The influence of protein:energy value of the ration and level of feed intake on the energy and nitrogen metabolism of the growing pig

2.* N metabolism at two environmental temperatures

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(*Received 28 July 1982 – Accepted 22 October 1982*)

1. The nitrogen balances of thirty-six individually-housed, entire male pigs (body-weight range 19–50 kg) were measured over 7 d periods when the animals were kept initially at an environmental temperature of 22° and then at 10° while fed on rations containing 153, 201 and 258 g crude protein (N × 6·25; CP)/kg dry matter (DM). The respective metabolizable energy (ME) contents were 16·29, 16·96 and 17·24 MJ/kg DM. Each ration was given at three levels, 20, 35 and 50 g feed/kg body-weight per d. The animals fed on the 20 and 35 g/kg feeding level were catheterized and blood samples withdrawn on two consecutive days within the N-balance periods for the determination of blood urea (BU) concentration both before and at hourly intervals for 7 h following the morning feed.

2. An increase in feed intake resulted in a significant increase in N retention (NR) at each environmental temperature. However, NR as a proportion of N intake was higher the lower the protein content of the ration. With the exception of the animals fed on the low-protein ration, NR at any given feed intake was lower at 10° than at 22° and these differences were reflected in the animal's body-weight gain.

3. Values for the fasting N metabolism (N_f), calculated from the relationship between NR and intake of digestible N (IDN), were temperature-dependent. At 22°, a constant N_f value of 0·255 g N/kg body-weight$^{0.75}$ per d was found appropriate, while at 10° N_f increased with increase in protein content of the ration from 0·380 on the low protein ration to 0·533 and 0·753 g N/kg body-weight$^{0.75}$ per d on the medium- and high-protein rations respectively.

4. The efficiency of N utilization (k_N) reflected the differences in the relationships between NR and IDN. At 22° the relationship was curvilinear so that k_N decreased with increase in both the level of feed intake and the protein content of the ration. At 10° the relationship was linear, hence k_N was independent of feed intake within rations. However, it decreased from 0·909 to 0·679 as the protein content of the ration was increased.

5. The concentration of BU attained a maximal value some 3–5 h after the ingestion of the feed, with the values at 10° being higher than those at 22°. BU increased as the level of protein in the ration increased but decreased with the level of feed intake when dietary protein concentration was held constant. There was a significant correlation between BU and k_N, indicating that BU is a useful criterion for assessing the efficiency of N utilization.

The calculation of the protein requirements of farm animals by the factorial method requires knowledge of the efficiency with which dietary protein intake is utilized for tissue protein accretion and of the factors which influence it. Individuals differ in their rate and capacity for protein deposition depending upon several endogeneous and exogeneous factors which interact to influence the efficiency with which dietary protein is retained. At any given protein intake, the rate and extent of protein deposition is dependent on the age and body-weight of the animal (Gebhardt *et al.* 1973; Thorbek, 1975), its sex (Piatkowski & Jung, 1966; Davis & Lucas, 1972), breed (Curran *et al.* 1972; Fuller *et al.* 1976; Petersen, 1978) and previous nutritional history, that is the extent of under- or over-feeding (Wyllie *et al.* 1969; Zimmerman & Khajarern, 1973; Gädeken *et al.* 1980). It is also dependent on

* Paper no. 1: *Br. J. Nutr.* (1983) **49**, 255.

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the extent to which nutrients supplied in the diet are available to meet the requirements of the animal. This implies that nutritional factors are especially important and the protein, amino acid and energy contents of the feed and the levels at which they are applied have been shown to influence the rate and efficiency of protein utilization (Menke, 1979; Berschauer, Gaus, Ehrensvärd *et al.* 1980; Holmes *et al.* 1980).

In many experiments in which these variables have been investigated only the growth and carcass characteristics of the animal have been measured. There is little available information to show the relation which exists between the efficiency of protein utilization, on the one hand, and dietary intake on the other, particularly when there are alterations in the protein and energy contents of the ration and in the environmental temperature. The objective of the present experiment was to provide such information. Part of this work has been the subject of a preliminary communication (Berschauer *et al.* 1981).

MATERIALS AND METHODS

Animals

The animals in the present investigations were those which had been used for the calorimetric determination of heat loss and energy and N balance, reported by Close *et al.* (1983). The animals were growing, entire male pigs maintained at two environmental temperatures and fed on three diets varying in their protein and energy concentrations.

Plan of experiments

The experiments were designed in a $2 \times 3 \times 3$ factorial arrangement involving two environmental temperatures with three rations each of different protein content being given at three levels of intake at each environmental temperature. There were, therefore, eighteen different environmental temperature–protein intake–feed intake combinations. The experiments involved a total of thirty-six animals, with four animals being allocated to each of the different protein intake–energy intake combinations. However, the same four animals were exposed to each of the environmental temperatures at each dietary treatment. The environmental temperatures investigated were 22 and 10 (± 1)°; the crude protein (N × 6·25; CP) contents of the rations were 153 (L), 201 (M) and 258 (H) g/kg dry matter (DM) and each ration was given at three different intake levels, 20 (low), 35 (medium) and 50 (high) g feed/kg body-weight per d. The metabolizable energy (ME) contents of the rations were 16·29, 16·96 and 17·24 MJ/kg DM respectively.

Nutrition

The nutrition of the animals and the ingredients and chemical compositions of the rations were similar to those reported by Close *et al.* (1983). The composition of each ration was so arranged that the relative proportion of the protein-supplying ingredients was kept constant. In this way, large differences in the quality of protein could be avoided. This was achieved as illustrated from the amino acid analyses of the rations presented by Close *et al.* (1983).

