Effect of Protein Deprivation on Subsequent Efficiency of Dietary Protein Utilization in Finishing Pigs

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ABSTRACT : A nitrogen (N) balance trial was conducted to examine the effect of N deprivation on subsequent N retention, blood urea nitrogen (BUN) and IGF-I levels and the ratio of IGF binding protein (IGFBP)-3 to IGFBP-1 and -2. Pigs in treatment (T) 1 were given diet A (2.39% N) and those in T2 and T3 were given diet B (1.31% N) and excreta were collected (period 1 (P1)). Pigs in T1 continued to receive diet A while diets for T2 and T3 were changed to diets A and C (2.74% N), respectively. The excreta were collected for two more periods (P2 and P3). During P1, pigs in T2 and T3 retained 50% less N ($p<0.001$) than those in T1. However, pigs provided T2 ($p<0.01$) and T3 ($p<0.05$) retained more N than those assigned to T1 during P2. Pigs in T3 tended to retain more ($p=0.10$) N than those receiving T2 for the same period. The BUN values were lower ($p<0.05$) for pigs assigned to T2 and T3 than T1 during P1 and P2. Both IGF-I and IGFBP ratios of pigs assigned to T1 were higher ($p<0.05$) than those given T2 and T3 during P1 but no differences were found during P2 and P3. (*Asian-Aus. J. Anim. Sci. 2000. Vol. 13, No. 5 : 659-665*)

Key Words : Pigs, Compensatory Nitrogen Retention, Blood Urea Nitrogen, IGF-I, IGF Binding Proteins

INTRODUCTION

Compensatory growth in swine is not well understood. In previous studies (Whang and Easter, 1994, 1995; Whang et al., 1994a), it was demonstrated that retarded growth in early life was compensated in later periods. Some work (Campbell and Biden, 1978; Kornegay et al., 1990) agrees with this finding. However other investigators (Stairs et al., 1991; Hancock et al., 1994) failed to show compensatory growth. The capacity of an animal to compensate may be dependent on gender, genotype, feed intake or possibly other factors. In the previous studies, lean gain was compensated regardless of gender or genotype (Whang and Easter, 1995). Because the growth component of interest is lean muscle, compensatory lean gain rather than compensatory body weight gain should be emphasized. Nitrogen retention is increased during compensatory growth (Whittemore et al., 1978) and should be a valid indicator of changes in lean growth (Whang et al., 1994b, c). Growth regulators, i.e., IGF-I and its binding protein (IGFBP) ratios have not been investigated during compensatory growth. In the present experiment, dietary protein depletion was used to test the hypothesis that the efficiency of N retention would increase during repletion and that this compensatory response would be indicated by changes in BUN, IGF-I and the IGFBP ratio.

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MATERIALS AND METHODS

Animals and feeding

Twelve Landrace-Duroc barrows (initial weight= 56.86 kg) were used in a randomized, complete-block design experiment. Pigs were housed in metabolism crates in an environmentally-regulated room with continuous lighting. Animals within a block were allocated from outcome groups formed on the basis of litter of origin and weight. Pigs were adapted to diet, environment and feeding method (three meals per day at 0600 h, 1200 h, and 1800 h; addition of water at 1:1 (w:w) ratio to feed) for a 5-d period. The experimental diets were formulated to meet amino acid requirements (Diet A), to reduce the growth through feeding protein/amino acid-deficient diet (Diet B), and to investigate if animals require greater nutrient intake during compensatory growth (Diet C). The composition of experimental diets is shown in table 1. Orts were collected to establish absolute feed intake. Water was provided *ad libitum*.

