was measured with a paramagnetic differential analyser (Oxygor 6N, Maihak AG, Hamburg, Germany), whereas CO_2 and CH_4 were measured with infrared analysers (Unor 6N, Maihak AG, Hamburg, Germany). As only one CH_4 analyzer was available, CH_4 production was measured in every other animal for each treatment. The gas extraction rate was measured with a mass gas meter (Hasting, HFM 200B, Hampton, USA). Gas concentrations, signals of the force sensors, weight of the trough and physical characteristics of gas in the chamber (temperature, relative humidity, barometric pressure) were measured 60 times per second, averaged over 10 s intervals, and recorded for further calculations.

2.4. Chemical analyses

Samples of feed (one per diet) were analysed for DM, ash, CP (nitrogen × 6.25), starch, ether extract and Weende crude fibre contents [1]. The gross energy content was measured using an adiabatic bomb calorimeter (IKA, C5000, Staufen, Germany). The NDF, ADF and ADL contents were determined according to van Soest and Wine [29] with prior amylolytic treatment. Total AA contents of the diets were analysed at the Ajinomoto Eurolysine laboratory (Amiens, France), using ion-exchange chromatography, except for tryptophan, which was analysed using high performance liquid chromatography (Tab. II). Similarly, samples of faeces were analysed for DM, ash, CP, and gross energy. In order to save time, ether extract and crude fibre of faeces were analysed on pooled samples per dietary treatment. Consequently, only one digestibility value per treatment was available precluding statistical analysis on these variables. Samples of urine, condensed water and extracted air were analysed for nitrogen using fresh material. The energy content of urine was obtained after freeze-drying approximately 50 mL in polyethylene bags.

2.5. Calculations

Apparent digestibility coefficients of nutrients and energy were calculated according to standard procedures. Nitrogen retention of each pig was calculated as the difference between nitrogen intake and nitrogen losses in faeces, urine and gas. The digestible

(DE) and metabolisable (ME) energy values of diets were calculated as previously described [14]. For the ME calculation, the average CH_4 production measured for each diet (measured in half of the animals) was applied to all animals fed this diet.

Heat production (HP) was calculated from gas exchanges (indirect calorimetry) according to the formula of Brouwer [3] including methane production and urinary nitrogen. The first day in the respiration chamber was considered as an adaptation day and was not considered in the calculations. Energy retention (RE) was calculated as the difference between ME intake and average HP over the measurement period. Energy retained as protein was calculated from nitrogen balance, and the quantity of energy retained as lipids was calculated as the difference between RE and the energy retained as protein [15].

Simultaneous measurements of O_2 and CO_2 concentrations, physical activity (signal of force sensors) and eating events (signal of load-cell) in the respiration chamber and physical characteristics of gas in the chamber were used as inputs for calculating the components of HP [26, 27]. The principle of the model is to relate the dynamics of O_2 and CO_2 concentrations in the chamber to events in the respiration chamber. In practice, on days when the animals were fed, the model provided estimates of gas exchanges due to resting (L/h), physical activity (L/unit of force) and feed intake (L/g). During fasting, it provided estimates of gas exchanges due to fasting (L/h) and physical activity during fasting. Parameter estimates for gas exchange components were obtained using SimuSolv (The DOW Chemical Company, 1990).

Components of total HP were calculated from the respective estimated O_2 consumption and CO_2 production [3], excluding the correction for urinary nitrogen and methane production. On days when the animals were fed, HP was considered as the sum of resting heat production (RHP), short-term thermic effect of feed (TEF_{st}) and HP due to physical activity (HP_{act}). The difference between the resting heat production (when fed) and asymptotic fasting HP (FHP) was used to calculate the long-term thermic effect of feed (TEF_{lt}). Four components of daily HP were then obtained: FHP, TEF_{lt}, TEF_{st} and HP_{act} [27]. The total TEF corresponds to the sum of TEF_{lt} and TEF_{st}. Due to the experimental design, a single estimation of FHP was available for each animal whereas the other components were estimated for at least four days that were averaged for each animal. The respiratory quotient was calculated as the ratio between CO_2 production and O_2 consumption.