Experimental routine

At the end of the 7 d calorimetric period, the animals were removed to a clean metabolism pen and transferred to a temperature-controlled room maintained at 22°, that is, a similar temperature to which they had previously been exposed. The feed intake and the protein content of the feed for each animal were also maintained at similar levels. On the following morning, i.e. day 2, a siliconized polyethylene catheter was implanted in the external jugular vein of each animal under surgical conditions. The animals recovered quickly following catheterization so that on the same evening they consumed all their allocated feed on the low- and medium-feeding level. On succeeding days (day 3 and 4) blood samples were

withdrawn from the catheters immediately before the morning feed (08.30 hours) and then sequentially at intervals of 1 h for the following 7 h period. Faeces and urine were not collected during this period and the determination of N balance during the calorimetric period was taken to represent that during the period of catheterization at 22°.

On the morning of day 5, the catheters were removed from the animals and during the next 2 d the temperature was reduced to 10 (±1)°. The animals were allowed a 6 d period to acclimatize to the new environmental conditions. Following this habituation period a 7 d N balance was carried out (days 12–19). On the morning of day 16, the animals were catheterized again so that blood samples could be withdrawn hourly on days 17 and 18 as previously. On the morning of day 19, the N balance was terminated. During this 19 d period the metabolism cages were cleaned at intervals of 2–3 d. On these days the animals were also weighed.

It was originally intended that all animals on each treatment be catheterized and blood urea (BU) concentrations measured. However, following catheterization of the animals fed on the highest level of the H ration at 22°, that is the first series of animals investigated, there was a marked reduction in feed intake compared to that within the calorimeter. The latter finding meant that the BU concentrations measured in this period were not representative of the N balance measured within the calorimeter. Because of this effect the animals on the high feeding level of both the L and M rations were not catheterized. Thus, while N balance was measured for each treatment only those animals on the low and medium feed intakes were catheterized.

Blood sampling

With the exception of two animals where the catheters broke or became blocked, little difficulty was experienced with the withdrawal of blood. Blood samples were taken without restraining or exciting the animal and always by the same experimenter. Heparinized saline (9 g sodium chloride/l) was infused continuously through the catheters. Each blood sample was centrifuged for 15 min at 3000 rev./min. Duplicate samples of plasma were withdrawn and transferred to plastic vials and stored at −20° until later analysed for their urea concentration.

Analytical procedures

N balance. The collection, sampling and analysis of feed, faeces and urine at 10° was similar to those at 22° previously described by Close *et al.* (1983). Although the ammonia generated within the metabolism pens at 10° was not measured, estimates of N balance were corrected on the assumption that it represented 1·2% of total N intake (IN), i.e. the mean value determined in the experiments at 22°.

BU concentration. BU concentration in the plasma was measured using a Technicon AutoAnalyzer (Technicon, Basingstoke) with a modification of the method described by Marsh *et al.* (1965).

Statistical analysis. The results of the experiments were statistically analysed according to the Student's *t* test and split plot analysis of variance. Linear and quadratic regression analyses were also carried out.

RESULTS

Feed intake and N balance

As reported previously (Close *et al.* 1983) there was little difficulty with the animals' acceptance of the rations offered at 22°. Only the animals fed on the highest level of the high-protein ration refused feed. On this treatment the animals' *ad lib.* intake was 43 g feed/kg body-weight per d. At 10° the animals consumed all the feed offered at the low

and medium intake levels on all three rations. On the highest intake, however, there were always feed refusals and the *ad lib.* intakes corresponded to 41, 45 and 33 g feed/kg body-weight per d on the L, M and H rations respectively. Although the *ad lib.* feed intake of the animals on the L and M rations decreased relative to body-weight, in real terms it increased so that each 1° decrease in temperature from 22 to 10° resulted in a 25·3 and 40·2 g/d increase in feed intake respectively. Body-weight also increased so that per kg increase in body-weight, the *ad lib.* feed intakes increased by 1·80 and 3·27 g/d per 1° on the L and M rations respectively. The reduction in the *ad lib.* intake of the animals on the H ration was probably a result of the effects of catheterization.

For each of the rations fed at each of the two environmental temperatures, increasing the level of feed or IN resulted in an increase in N retention (NR) ($P < 0{\cdot}01$), even though both the faecal and urinary losses increased significantly ($P < 0{\cdot}001$; $P < 0{\cdot}001$) (Table 1). The significantly lower NR of the animals at 10° ($P < 0{\cdot}01$), compared to that at the same feeding level and ration at 22°, resulted from the significantly higher urinary N losses ($P < 0{\cdot}01$). Faecal N loss, and hence apparent digestibility of N (ADN), appeared to be independent of temperature. However, when the losses were expressed relative to IN, the pattern of increasing faecal and decreasing urinary losses was observed with increase in intake. As a result, the proportion of N retained was maximal on all rations at the medium level of feeding.