There were three periods (P) in this experiment. Table 2 shows the experimental diet assignments and periods. The first period (P1) was used to establish a protein deficiency in treatment 2 (T2) and treatment 3 (T3). Period 2 and P3 provided repletion either (T2) at the level of protein fed in T1 (control) or at an excessive level (T3). The division of time between P2 and P3 was admittedly arbitrary but was done with

Table 1. Percentage composition and calculated values of experimental diets

	Diet A	Diet B	Diet C
Ingredients (%):			
Corn	68.35	77.99	61.38
Dehulled soybean meal	21.68	2.92	31.45
Cornstarch	5.00	15.00	2.00
Soybean oil	2.00	0.70	2.40
Lysine-HCl	0.07	0.21	-
Dicalcium phosphate	1.49	2.00	1.25
Ground limestone	0.61	0.38	0.71
Vitamin premix[a]	0.20	0.20	0.20
Trace-mineral salt[b]	0.35	0.35	0.35
ASP-250c	0.25	0.25	0.25
Analyzed nitrogen	2.39	1.31	2.74
Calculated values			
Lysine	0.90	0.45	1.13
Ca	0.70	0.70	0.70
P	0.60	0.60	0.60
DE (Mcal per kg diet)	3.57	3.52	3.59
ME (Mcal per kg diet)	3.42	3.42	3.42

[a] Provided per kilogram of diet: 6,600 IU vitamin A, 660 IU vitamin D_3, 88 IU vitamin E, 4.4 mg vitamin K, 0.0352 mg vitamin B_{12}, 8.8 mg riboflavin, 24.2 mg D-pantothenic acid, 33.0 mg niacin and 330 mg choline chloride.

[b] Provided per kilogram of diet: 20.05 mg Mn, 90.38 mg Fe, 100.58 mg Zn, 8.09 mg Cu, 0.35 mg I and 0.30 mg Se.

[c] Supplied per kilogram of diet: 110 mg chlortetracycline, 110 mg sulfamethazine and 55 mg penicillin (American Cynamid Co., Princeton, NJ, USA).

Table 2. Experimental diet assignment and periods

Period	Day of Exp.	Description	Dietary treatment[a]		
			1	2	3
1	1-5	Adaptation	A	A	A
	6-12	Pre-collection[b]	A	B	B
	13-17	Collection	A	B	B
2	18-20	Break	A	A	C
	21-25	Collection	A	A	C
3	26-28	Break	A	A	C
	29-33	Collection	A	A	C

[a] Diet A: Protein-adequate diet (2.39% N); Diet B: Protein-deficient diet (1.31% N); Diet C: High protein diet (2.74% N).

[b] Dietary treatment was applied but excreta were not collected.

intent of observing immediate (P2) and subsequent (P3) compensatory response.

Balance trial

To examine the effect of nitrogen-deficient diets on nitrogen retention, a meal containing 0.25% chromium oxide as an initial fecal marker was fed on d-14 and urine collection was initiated. The last meal for the collection contained 0.25% ferric oxide as a final fecal marker. During the 5-d collection period (P1), urine and fecal material were collected and stored at -20℃. The green-colored chromium oxide and red-colored ferric oxide, two-marker approach was used to avoid the possible confusion in fecal collection because there was only 3-d break between collection periods.

Experimental diets were switched on d-18 to determine if pigs previously fed a protein-deficient diet would retain nitrogen more efficiently than pigs previously fed an adequate diet. During this period (P2), experimental diets were diets A for T1 and T2, and diet C for T3. After a 3-d adaptation, the urine and fecal material were collected for 5 d (P2).

If pigs previously fed the protein-deficient diet exhibit compensatory nitrogen retention, it is important to determine how long it will persist. Thus, urine and fecal material were collected for an additional 5 d (P3) after 3-d collection break.

Proximate analysis

The collected urine and fecal samples were analyzed as described by Carr (1994). Urine was collected into a 8 L-plastic bucket containing 20 mL of 12 N HCl. The daily urine collection was measured, recorded and aliquot was retained. The daily aliquots were frozen individually at -20℃ until pooled. The pooling consisted of combining 1% of each days total urine production from each pig. The pooled samples were refrigerated at 4℃ until nitrogen analysis was conducted.

For fecal collection, chromium oxide and ferric oxide were used (0.25%) as color markers to identify the initiation (chromium oxide) and termination (ferric oxide) of the collection periods. Fecal material was collected daily, placed in plastic bags and frozen. At the end of the experiment, all feces collected during each period from each pig were mixed and fecal samples were freeze-dried. The dried fecal samples were then ground in a Wiley mill through a 1 mm screen and stored at 4℃ until analysis. Urine, feed, and fecal samples were analyzed for nitrogen by the macro-Kjeldahl procedure (AOAC, 1990).