The individual data for ME and HP were also adjusted for mean levels of physical activity (mean value of each trial) by adding the mean value of physical activity of the trial to activity-free ME and HP levels. Similarly, RE adjusted for mean level of physical activity was obtained as the difference between ME and HP corrected for mean level of physical activity. As indicated by Noblet et al. [14], NE can be calculated as the sum of FHP and RE. In the present study, RE was calculated as the difference between ME and HP (adjusted for mean levels of activity), whereas FHP was the mean of all animals in the trial. Energy balance data were expressed as MJ per day and per kg of metabolic body weight ($MJ \cdot d^{-1} \cdot kg^{-0.60}$) [16].

2.6. Statistical analyses

Data of trial 1 were subjected to analysis of variance using diet (D; $n = 3$) as the main effect. Data of trial 2 were subjected to analysis of variance using diet (D; $n = 3$) and block (B; $n = 5$) as main effects. Energy balance data were adjusted for each trial by covariance analysis for similar ME intakes ($MJ \cdot d^{-1} \cdot kg^{-0.60}$); they were also corrected for similar levels of physical activity in order to reduce variability. The GLM procedure of SAS was used for all statistical analyses [24].

3. RESULTS

The chemical composition of the diets is given in Table II and is in agreement with the objectives of the experiment, especially for AA levels. In addition, levels of free AA in diets (data not reported) agreed with amounts of industrial amino acids that were added to diets.

All animals performed satisfactorily and BW gain did not differ between treatments for each trial. Nutrients and energy digestibility did not differ markedly between treatments in each trial (Tab. III). However, in trial 1, digestibility coefficients were higher ($P < 0.05$) for diets 2 and 3 than for diet 1. In addition, higher digestibility coefficients of fat (statistical analysis not

Table III. Effect of dietary protein and fat levels on performance, digestive utilisation of nutrients and energy, and nitrogen balance in growing pigs.

	Trial 1					Trial 2				
	Diet			RSD[1]	Statistical analysis[2]	Diet			RSD[1]	Statistical analysis[3]
	1	2	3			1	2	3		
Number of animals	6	6	6	–	–	5	5	5	–	–
Average body weight (kg)	65.2	65.2	64.1	2.2	–	64.0	60.8	60.7	2.6	–
Dry matter intake ($g \cdot d^{-1}$)	2012^{a}	1980^{a}	1830^{b}	60	D**	1953^{a}	1835^{b}	1780^{c}	32	D**
Daily gain ($g \cdot d^{-1}$)	1064	1050	1054	126	–	950	1050	985	120	–
Digestibility coefficients (%)										
Dry matter	90.0^{a}	90.9^{b}	90.7^{b}	0.5	D*	89.8	90.1	89.5	0.8	
Organic matter	92.0^{a}	92.7^{b}	92.5^{b}	0.4	D*	91.8	91.9	91.3	0.7	
Nitrogen	91.5^{a}	89.4^{b}	89.4^{b}	1.2	D*	89.8	88.7	89.4	1.2	
Fat[4]	63	68	84	–	–	70	68	84	–	–
Crude fibre[4]	51	54	52	–	–	62	51	55	–	–
Energy	90.7^{a}	91.5^{b}	91.4^{b}	0.4	D**	90.5	90.4	90.0	0.8	
Nitrogen intake ($g \cdot d^{-1}$)	69.7^{a}	44.7^{b}	45.7^{b}	1.6	D**	62.4^{a}	46.7^{c}	48.6^{b}	0.9	D**
Nitrogen excretion ($g \cdot d^{-1}$)										
Faeces	6.0^{a}	4.7^{b}	4.8^{b}	0.5	D**	6.4^{a}	5.3^{b}	5.1^{b}	0.7	D*
Urine	30.4^{a}	10.7^{c}	14.3^{b}	2.4	D**	26.4^{a}	14.9^{b}	15.9^{b}	2.2	D**
Evaporated	0.6	0.3	0.3	0.3		0.4	0.3	0.5	0.2	
Total	37.0^{a}	15.7^{c}	19.4^{b}	2.7	D**	33.2^{a}	20.5^{b}	21.5^{b}	2.2	D**
Nitrogen retention ($g \cdot d^{-1}$)	32.7^{a}	29.0^{a}	26.3^{b}	3.1	D**	29.2	26.2	27.1	2.1	
Methane energy (% DE)[4]	0.70	0.50	0.52	–	–	0.72	0.41	0.33	–	–
Urinary energy (% DE)	3.80^{a}	2.27^{c}	2.61^{b}	0.23	D**	3.79^{a}	2.85^{b}	2.79^{b}	0.19	D**
ME (% DE)[5]	95.5^{a}	97.2^{b}	96.9^{c}	0.2	D**	95.5^{a}	96.7^{b}	96.9^{b}	0.2	D**