The efficiency of N utilization (k_N)

To estimate an animal's N requirements it is necessary to have some knowledge of k_N. Estimates of k_N have therefore been determined in the present experiments for each diet from equations relating NR to the intake of digestible N (IDN). At 22°, the relationship between NR (g/kg body-weight$^{0{\cdot}75}$ per d; y) and IDN (g/kg body-weight$^{0{\cdot}75}$ per d; x) may be described by the following quadratic equations:

$$\text{L:}\quad y = -0{\cdot}189\ (\pm 0{\cdot}218) + 0{\cdot}818\ (\pm 0{\cdot}347)\ x - 0{\cdot}0191\ (\pm 0{\cdot}124)\ x^2 \quad (r\ 0{\cdot}97), \qquad (1)$$

$$\text{M:}\quad y = -0{\cdot}364\ (\pm 0{\cdot}338) + 0{\cdot}963\ (\pm 0{\cdot}359)\ x - 0{\cdot}0726\ (\pm 0{\cdot}086)\ x^2 \quad (r\ 0{\cdot}94), \qquad (2)$$

$$\text{H:}\quad y = -0{\cdot}211\ (\pm 0{\cdot}341) + 0{\cdot}725\ (\pm 0{\cdot}307)\ x - 0{\cdot}041\ (\pm 0{\cdot}061)\ x^2 \quad (r\ 0{\cdot}97). \qquad (3)$$

Although the quadratic terms in the eqns (1)–(3) were not significant ($P > 0{\cdot}05$), the use of this model to describe the relationship between NR and IDN is in agreement with a large number of experiments (Agricultural Research Council, 1981). In these equations the intercept term represents the endogenous N loss at zero feed intake and is therefore an estimate of fasting N metabolism (N_f). The mean value for all three rations, 0·255 g/kg body-weight$^{0{\cdot}75}$ per d, was quite similar to that of 0·23 g/kg body-weight$^{0{\cdot}75}$ per d, calculated in other experiments (Gebhardt & Stein, 1970; Menke, 1979). Similarly, estimates of the maintenance requirement for N (N_m) were determined as that intake corresponding to zero NR. Values of 0·236, 0·393 and 0·293 g/kg body-weight$^{0{\cdot}75}$ per d, were calculated on the L, M and H rations respectively, with an overall mean value of 0·307 g/kg body-weight$^{0{\cdot}75}$ per d. The efficiency of N utilization for maintenance calculated as the ratio $N_f : N_m$ was, therefore, 0·83.

Estimates of k_N were calculated from the first derivative of eqns (1), (2) and (3) for each ration at known IDN values. As expected, for each feed type, k_N decreased with increase in IDN. However, over similar ranges of intake the rate at which k_N decreased increased with the protein content of the ration. Thus between 1·0 and 3·0 g IDN/kg body-weight$^{0{\cdot}75}$ per d, k_N decreased from 0·78 to 0·67 on the L, compared with 0·64 to 0·48 on the H ration. In addition, at any given level of IDN, the values of k_N were higher the lower the N content of the ration.

At 10° the range of feed intakes was less than that at 22° with the result that the

Table 1. *The partition of dietary nitrogen intake (IN) into its faecal (FN) and urinary (UN) losses (g/kg body-weight$^{0.75}$ per d) and N retention (g/kg body-weight$^{0.75}$ per d, NR) in growing pigs at three levels of feeding on each of three rations of differing protein content at environmental temperatures of 10 and 22°. The mean body-weight (kg; BW), body-weight gain (g/kg body-weight$^{0.75}$ per d; G), and the apparent digestibility of nitrogen (ADN) are also given*

(Mean values with their standard errors)

Protein content of ration (g/kg dry matter)	Level of feed intake	BW (kg)		*G*		IN		FN		UN		NR		ADN	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
							22°								
153	Low	19·4	0·1	13·1	0·7	0·92	0·01	0·12	0·02	0·33	0·02	0·46	0·05	0·88	0·020
	Medium	28·2	1·2	43·8	3·3	1·76	0·01	0·27	0·02	0·48	0·05	1·01	0·03	0·86	0·010
	High	30·3	0·8	62·4	2·5	2·37	0·02	0·40	0·02	0·61	0·03	1·36	0·05	0·83	0·013
201	Low	24·3	0·3	27·1	2·4	1·27	0·01	0·15	0·01	0·47	0·02	0·65	0·03	0·90	0·005
	Medium	35·6	0·6	59·0	2·2	2·32	0·06	0·32	0·02	0·73	0·05	1·27	0·08	0·87	0·011
	High	37·7	0·8	80·5	4·2	3·52	0·11	0·60	0·04	1·07	0·11	1·85	0·09	0·84	0·010
258	Low	20·9	0·1	23·8	2·0	1·49	0·03	0·19	0·01	0·62	0·05	0·67	0·08	0·88	0·010
	Medium	21·9	1·1	53·6	4·9	2·66	0·06	0·35	0·02	1·02	0·03	1·29	0·06	0·88	0·008
	High	33·8	1·4	68·3	4·1	4·21	0·14	0·70	0·01	1·69	0·07	1·82	0·14	0·84	0·003
							10°								
153	Low	22·8	0·5	12·2	1·7	0·94	0·02	0·14	0·01	0·44	0·05	0·36	0·03	0·87	0·006
	Medium	39·6	1·1	30·9	4·8	1·68	0·04	0·22	0·01	0·65	0·10	0·81	0·07	0·88	0·003
	High	41·7	1·1	48·9	5·2	2·00	0·11	0·35	0·02	0·41	0·04	1·23	0·07	0·84	0·005
201	Low	27·9	0·3	10·6	4·5	1·23	0·15	0·13	0·02	0·96	0·11	0·14	0·04	0·91	0·005
	Medium	47·6	0·7	49·0	2·6	2·57	0·05	0·38	0·02	1·00	0·03	1·19	0·05	0·87	0·006
	High	50·0	1·5	48·6	3·3	3·41	0·10	0·58	0·06	1·62	0·10	1·21	0·06	0·84	0·006
258	Low	23·7	0·3	10·0	2·5	1·63	0·01	0·19	0·01	1·25	0·03	0·20	0·02	0·90	0·007
	Medium	31·4	1·7	39·5	7·8	3·04	0·08	0·37	0·03	1·59	0·08	1·08	0·08	0·89	0·009
	High	45·0	1·0	39·0	6·3	2·94	0·16	0·46	0·05	1·57	0·19	0·91	0·18	0·86	0·016