Blood sampling

Pigs were bled by ear vein puncture at the end of the adaptation period (d 5), P1 (d 18), P2 (d 26) and P3 (d 34). A ten mL heparinized sample was obtained and centrifuged at 2,000×g for 20 min and the harvested plasma was frozen at -70℃ until analysis. The plasma samples were used for assays of IGF-I and IGFBP-1, -2 and -3. The ratios of IGF-3 to IGF-1 and -2 were calculated.

Pigs were also bled on d 6, d 19, d 27 and d 35 for BUN assays as described by Whang et al. (1994c). The animals were fasted for 12 h then fed a test meal (table 3) at 0600 h the following day. Pigs were bled 2 h, 3 h and 4 h after the meal to obtain peak post-prandial BUN values (Whang et al., 1994b, c). The quantity of diet fed was calculated from 0.58 g N per kg BW^{75}. Plasma samples were harvested as described above.

Table 3. Percentage composition and calculated values of the test diet for blood urea nitrogen determinations

Ingredients	%
Corn	67.22
Dehulled soybean meal	1.49
Fish meal, Menh.	7.00
Plama protein (AP-820)[a]	5.00
Casein, Erie	7.50
Sucrose	10.00
Dicalcium phosphate	0.97
Ground limestone	0.27
Vitamin premix[a]	0.20
Trace-mineral salt[b]	0.35
Calculated values	
Crude protein	22.00
Lysine	1.43
Ca	0.65
P	0.55
DE (Mcal per kg diet)	3.50
ME (Mcal per kg diet)	3.31

[a] Contains 70.00% crude protein, 13.00% ash, 2.00% fat, 0.14% calcium, 0.13% phosphorus, 3.01% alanine, 6.36% aspartate, 4.79% arginine, 2.24% cystine, 3.70% phenyl-alanine, 2.44% glycine, 8.85% glutamate, 2.50% histidine, 1.96% isoleucine, 5.56% leucine, 6.10% lysine, 0.53% methionine, 4.09% proline, 3.86% serine, 4.13% threonine, 1.33% tryptophan, 3.50% tyrosine and 4.12% valine (American Protein Corporation, Ames, IA, USA).

[b] Provided per kilogram of diet: 6,600 IU vitamin A, 660 IU vitamin D_3, 88 IU vitamin E, 4.4 mg vitamin K, 0.0352 mg vitamin B_{12}, 8.8 mg riboflavin, 24.2 mg D-pantothenic acid, 33.0 mg niacin and 330 mg choline chloride.

[c] Provided per kilogram of diet: 20.05 mg Mn, 90.38 mg Fe, 100.58 mg Zn, 8.09 mg Cu, 0.35 mg I and 0.30 mg Se.

Plasma analyses

An autoanalyzer (Boehringer Mannheim Diagnosis, Indianapolis, IN, USA.) was used to measure BUN employing a method described by Skeggs (1957) and Marsh et al. (1965).

Plasma IGF-I concentration was measured by specific radioimmunoassay (RIA) according to Zhao et al. (1995). A 500 μL sample of plasma was chromatographed in 0.25 mol/L formic acid on a 0.9 $\times$100 cm column containing Sephadex G-50 (Pharmacia LKB, Piscata- way, NJ, USA) to separate IGF-I from IGFBP. Eluent containing IGF-I was collected between 47 mL and 72 mL, lyophilized and resuspended to the original sample volume (500 μL) using RIA buffer (0.03 mol/L sodium phosphate, 2.5 g/L bovine serum albumin, 0.2 g/L sodium azide, pH 7.5). The recovery of IGF-I from the column measured by Zhao et al. (1995) was more than 90%. The IGF-I concentration was measured using ^{125}IGF-I as the radioligand and a polyclonal anti-rabbit somatomedin-C-IGF-I antibody distributed through the Hormone Distribution Program of the National Institute of Diabetes, Digestive and Kidney Diseases to the National Hormone and Pituitary Program. The assay was conducted using duplicate 25 μL, 50 μL and 100 μL samples and binding was determined by a gamma counter (COBRA Auto-Gamma 5000, Packard Instrument, Meriden, CT, USA). Samples were analyzed within a single assay with intra-coefficient of variation of 6% for IGF-I.