[1] RSD: Residual Standard Deviation.
[2] Analysis of variance with diet (D) as main effect. Levels of significance: * $P < 0.05$; ** $P < 0.01$. Different superscripts indicate statistically different means ($P < 0.05$).
[3] Analysis of variance with diet (D) and 'block' (B) as main effects. Levels of significance: * $P < 0.05$; ** $P < 0.01$. Different superscripts indicate statistically different means ($P < 0.05$).
[4] Crude fibre and fat were analysed on pooled samples of faeces (one per diet) and methane energy loss was measured in half of the animals; statistical analyses were not performed on these data.
[5] See Table II for abbreviations used.

applicable) were observed in fat-enriched diets (diet 3). Methane energy loss appeared lower with low-protein diets (statistical analysis not applicable). Nitrogen excretion levels were significantly lower in the low-protein diets (diets 2 and 3). The difference with diet 1 was more important in trial 1 (minus 53%) than in trial 2 (minus 37%). Most of the variation in nitrogen excretion originated from a variation of urinary nitrogen. Accordingly, urinary energy loss was markedly reduced in diets 2 and 3, so that the ME/DE ratio was higher for these diets than for diet 1. Nitrogen gain was lower ($P < 0.01$ in trial 1) with the low CP diets (Tab. III).

The FHP and HP_{act} components of heat production were quite similar between treatments for each trial (Tab. IV); HP_{act} represented about 15% of total heat production or 8% of ME intake across trials whereas FHP averaged 765 $kJ \cdot kg^{-0.60}$. The TEF component, expressed either as $kJ \cdot kg^{-0.60}$ or as percentage of ME intake, was the lowest in diet 3 and the highest in diet 1. Ranking between diets was similar for both trials but differences were significant only in trial 1. Both components of TEF (TEF_{st} and TEF_{lt}) contributed to the changes of TEF but only TEF_{st} in trial 1 was significantly affected by diet composition. According to these variations of components of TEF with diet composition, total HP or HP as a proportion of ME was highest for diet 1 and lowest for diet 3 ($P < 0.01$). These differences are even more significant when HP values are adjusted for similar ME intakes. As a consequence, retained energy was affected by diet composition with the highest deposition rate for diet 3 and the lowest rate for diet 1 (Tab. IV). The respiratory quotient was affected by diet composition but the effect was significant only in trial 1; the higher values obtained with diet 1 correspond to a higher rate of fat synthesis from dietary starch.

Energy values of diets are presented in Table IV. Within each trial, they differed significantly irrespective of the expression system used (DE or ME or NE). However, the relative order of the diets differed between the three systems with ME and, to a greater extent, NE providing higher relative energy values for the low-protein diets. The difference was most pronounced for diet 3 (Tab. IV).