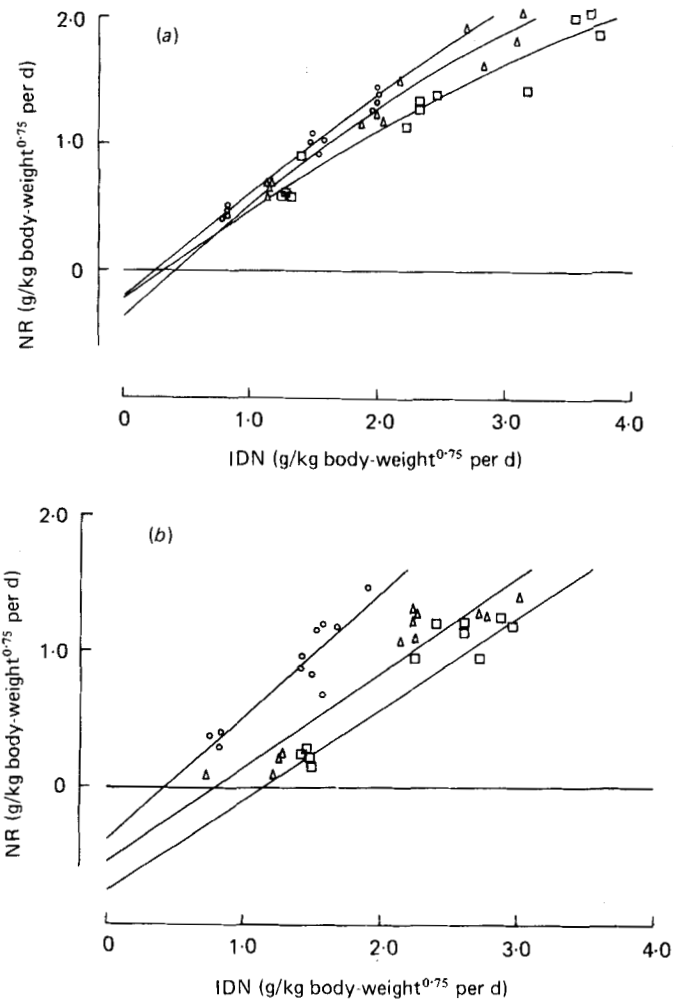

Fig. 1. The relationship between nitrogen retention (g/kg body-weight$^{0·75}$ per d; NR) and intake of digestible N (g/kg body-weight$^{0·75}$ per d; IDN) for pigs fed on rations differing in protein content and maintained at environmental temperatures of (*a*) 22° and (*b*) 10°. (○), Low-protein ration (153 g crude protein (N ×6·25; CP)/kg dry matter (DM)); (△), medium-protein ration (201 g CP/kg DM); (□), high-protein ration (258 g CP/kg DM). The lines are drawn from the regression equations presented on pp. 274 and 276.

relationship betwen NR (g/kg body-weight$^{0·75}$ per d; y) and IDN (g/kg body-weight$^{0·75}$ per d; x) was best described by a series of linear functions. When the quadratic terms were included they were clearly non-significant ($P > 0·05$) and varied in size between the various rations so that little reliance could be placed upon them. The equations were:

L: $y = -0·380\ (\pm 0·208) + 0·909\ (\pm 0·147)\ x$ (r 0·90), (4)

M: $y = -0·533\ (\pm 0·166) + 0·701\ (\pm 0·078)\ x$ (r 0·94), (5)

H: $y = -0·753\ (\pm 0·237) + 0·679\ (\pm 0·103)\ x$ (r 0·90). (6)

These relationships are compared with those determined at 22° in Fig. 1 (*a*, *b*). The intercept terms, that is N_t, calculated at 10°, were rather variable, increasing with increase in protein content of the ration. When all estimates were considered together the mean value was 0·555