Plasma IGFBP profiles were characterized by Western ligand blotting as described by Zhao et al. (1995). Thirty microliters of a 1:10 dilution of plasma were prepared for SDS-PAGE by the addition of sample buffer (Laemmli, 1970), applied to a 4% stacking gel and separated through a 12% gel under nonreducing conditions overnight at 50 V, 4℃. Following the electrophoresis, proteins were electro-transferred onto .45-μm nitrocellulose membranes (Micron Separations, Westborough, MA, USA) using a Buchler semidry electrophoresis transfer unit (Labconco, Kansas City, MO, USA) at 200 mA for 1 h. Nitrocellulose membranes were sequentially blocked with Tris-buffered saline (0.15 mol/L sodium chloride, 0.01 mol/L Tris HCl, pH 7.5) containing 30 g/L Tergitol NP-40, Tris-buffered saline containing 10 g/L bovine serum albumin and Tris-buffered saline containing 1 g/L Tween. Membranes were incubated overnight at 4℃ with [^{125}I] IGF-I in Tris-buffered saline containing 10 g/L bovine serum albumin and 1 g/L Tween. Membranes were washed with Tris-buffered saline, air-dried and IGFBP visualized by exposure to Kodak X-Omat AR film (Rochester, NY, USA.) with an intensifying screen for 7 d at -70℃.

Statistical analysis

All data were analyzed using the GLM procedure of SAS (1985). Nitrogen balance, BUN, IGF-I and IGFBP ratio data were analyzed by ANOVA appropriate for randomized complete-block designs. A one-way ANOVA using GLM was used to determine treatment effects between protein-deficient feeding and protein-adequate feeding and between protein-adequate feeding and high-protein feeding during P1, P2 and P3.

Table 4. Nitrogen metabolism in periods 1, 2 and 3 for pigs given dietary treatments 1, 2 and 3[a]

Period	1			2			3			Pooled SEM
Treatment	1	2	3	1	2	3	1	2	3	
Diet	A	B	B	A	A	C	A	A	C	
Dietary N, %	2.39	1.31	1.31	2.39	2.39	2.74	2.39	2.39	2.74	-
N intake, g/d	50.14	27.60	27.60	60.88	60.88	69.87	71.63	71.63	82.20	-
Fecal N, g/d	8.99	8.16	8.51	9.97	10.90	10.95	14.15	12.47	14.46	0.862
Urinary N, g/d	8.00	3.24	3.03	8.85	5.49	10.52	12.04	11.47	18.15	1.696
Digestable N, % of intake	82.07	70.44	69.15	83.62	82.09	84.33	80.10	82.59	82.29	1.548
Retained N, g/d	33.15	16.21	16.06	42.06	44.49	48.40	44.88	47.68	49.01	0.140
Retained $N/kg^{0.75} \cdot d^{-1}$, g/d	1.47	0.72	0.71	1.72	1.85	1.96	1.65	1.76	1.80	0.041
Retained N, % of digested N	80.60	83.13	84.10	82.60	89.03	82.09	78.88	80.69	73.00	3.173

[a] Data represent means of three pigs. Each period was a 5-d collection and 3-d adaptation between collection periods. Animals were adapted for 5 d before dietary treatment. Average initial body weight was 56.86 kg and average ending body weight was 87.26 kg.