4. DISCUSSION

In agreement with the results of the study of Le Bellego et al. [12] and with results of growth trials [2, 4], the results of the present study demonstrate that similar levels of nitrogen gain and subsequently BW gain can be achieved with low-protein diets when essential AA supplies meet animal requirements. The lower nitrogen gain observed in trial 1 with diets 2 and 3 is probably related to methodological problems [12, 18], i.e., an underestimation of nitrogen losses and a subsequent overestimation of nitrogen gain as important as nitrogen losses are high. It is important to note that the low-protein diets in trial 2 were supplemented with valine and isoleucine, both of which are currently not available at a competitive price for animal feeds. The levels of supplementation for these two AA were not fully justified according to optimal AA balance (or ideal protein), but were included to ensure that the requirements of all essential amino acids were met. The levels of supplementation were also determined in order to avoid a shortage of non-essential N; the ratio between non-essential protein (as nitrogen $\times$ 6.25) and CP was slightly above 50% in trial 1; a value often considered as minimal [13]. This ratio exceeded 50% in the low-protein diets of trial 2. In other words, diets 2 and 3 in trial 2 are similar to practical diets and can be produced under present economical and technical conditions. Therefore, they represent the potential reduction of nitrogen excretion that can be achieved under practical conditions, when compared to diets with conventional CP levels and/or no AA

Table IV. Effect of dietary protein and fat levels on performance, digestive utilisation of nutrients and energy, and nitrogen balance in growing pigs.

	Trial 1					Trial 2				
	Diet			RSD[1]	Statistical analysis[2]	Diet			RSD[1]	Statistical analysis[3]
	1	2	3			1	2	3		
Average BW[4] (kg)	67.6	67.1	65.7	2.5		65.8	62.8	62.4	2.6	
Energy balance ($MJ \cdot d^{-1} \cdot kg^{-0.60}$)										
Digestible energy	2.735^{a}	2.671^{a}	2.618^{b}	0.054	D**	2.608	2.536	2.611	0.078	
Metabolisable energy	2.613^{a}	2.598^{a}	2.538^{b}	0.052	D*	2.489	2.455	2.531	0.079	
Heat production										
As FHP[5]	0.787	0.778	0.753	0.061		0.777	0.756	0.740	0.067	
As activity	0.205	0.199	0.193	0.026		0.223	0.201	0.217	0.039	
As TEF[5]	0.490^{a}	0.396^{b}	0.366^{b}	0.076	D*	0.470	0.432	0.391	0.061	
Total	1.482^{a}	1.373^{b}	1.312^{b}	0.050	D**	1.470^{a}	1.389^{b}	1.348^{b}	0.056	D*
Retained energy										
As protein	0.394^{a}	0.350^{b}	0.323^{b}	0.031	D**	0.353	0.330	0.345	0.033	
As fat	0.737^{a}	0.875^{b}	0.903^{b}	0.072	D**	0.666^{a}	0.736^{a}	0.838^{b}	0.066	D**
Total	1.131^{a}	1.225^{b}	1.226^{b}	0.055	D*	1.019^{a}	1.066^{a}	1.183^{b}	0.064	D**
Respiratory quotient	1.13^{a}	1.19^{b}	1.16^{b}	0.02	D**	1.11	1.14	1.12	0.02	
Heat production (% ME)	56.7^{a}	52.8^{b}	51.7^{b}	1.8	D**	59.1^{a}	56.6^{a}	53.3^{b}	1.9	D**
TEF (% ME)[5]										
As short-term	9.2^{a}	7.6^{b}	7.6^{b}	1.1	D*	10.5	10.4	9.8	2.1	
As long-term	9.5	7.6	6.8	2.6		8.4	7.2	5.7	1.8	
Total	18.7^{a}	15.2^{b}	14.4^{b}	2.7	D*	18.9	17.6	15.5	2.6	
Energy values ($MJ \cdot kg^{-1}$ DM)										
Digestible energy	16.84^{b}	16.60^{a}	17.33^{c}	0.08	D**	16.47^{a}	16.40^{a}	17.19^{b}	0.15	D**
Metabolisable energy	16.08^{a}	16.14^{a}	16.79^{b}	0.10	D**	15.73^{a}	15.87^{a}	16.65^{b}	0.12	D**
Net energy[6]	11.76^{a}	12.43^{b}	13.20^{c}	0.29	D**	11.37^{a}	11.82^{b}	12.89^{c}	0.26	D**
Energy utilisation										
NE/DE (%)	69.8^{a}	74.8^{b}	76.2^{b}	1.7	D**	69.0^{a}	72.1^{b}	75.0^{c}	1.5	D**
NE/ME (%)	73.1^{a}	76.9^{b}	78.6^{b}	1.8	D**	72.3^{a}	74.5^{b}	77.4^{c}	1.5	D**
NE/NEg[7] (%)	98.3^{a}	101.4^{b}	102.1^{b}	2.3	D*	97.0^{a}	98.2^{a}	101.1^{b}	2.1	D*
Adjusted energy balance ($MJ \cdot d^{-1} \cdot kg^{-0.60}$) [8]										
Heat production	1.466^{a}	1.367^{b}	1.337^{b}	0.045	D**	1.462^{a}	1.406^{b}	1.338^{c}	0.030	D**
Retained energy	1.118^{a}	1.217^{b}	1.247^{b}	0.045	D**	1.029^{a}	1.085^{b}	1.153^{c}	0.030	D**