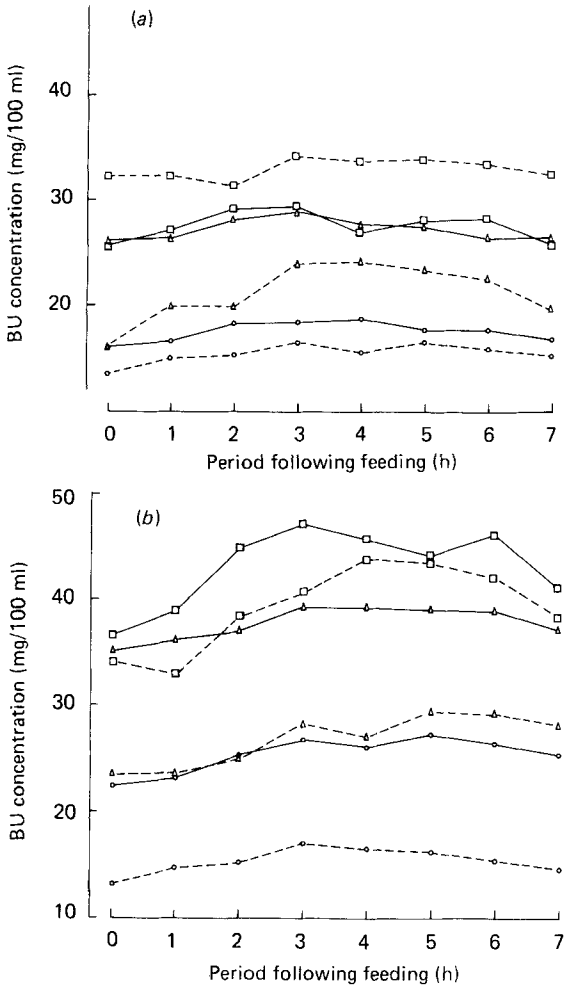

Fig. 2. Blood urea concentration (mg/100 ml; BU) of pigs in relation to the period of time following feeding of rations differing in protein content when the animals were maintained at environmental temperatures of (*a*) 22° and (*b*) 10°. (○), Low-protein ration (153 g crude protein (N × 6·25; CP)/kg dry matter (DM)); (△), medium-protein ration (201 g CP/kg DM); (□), high-protein ration (258 g CP/kg DM). (——), Low intake (20 g feed/kg body-weight per d); (– – – –), medium intake (35 g feed/kg body-weight per d).

which compares with that of 0·486 g/kg body-weight$^{0·75}$ per d calculated at 10° from the results of Close *et al.* (1978). The mean estimate of N_m was 0·762 g/kg body-weight$^{0·75}$ per d, so that the efficiency of N utilization for maintenance at 10° was 0·73. Because of the relatively lower values of IDN at 10° compared with that at 22°, k_N, that is the coefficient of x, was constant over the intakes investigated. However, as at 22°, k_N decreased as the protein content of the ration was increased.

BU concentration

There were significant changes in the BU concentrations of the animals depending on the dietary treatments imposed and the temperature of exposure. The extent to which BU changed over the 7 h period following feeding is illustrated in Fig. 2(*a*, *b*). Following feeding, BU increased to attain maximal values some 3–5 h after the ingestion of the meal.

Table 2. *Blood urea (mg/100 ml; BU) in growing pigs at two levels of feeding on each of three rations of differing protein content at environmental temperatures of 10 and 22°*

(Mean values with their standard errors)

Protein content of ration (g/kg dry matter	Level of feed intake	Environmental temperature (°)	Period after feeding (h) 0 Mean	0 SE	3·5 Mean	3·5 SE	7 Mean	7 SE	Mean (0–7) Mean	Mean (0–7) SE
153	Low	22	16·2	1·0	18·5	1·1	16·9	1·6	17·6	1·3
		10	22·4	3·6	26·7	5·3	25·2	5·2	25·3	5·0
	Medium	22	13·7	0·6	16·1	1·0	15·3	1·3	15·5	0·8
		10	13·2	1·5	16·8	1·4	14·6	1·4	15·4	1·4
201	Low	22	26·2	2·1	28·3	0·9	26·5	1·9	27·1	1·4
		10	35·3	3·5	39·2	2·3	37·0	3·5	37·7	3·0
	Medium	22	16·1	0·1	24·2	3·4	19·8	1·0	21·6	2·1
		10	23·5	2·2	27·7	0·9	28·2	1·8	26·8	0·7
258	Low	22	25·8	1·8	28·1	1·9	25·6	0·4	27·5	1·6
		10	36·6	1·7	46·2	2·2	40·9	2·8	42·9	1·6
	Medium	22	32·3	3·3	33·9	3·0	32·5	1·6	32·6	2·3
		10	34·0	9·2	42·0	3·8	38·2	3·3	39·1	4·3
		—	—	4·2*	—	2·9*	—	3·0*	—	3·3*
		—	—	4·7†	—	1·9†	—	2·1†	—	2·1†

* Approximate SE of differences for comparisons between ration/feed level means at the same or different temperatures.

† Approximate SE of differences for comparisons between treatment means within ration/feed level combination.

Subsequently the concentration fell but the values recorded 7 h after feeding were in general higher than those just before feeding, that is some 16 h after the last meal. The mean rate at which BU increased following feeding was greater for the animals kept at 10°, the percentage increase being 18·8 and 23·2% on the low and medium feeding levels respectively. The corresponding values at 22° were 10·4 and 24·3%.

Split plot analysis of variance showed that at any given level of feeding and at each environmental temperature there was a significant increase ($P < 0·05$) in BU with increase in the protein content of the diet, that is, from the L to the H ration (Table 2). However, when the feeding level within each ration was increased there was usually a reduction in BU concentration. However, these reductions were only significant on the M ration at 10° ($P < 0·05$). The values of BU were temperature-dependent, since for any given intake and ration they were generally higher at 10° compared with that at 22°. The differences were, however, only significant ($P < 0·05$) on the low feeding level of the H ration.

Body-weight gain (G)

The results presented in Table 1 show that although *G* determined within each 7 d balance period was higher at 22° than at 10°, there were differences dependent on the ration offered, so that *G*, when compared at similar levels of IN, was less the higher the protein content of the ration at each environmental temperature. Within each environmental temperature *G* increased with increase in IN or IDN, but the response varied depending on the temperature of exposure and the protein content of the ration offered to the animals. This is illustrated in Fig. 3 (*a*, *b*) where *G*, at both 10 and 22°, is shown in relation to IDN.