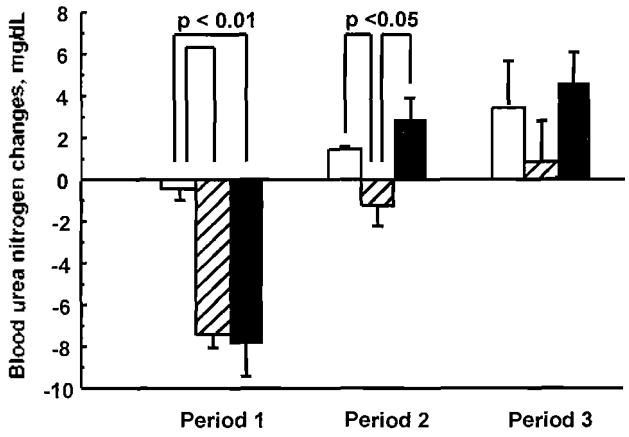

Figure 1. Changes of blood urea nitrogen (BUN) changes from pre-treatment initial BUN in period 1, 2 and 3. Data points represent means±SEM of three pigs. Treatment 1 (pigs fed adequate diet (diet A) during periods 1, 2 and 3)=□; Treatment 2 (pigs fed nitrogen-deficient diet (diet B) during period 1 and fed adequate diet (diet A) during periods 2 and 3)=▨; Treatment 3 (pigs fed nitrogen-deficient diet (diet B) during period 1 and fed high-nitrogen diet (diet C) during periods 2 and 3)=■.

RESULTS

Nitrogen balance data for each period are shown in table 4. Average daily N retentions for pigs receiving T2 (16.21±1.36 g/d) and T3 (16.06±0.47 g/d) were lower ($p<0.001$) than that of those fed T1 (33.15± 1.59 g/d) during P1. Apparent N digestibilities for T2 and T3 were also lower ($p<0.001$) than for T1 during the same period. However, pigs fed T2 and T3 showed less ($p<0.01$) urinary N loss than pigs fed T1.

During P2, animals fed T2 (44.49±0.18 g/d) and T3 (48.40±1.56 g/d) retained more ($p<0.05$) N than those receiving T1 (42.06±0.59 g/d). Pigs fed the high protein diet (diet C; T3) tended to retain more N than pigs fed T2 ($p=0.10$). Because N intake was adjusted to body weight, N retention for all treatments during P2 was increased ($p<0.01$). But N losses and apparent N digestibilities were not different among treatments.

Although pigs assigned to T2 and T3 tended to maintain higher N retention levels than pigs fed T1 during P3 ($p<0.10$), N retention among treatments was not different. Also, those assigned to T3 tended to retain more N than those fed T2 but the difference was not significant. Again protein intake was adjusted to the body weight during P3, but unlike P2, N retention during P3 was not higher than that achieved during P2.

Blood urea nitrogen data are shown in figure 1. The BUN values are expressed as changes in level from pre-treatment measurement. This was done to eliminate the effect of the different BUN levels among individual animals. The BUN levels for pigs assigned to T2 and T3 were dramatically reduced ($p<0.01$) during P1. During P2, BUN for T2 was lower ($p<0.05$) than T1 and T3. The BUN values for T1 and T3 were not different. Although BUN in pigs assigned to T2 tended to be lower than those on T1 or T3 during P3 ($p<0.10$), BUN values among treatments were not different.

The plasma IGF-I concentrations of pigs assigned to T1 (217.00±22.32 ng/mL) were higher ($p<0.01$) than in those fed T2 (107.51±16.80 ng/mL) and T3 (138.51±20.56 ng/mL) during P1 (figure 2). Plasma IGFBP-3 to IGF-1 and 2 ratios for T1 (1.57±0.22) were also higher ($p<0.05$) than for T2 (1.08±0.20) and T3 (1.14±0.19) during P1 (figure 3). However, IGF-I concentration and IGFBP ratio were not affected by dietary treatment during either P2 or P3.