[1, 2, 3] See Table III.
[4] Average body weight during the respiration chamber period.
[5] FHP: fasting heat production; TEF: thermic effect of feed; see Table II for other abbreviations.
[6] Adjusted for activity heat production and zero activity fasting heat production equal to 0.200 and 0.780 $MJ \cdot d^{-1} \cdot kg^{-0.60}$ for trial 1 and 0.214 and 0.760 $MJ \cdot d^{-1} \cdot kg^{-0.60}$ for trial 2, respectively (mean values of the trial); calculated as (zero activity fasting heat production + retained energy)/DM intake.
[7] NEg = average of NEg2, NEg4 and NEg7 values (Noblet et al., 1994; [14]).
[8] Adjusted for constant activity heat production and ME intake of 0.200 and 2.584 $MJ \cdot d^{-1} \cdot kg^{-0.60}$ for trial 1 and 0.214 and 2.491 $MJ \cdot d^{-1} \cdot kg^{-0.60}$ for trial 2, respectively.

supplementation. These results suggest that nitrogen excretion can be reduced by 10% for each percent reduction of the dietary CP level. This value is similar to a previous estimate of Dourmad et al. [6].

The value of FHP (for zero physical activity) obtained in the present study is similar to those obtained by van Milgen et al. [28] with similar pigs and methodologies or the value estimated by Noblet et al. [14] (750 kJ·kg $BW^{-0.60}$) from a regression approach. In agreement with Schiemann et al. [25], FHP was not affected by dietary protein level. In our experimental conditions (i.e., pigs are meal-fed and individually housed in cages), activity levels were not affected by diet characteristics and pigs used about 8% of the ME intake for physical activity. This value is similar to that found by Quiniou et al. [20] in ad libitum and group-housed growing pigs (7.5%) but lower than in ad libitum and group-housed 20- to 30-kg piglets (11%; [5]) and in restrictively fed pregnant sows (18–20%; [21]). Van Milgen et al. [28] also showed that daily HP_{act} was higher in energy-restricted pigs and in this case represented a much higher proportion of ME intake (13%). These results show that, at any stage of production, physical activity represents a considerable quantity of feed energy; a fraction that is variable with stage of production, housing system, and feeding level. It can also be quite variable between animals, especially in adult pigs [17, 21].