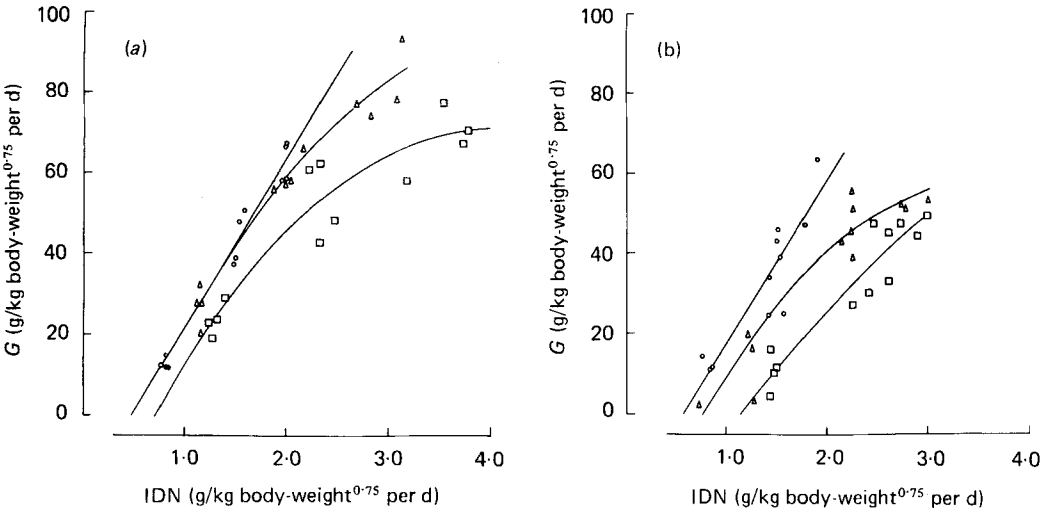

Fig. 3. The relationship between body-weight gain (g/kg body-weight$^{0.75}$ per d; *G*) and intake of digestible N (g/kg body-weight$^{0.75}$ per d; IDN) for pigs fed on rations differing in protein content and maintained at environmental temperatures of (*a*) 22° and (*b*) 10°. (○), Low-protein ration (153 g crude protein (N × 6·25; CP)/kg dry matter (DM); (△), medium-protein ration (201 g CP/kg DM); (□), high-protein ration (258 g CP/kg DM). The lines are drawn from the regression equations presented below.

The equations relating *G* (g/kg body-weight$^{0.75}$ per d; *y*) to IDN (g/kg body-weight$^{0.75}$ per d; *x*) were:

at 22°

$$\text{L:}\quad y = -20{\cdot}93\ (\pm 3{\cdot}26) + 42{\cdot}04\ (\pm 2{\cdot}14)\ x \quad (r\ 0{\cdot}99), \tag{7}$$

$$\text{M:}\quad y = -26{\cdot}48\ (\pm 12{\cdot}96) + 53{\cdot}65\ (\pm 13{\cdot}75)\ x - 5{\cdot}80\ (\pm 3{\cdot}29)\ x^2 \quad (r\ 0{\cdot}98), \tag{8}$$

$$\text{H:}\quad y = -32{\cdot}31\ (\pm 19{\cdot}2) + 51{\cdot}60\ (\pm 17{\cdot}27)\ x - 6{\cdot}49\ (\pm 3{\cdot}46)\ x^2 \quad (r\ 0{\cdot}94), \tag{9}$$

at 10°:

$$\text{L:}\quad y = -21{\cdot}57\ (\pm 10{\cdot}10) + 39{\cdot}54\ (\pm 7{\cdot}16)\ x \quad (r\ 0{\cdot}88), \tag{10}$$

$$\text{M:}\quad y = -39{\cdot}00\ (\pm 15{\cdot}80) + 55{\cdot}35\ (\pm 18{\cdot}27)\ x - 8{\cdot}01\ (\pm 4{\cdot}81)\ x^2 \quad (r\ 0{\cdot}94), \tag{11}$$

$$\text{H:}\quad y = -42{\cdot}11\ (\pm 12{\cdot}07) + 40{\cdot}44\ (\pm 31{\cdot}50\ x - 3{\cdot}37\ (\pm 9{\cdot}96)\ x^2 \quad (r\ 0{\cdot}92). \tag{12}$$

In all instances there was a high degree of correlation between the variables investigated. It is interesting to note from Fig. 3(*a*, *b*) that the difference in growth rate between 22 and 10°, when compared over similar intakes, increased with increasing protein content of the ration. Thus, at an IDN of 2 g/kg body-weight$^{0.75}$ per d, the growth rate at 22° was 9, 45 and 77% higher than at 10° on the L, M and H rations respectively. This reflects differences in the composition of *G*, particularly changes in the protein and its associated water content (Close *et al.* 1983).

DISCUSSION

N retention (NR) and its efficiency of utilization (k_N)

The rate and efficiency with which dietary N was retained depended upon both the supply of N and energy in the ration. Thus at any given intake of N, the higher the energy supplied in the ration the higher was NR. When, for example, non-protein energy is limited, dietary protein is utilized for energetic purposes and the utilization of dietary protein for protein accretion diminishes with decrease in energy intake. (Munro, 1951; Fuller & Crofts, 1977). Similarly, dietary protein is utilized to its maximum extent only when sufficient amounts of non-protein energy are supplied. This phenomenon has been observed in both lambs

(Black & Griffiths, 1975) and pigs (Wiesemüller & Poppe, 1969; Wenk *et al.* 1976; Berschauer, 1977; Fuller & Crofts, 1977) and can be inferred from the results of the present investigations. However, it is not just the levels of protein and energy and protein:energy *per se* which influence NR and k_N, but the extent to which the composition of these fractions vary, particularly the amino acid pattern (Miller & Payne, 1964; Berschauer, Gaus, Ehrensvärd *et al.* 1980).