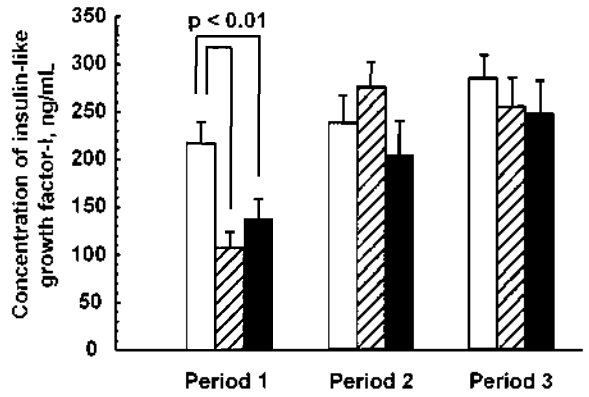

Figure 2. Insulin-like growth factor-I concentrations in periods 1, 2 and 3. Data points represent means ± SEM of three pigs. Treatment 1 (pigs fed adequate diet (diet A) during periods 1, 2 and 3)=□; Treatment 2 (pigs fed nitrogen-deficient diet (diet B) during period 1 and fed adequate diet (diet A) during periods 2 and 3)=▨; Treatment 3 (pigs fed nitrogen-deficient diet (diet B) during period 1 and fed high-nitrogen diet (diet C) during periods 2 and 3)=■.

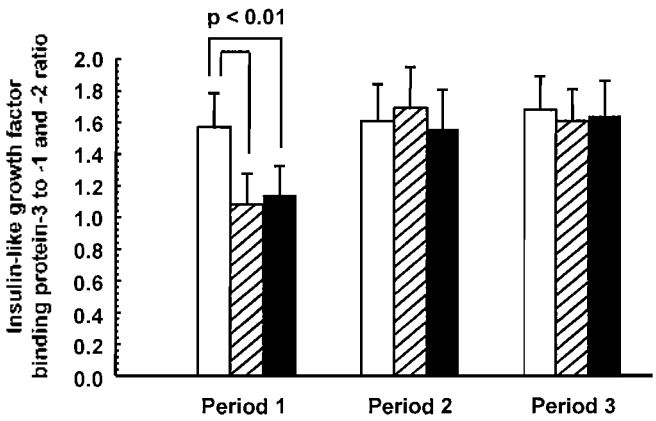

Figure 3. Insulin-like growth factor binding protein 3 to 1 and 2 ratio in periods 1, 2 and 3. Data points represent means ± SEM of three pigs. Treatment 1 (pigs fed adequate diet (diet A) during periods 1, 2 and 3)=□; Treatment 2 (pigs fed nitrogen-deficient diet (diet B) during period 1 and fed adequate diet (diet A) during periods 2 and 3)=▨; Treatment 3 (pigs fed nitrogen-deficient diet (diet B) during period 1 and fed high-nitrogen diet (diet C) during periods 2 and 3)=■.

DISCUSSION

The occurrence of compensatory N retention in growing pigs is not well accepted. In the present experiment, a protein-deficient diet was used to create a model to observe subsequent changes in metabolic efficiency of N utilization. In early studies it was observed that protein synthesis by N-deprived weanling rats is reduced (Waterlow and Stephen, 1968) and loss of body N is seen in severely protein-deficient growing pigs (Whittemore et al., 1978). In this study, pigs assigned to T2 and T3 retained less N during the protein-deficient period (P1). Regulation of protein balance, especially in the liver, is achieved by a decrease in the protein breakdown rate rather than a decrease of the protein synthesis rate (Garlick et al., 1973; Roobol and Alleyne, 1974).

Although N retention is decreased during a period of protein-deficient feeding, the efficiency of dietary utilization is enhanced. A study conducted by Golden et al. (1977) demonstrated that the efficiency of protein utilization is increased in malnourished children. Rats fed a protein-deficient diet also exhibited a slower wasting of muscle mass (Coward et al., 1977). Reduced urinary N loss by pigs assigned to T2 and T3 during P1 supports the concept of increased utilization of dietary protein in the period of protein deprivation. This may result from a decrease in the overall protein flux rate (Shipley and Clark, 1972), or a decrease in the proportion of the flux which is excreted (Millward et al., 1976). Apparent N digestibility in pigs assigned to T2 and T3 was lower than in pigs fed T1, possibly due to a relatively higher excretion of metabolic fecal N relative to N intake. The same finding was observed by Whittemore et al. (1978).