In agreement with most literature results [9, 14, 25], heat production was reduced when dietary CP was reduced (i.e. partial replacement of CP by starch) or when fat was added. This indicates that the efficiency of utilisation of ME for retained energy depends on diet composition which confirms the interest of estimating energy values of pig feeds according to their NE value. As indicated in Table IV, the NE value as measured in the present study was, on average, equal to the NEg value calculated from equations proposed by Noblet et al. [14] (see NE/NEg ratio). However, the NE/NEg ratio is not constant but increases when dietary CP is reduced and/or fat is added, which means that the NE content of CP could be slightly overestimated by the NEg prediction equations while NE of fat could be underestimated. With regard to dietary CP, it is important to mention that the pigs used in the present study and those used by Noblet et al. [14] differed in BW (65 and 45 kg, respectively). In addition, recent results obtained in 20-kg piglets (Le Bellego and Noblet, unpublished data) indicate that heat production was little affected by dietary CP level. It can be hypothesised that the increase in heat production associated with increase of dietary CP level may depend on the BW of pigs; in other words, the change in body protein turnover with dietary CP level that has been quantified in 50-kg pigs [23] may depend on the BW of the pig. This aspect deserves further investigation.

In conclusion, our data indicate that energy utilisation is improved (i.e., heat production is reduced) when dietary CP level is reduced. This effect is accentuated when fat is added in the feed. Our data also confirm the superiority of the NE system (compared to DE or ME systems) proposed in previous studies. Finally, the results of this study and those of the literature demonstrate that nitrogen output in growing-finishing pigs can be markedly reduced without impairing performance by using low-protein diets supplemented with the most limiting essential amino acids. However, complementary growth trials looking at the effects of low-protein diets on voluntary feed intake and body composition are required.

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REFERENCES

[1] AOAC, Official Methods of Analysis (15th ed.), Association of Official Analytical Chemists, Washington DC, 1990.

[2] Bourdon D., Dourmad J.Y., Henry Y., Réduction des rejets azotés chez le porc en croissance par la mise en œuvre de l'alimentation multiphase, associée à l'abaissement du taux azoté, Journ. Rech. Porcine Fr. 27 (1995) 269–278.

[3] Brouwer E., Report of sub-committee on constants and factors, in: Blaxter K.L. (Ed.), Energy metabolism of farm animals, Academic Press, London, 1965, pp. 441–443.

[4] Canh T.T., Aarnink A.J.A., Schutte J.B., Sutton J.D., Langhout D.J., Verstegen M.W.A., Dietary protein affects nitrogen excretion and ammonia emission from slurry of growing-finishing pigs, Livest. Prod. Sci. 56 (1998) 181–191.

[5] Collin A., van Milgen J., Dubois S., Noblet J., Effect of high temperature on feeding behavior and heat production in group-housed piglets, Brit. J. Nutr. (2001) (in press).

[6] Dourmad J.Y., Henry Y., Bourdon D., Quiniou N., Guillou D., Effect of growth potential and dietary protein input on growth performance, carcass characteristics and nitrogen output in growing-finishing pigs, in: Verstegen M.W.A., den Hartog L.A., van Kempen G.J.M., Metz J.H.M. (Eds.), Nitrogen flow in pig production and environmental consequences: Proceedings of the First International Symposium PUDOC, Wageningen, 1993, pp. 206–211.

[7] Eurolysine and ITCF, Ileal digestibility of amino acids in feedstuffs for pigs, Paris, 1995.

[8] Henry Y., Affinement du concept de la protéine idéale pour le porc en croissance, INRA Prod. Anim. 6 (1993) 199–212.

[9] Just A., The net energy value of crude (catabolized) protein for growth in pigs, Livest. Prod. Sci. 9 (1982) 349–360.

[10] Kerr B.J., McKeith F.K., Easter R.A., Effect of performance and carcass characteristics of nursery to finisher pigs fed reduced crude protein, amino acid-supplemented diets, J. Anim. Sci. 73 (1995) 433–440.

[11] Le Bellego L., van Milgen J., Noblet J., Effect of high temperature and low protein diets on performance of growing-finishing pigs, J. Anim. Sci. (2001) (accepted for publication).

[12] Le Bellego L., van Milgen J., Dubois S., Noblet J., Energy utilization of low protein diets in growing pigs, J. Anim. Sci. 79 (2001) 1259–1271.