For maximum utilization of protein the diet must, therefore, supply protein and energy in the correct proportion. An indication of the relationship between protein and energy may be gauged from the present results. Fig. 1 shows that at any given IDN, NR was higher the lower the CP:ME value of the ration. The increase in NR may, therefore, be related to the additional energy supplied. Comparison between the L and H rations at a mean IDN of 2·0 g/kg body-weight$^{0.75}$ per d, showed that each 1 g increase in protein retention at 22° was associated with a 310 kJ increase in ME. Similarly, it was possible to relate the differences in IDN to differences in ME at similar rates of NR. Comparison between the L and H rations at 22° showed that at an NR of 1 g/kg body-weight$^{0.75}$ per d, each 1 g change in dietary protein was equivalent to a 106 kJ change in ME. When NR = 2, that is the highest value attained, the equivalence was 44 kJ ME/g. In energetic terms these represent efficiences of 0·22 and 0·54 respectively. This shows the sensitivity of protein metabolism to change in energy intake and reiterates the dynamic relationship that exists between them. This is not always recognized in the assessment of nutrient requirements.

Over similar ranges of N intake, NR was reduced on the M and H rations at 10°, compared with that at 22°, unlike that on the L ration when NR appeared independent of environmental temperature. The latter observation is consistent with that previously determined in our laboratory (Verstegen *et al.* 1973; Close *et al.* 1978). The decrease in NR at 10° was associated with an increase in urinary N excretion. Increased urinary N losses are indicative of high rates of dietary protein degradation associated with excess IN, an imbalanced amino acid pattern of the dietary protein or oxidation of muscle amino acids for thermoregulatory purposes. Under cold conditions the animal's energy requirements increase and this additional requirement is normally met from the carbohydrate and fat fractions of the diet, if provided in sufficient quantity. However, when dietary protein content is increased while maintaining a constant energy content, less energy is available as carbohydrate and fat to meet the thermoregulatory demand of the animal so that the protein fraction is then increasingly used for energetic purposes. This would result in the higher BU levels and increased urinary N losses with increase in protein content of the ration at 10°, compared with those at 22° (Table 1):

At 22° there was little difference in the estimates of N_f and N_m between rations, with the mean values being 0·255 and 0·307 g/kg body-weight$^{0.75}$ per d. At 10° both N_f and N_m increased with the protein content of the ration suggesting that they are dietary dependent, although they may also be related to changes in the body composition of the animals on the different rations. From the results of Close *et al.* (1983) it can be inferred that the animals given the H ration have lower fat reserves than the animals on the L or M rations, so less fat will be available for mobilization purposes to provide energy for the increase in the maintenance energy requirement associated with the increased thermal demand under cold conditions (Close *et al.* 1978). Under such circumstances, and particularly following the prolonged application of the lowest feeding level in the present experiments, it is possible that catabolism of tissue protein occurs to meet the increased thermoregulatory demand as a result of which the endogenous N losses will be increased to reflect the extent of protein catabolism. As a result, the maintenance of a given rate of NR at 10° necessitates a higher IDN than at 22° and this will influence the assessment of the nutrient requirements of pigs under different environmental conditions.

Blood urea (BU)

BU concentration in animals is a useful indicator of the protein status of an animal and those factors which influence it. Other than factors associated with the body-weight, age, sex and breed of the animal, variations in BU concentration have been shown to reflect changes in protein intake (Fonnesbeck & Symons, 1969; Eggum, 1970; Kirchgessner & Kellner, 1972; Müller & Kirchgessner, 1974; Risse *et al.* 1975; Zamora *et al.* 1975), protein quality (Kumta & Harper, 1961; Münchow & Bergner, 1967, 1968; Bergner *et al.* 1970; Eggum, 1970; Braude *et al.* 1974; Williams & Smith, 1975) and protein:energy of the ration (Berschauer, 1977). If it is to be used in assessing the efficiency of protein utilization, then the time at which the blood samples are taken relative to the meal will be of critical importance. In the present experiments maximum BU values were obtained some 3–5 h following feeding in agreement with the results of Menke *et al.* (1969), Eggum (1970) and Berschauer (1977). However, in contrast to the results of Orok & Bowland (1975) there were no differences in either the absolute concentration or the pattern of BU concentration following feeding as a result of the nature of the protein ingested. There was also little difference in the rates at which BU concentration increased following feeding, although from the results of Berschauer (1977) it could have been anticipated that the rate of increase would be related to the protein content of the rations.

Differences in BU concentration reflect changes in the metabolism of dietary N and hence differences in k_N. The extent to which BU concentration is an index of this efficiency can, therefore, be compared by relating it to k_N. Only the values at 22° have been used in the comparison. For this purpose, the mean concentration has been calculated as that throughout the 0–7 h period on each of the consecutive sampling days. The relationship between k_N (y) and BU concentration (mg/100 ml; x) at 22° was:

$$y = 0{\cdot}938\ (\pm 0{\cdot}057)\ -0{\cdot}0106\ (\pm 0{\cdot}0075)\ x \quad (r\ 0{\cdot}85). \tag{13}$$

This relationship is illustrated in Fig. 4 where it can be seen that a decrease in k_N was associated with a significant increase in BU concentration. It may therefore, be concluded that under the conditions of the present experiments those factors which influence BU concentration also influence k_N so that the former is a reliable criterion for assessing the k_N in animals.