According to Jeffreys and White (1975), Das and Waterlow (1974) and Schmike (1962), the concentration of urea cycle enzymes is reduced in response to a protein-deficient diet since the activity of urea cycle enzymes depends partly on left-over N for excretion after demands for protein synthesis have been met. Blood urea nitrogen levels in pigs fed T2 and T3 were much lower than in pigs fed an adequate diet (T1) which is an evidence of efficient utilization of dietary protein.

In the circumstance created in this experiment, growth hormone (GH) level should have increased (White et al., 1988, 1991). However, serum IGF-I level is believed to decrease in swine (White et al., 1988; Buonomo and Baile, 1991; White et al., 1991) because responsiveness to GH is reduced (Turner and Munday, 1974) or the GF-IGF-I axis is uncoupled during nutritional restriction (Buonomo and Baile, 1991). The present study supports this contention. The IGF-I level in the protein-deficient pigs (T2 and T3) was lower than in the adequately-fed pigs (T1). This study also confirms a correlation between IGF-I level and nitrogen retention in growing pigs (Fletcher et al., 1990).

Insulin-like growth factor binding proteins are also

GH-dependent in swine (Evock et al., 1990). It has been reported that malnutrition will decrease the level of IGFBP-3 and increase IGFBP-1 and -2 (Vicini et al., 1991; White et al., 1991; Cohick et al., 1992; McGuire et al., 1992). The ratio of IGFBP-3 to IGFBP-1 and -2 measured in this experiment was higher for T1 than T2 or T3 during the protein-deficient feeding period. Therefore, IGF-I concentrations and IGFBP ratios were positively related to N retention while BUN values were negatively related to efficiency of N retention during the period of protein-deficient feeding.

During rehabilitation (P2), pigs assigned to T2 were fed the same diet (diet A) as T1 and pigs assigned to T3 were fed a higher protein diet (diet C) to determine if compensatory N retention requires more dietary protein. Pigs assigned to T2 and T3 retained more N than those fed T1. Compensatory protein gain has been explained by enhanced activity of ribosomes in incorporating amino acids into protein (Omstedt and von der Decken, 1972) as well as any increased metabolic rate (Mount et al., 1963). Whittemore et al. (1978) reported that compensatory N retention requires more dietary protein to achieve maximal N retention. Pigs assigned to T3 in the present study tended to retain more N than those on T2. Pigs fed the protein-deficient diet exhibited negative N balance in the Whittemore experiment but pigs still retained about 50% of the N retained by adequately-fed pigs (T1) in the present experiment. It could be that protein-deprivation during P1 in this experiment was milder. We cannot refute the hypothesis that compensatory N retention may require a higher level of dietary protein, at least for a short period of time.

Lower BUN values in pigs on T2 during P2, as well as in P1, indicates that pigs in T2 retained N more efficiently than T1. Pigs fed the higher protein diet (T3) exhibited elevated BUN values compared to those on T2 but were similar to those fed the T1 regime. Higher protein feeding resulted in a greater N retention value during rehabilitation but retention was not as efficient as for those fed T2 regime. Whittemore et al. (1978) also reported a marked reduction in efficiency of protein utilization by pigs fed a higher protein diet. The levels of IGF-I and IGFBP ratio may not be sensitive enough to detect the regulatory basis for the small differences in N retention in this experimental circumstance. However, IGF-I and IGFBP ratio levels can possibly be recovered to normal level quickly. Or, the differences may have been present but undetectable.

During P3, pigs were fed the same diets as in P2 to examine the longer-term compensatory N retention. Nitrogen retention during P3 followed the same trend as in P2 but values were not different. This observation agrees with Whittemore et al. (1978) who reported that compensatory N retention declined as realimentation progressed.

The BUN values during P3 followed the same trends as in T2 but were not different among treatments. The levels of IGF-I and the IGFBP ratio during P3 were also not different amont treatments.

IMPLICATIONS

Pigs fed a protein-deficient diets retain less N but show greater efficiencies of dietary protein utilization. Pigs previously fed a protein-deficient diet exhibit compensatory N retention during realimentation. Compensatory N retention may require a higher level of dietary protein to maximize N retention. Blood urea nitrogen is an indicator of N retention efficiency while IGF-I levels and the IGFBP ratio are not predictors of compensatory N retention.

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