[13] Lenis N.P., van Diepen H.T.M., Bikker P., Jongbloed A.W., van der Meulen J., Effect of ratio between essential and nonessential amino acids in the diet on utilization of nitrogen and amino acids by growing pigs, J. Anim. Sci. 77 (1999) 1777–1787.

[14] Noblet J., Fortune H., Shi X.S., Dubois S., Prediction of net energy value of feeds for growing pigs, J. Anim. Sci. 72 (1994) 344–354.

[15] Noblet J., Henry Y., Dubois S., Effect of protein and lysine levels in the diet on body gain composition and energy utilization in growing pigs, J. Anim. Sci. 65 (1987) 717–726.

[16] Noblet J., Karege C., Dubois S., van Milgen J., Metabolic utilization of energy and maintenance requirements in growing pigs: Effects of sex and genotype, J. Anim. Sci. 77 (1999) 1208–1216.

[17] Noblet J., Shi X.S., Dubois S., Energy cost of standing activity in sows, Livest. Prod. Sci. 34 (1993) 127–136.

[18] Quiniou N., Dubois S., Noblet J., Effect of dietary crude protein level on protein and energy balances in growing pigs: comparison of two measurements methods, Livest. Prod. Sci. 41 (1995) 51–56.

[19] Quiniou N., Noblet J., Dubois S., Voluntary feed intake and feeding behaviour of group-housed growing pigs are affected by ambient temperature and body weight, Livest. Prod. Sci. 63 (2000) 245–253.

[20] Quiniou N., Noblet J., van Milgen J., Dubois S., Modeling heat production and energy balance in group-housed growing pigs exposed to low or high ambient temperatures, Brit. J. Nutr. 85 (2001) 97–106.

[21] Ramonet Y., van Milgen J., Dourmad J.Y., Meunier-Salaun M.C., Noblet J., The effect of dietary fibre on energy utilisation and partioning of heat production over pregnancy in sows, Brit. J. Nutr. 84 (2000) 85–94.

[22] Renaudeau D., Quiniou N., Noblet J., Effect of high ambient temperature and dietary protein level on performance of multiparous lactating sows, J. Anim. Sci. 79 (2000) 1240–1249.

[23] Roth F.X., Gotterbarm G.G., Windisch W., Kirchgessner M., Influence of dietary level of dispensable amino acids on nitrogen balance and whole-body protein turnover in growing pigs, J. Anim. Physiol. A Anim. Nutr. 81 (1999) 232–238.

[24] SAS, SAS/STAT User's Guide (version 6, 4th ed.), SAS Inst. Inc., Cary NC, 1990.

[25] Schiemann R., Jentsch W., Hoffmann L., Untersuchungen zum Energieerhaltungsbedarf wachsender Schweine verschiedenen Geschlechts bei normalen und hehen Proteingaben, Arch. Anim. Nutr. 39 (1989) 5–24.

[26] van Milgen J., Noblet J., Modelling energy expenditure in pigs, in: McNamara J.P., France J., Beever D.E. (Eds.), Modelling Nutrient Utilization in Farm Animals, CAB International, Wallingford, 2000, pp. 103–114.

[27] van Milgen J., Noblet J., Dubois S., Bernier J.F., Dynamic aspects of oxygen consumption and carbon dioxide production in swine, Brit. J. Nutr. 78 (1997) 397–410.

[28] van Milgen J., Noblet J., Dubois S., Energetic efficiency of starch, protein, and lipid utilization in growing pigs, J. Nutr. 131 (2001) 1309–1318.

[29] van Soest P.J., Wine R.H., Use of detergents in the analysis of fibrous feeds. IV. Determination of plant cell-wall constituents, J. AOAC 50 (1967) 50–55.

[30] Vermorel M., Bouvier J.C., Bonnet Y., Fauconneau G., Construction et fonctionnement de 2 chambres respiratoires du type « circuit ouvert » pour jeunes bovins, Ann. Biol. Anim. Bioch. Biophys. 13 (1973) 659–681.