Body-weight gain (G)

As anticipated, there were large differences in the rates of gain depending on the treatments imposed on the animals. Since variations in G are primarily caused by variations in lean tissue, that is protein and its associated water, it is interesting to investigate how variations in NR or protein retention influence the rate of gain of the animals fed on rations of varying protein content. Only the results at 22° have been subjected to this analysis because at 10° there was a limited range of NR values over which the relationship could be investigated. The relationships between rate of gain (g/kg body-weight$^{0{\cdot}75}$ per d; y) and NR (g/kg body-weight$^{0{\cdot}75}$ per d; x) at 22° were:

$$\text{L:}\quad y = -12{\cdot}05\ (\pm 2{\cdot}25)\ +56{\cdot}31\ (\pm 29{\cdot}3)\ x\ -1{\cdot}41\ (\pm 1{\cdot}60)\ x^2 \quad (r\ 0{\cdot}97) \tag{14}$$

$$\text{M:}\quad y = -12{\cdot}70\ (\pm 1{\cdot}81)\ +68{\cdot}45\ (\pm 16{\cdot}7)\ x\ -9{\cdot}68\ (\pm 6{\cdot}48)\ x^2 \quad (r\ 0{\cdot}99) \tag{15}$$

$$\text{H:}\quad y = -12{\cdot}21\ (\pm 3{\cdot}43)\ +64{\cdot}25\ (\pm 29{\cdot}2)\ x\ -10{\cdot}97\ (\pm 10{\cdot}80)\ x^2 \quad (r\ 0{\cdot}93) \tag{16}$$

For all three rations there was a high correlation between the variables with a remarkably constant intercept term (Fig. 5). Increasing the protein content of the ration resulted in a reduction in the rate at which growth increased per unit increment in NR with the rate of reduction decreasing with increase in NR. From eqns (14)–(16) it is possible to calculate

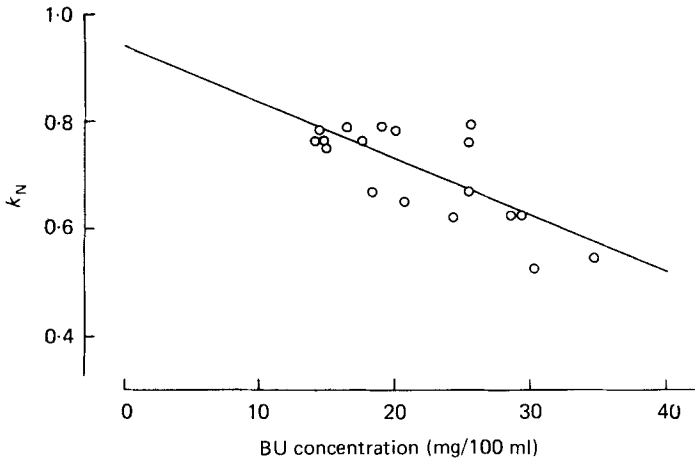

Fig. 4. The relationship between the efficiency of nitrogen utilization (k_N) and blood urea concentration (mg/100 ml; BU) in pigs at an environmental temperature of 22°. The line is drawn from the regression equations presented on p. 281.

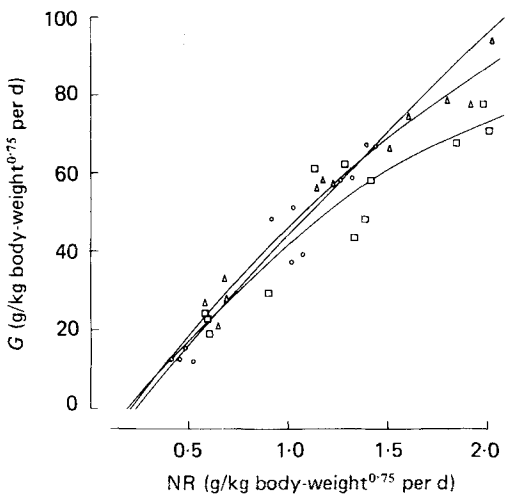

Fig. 5. The relationship between body-weight gain (g/kg body-weight$^{0·75}$ per d; *G*) and nitrogen retention (g/kg body-weight$^{0·75}$ per d; NR) for pigs fed on rations differing in protein content and maintained at an environmental temperature of 22°. (○), Low-protein ration (153 g crude protein (N × 6·25; CP)/kg dry matter (DM)); (△), medium-protein ration (201 g CP/kg DM); (□), high-protein ration (258 g CP/kg DM). The lines are drawn from the regression equations presented on p. 281.

the NR corresponding to zero *G*. The values were 0·216, 0·191 and 0·196 g/kg body-weight$^{0·75}$ per d from eqns (14), (15) and (16) respectively, and taking the mean value, 0·201 g/kg body-weight$^{0·75}$ per d, this corresponds to a retention rate of 16 g protein/d for a 30 kg pig. On the basis that lean meat comprises water and protein in the proportion 4:1 (Close *et al.* 1983) this is equivalent to 80 g lean meat/d. If ash and gut fill do not change then even at thermal neutrality an animal maintaining weight stasis is loosing approximately 80 g fat/d. An animal fed at its maintenance energy requirement would be expected to gain approximately 113 g/d (Close *et al.* 1983), showing that the maintenance of weight stasis and energy equilibrium are not synonomous with one another. The energy required to maintain weight status will underestimate that required to maintain energy equilibrium.

The authors thank Mr R. P. Heavens for the assistance he provided throughout the experiments. F.B. is grateful for the financial support of the Deutsche Forschungsgemeindschaft.

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Printed in Great Britain