Degree of amino acid restrictions during the grower phase and compensatory growth in pigs selected for lean growth efficiency[1]

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ABSTRACT: A total of 32 select line (SL) and 32 control line (CL) Duroc pigs were used in two trials to determine the effect of dietary amino acid contents during the grower (G) phase and selection for lean growth efficiency on growth performance, carcass traits, and meat quality. In each trial, pigs weighing 20 kg were assigned to 16 pens with two gilts or two castrated males per pen, and pens were randomly assigned within the genetic line to corn-soybean meal G diets formulated to contain 5.0, 7.0, 9.0, or 11.0 g lysine/kg. After 50 kg, all pigs were fed common finisher 1 (F1) and finisher 2 (F2) diets. Pigs were allowed ad libitum access to feed and water. After the initial statistical analyses, the data sets from the two trials were combined. During the G phase, pigs consumed less feed [linear (Ln), $P < 0.001$] and more lysine (Ln, $P < 0.001$), grew faster (Ln, $P < 0.05$) but utilized feed more and lysine less efficiently (Ln, $P < 0.001$) for weight gain as the amino acid content of G diets increased. Increasing dietary amino acids resulted in less ultrasound backfat (Ln, $P < 0.001$) and more serum urea nitrogen [Ln, $P < 0.001$; quadratic (Qd), $P < 0.01$] at the end of the G phase. Pigs grew more slowly during the F1 (Ln, $P < 0.01$ and Qd, $P = 0.05$) and F2 (Ln, $P = 0.07$) phases and utilized feed and lysine less efficiently (Ln, $P < 0.05$) for weight gain during the F1 phase as the amino acid content of G diets increased. The grower diet had no effect on overall weight gain and feed efficiency, carcass traits, or meat quality scores. The efficiency of lysine utilization for overall weight gain (Ln, $P < 0.001$) and lean accretion (Ln, $P < 0.05$) improved as the amino acid content of G diets decreased. The SL pigs grew faster ($P < 0.05$) and had less ($P < 0.001$) ultrasound backfat throughout the study compared with the CL pigs. The SL pigs had less 10th rib backfat ($P < 0.001$) and tended to have larger longissimus muscle area ($P = 0.09$) than the CL pigs, which were reflected in greater rate ($P < 0.001$) and efficiency ($P < 0.05$) of lean accretion. Marbling ($P < 0.05$) and meat color ($P = 0.07$) scores were lower in the SL pigs. No grower diet × genotype interactions were observed in response criteria of interest. The results indicate that pigs subjected to dietary amino acid restrictions during the G phase (as low as 5.0 g lysine/kg) compensated completely in terms of growth rate and body composition regardless of the genotype. Compensatory growth can have a positive impact not only on the overall efficiency of pig production but also on the environment by reducing excretion of unused nutrients.

Key Words: Amino Acids, Compensatory Growth, Pigs, Selection, Undernutrition

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Introduction

The main goal of diet formulation and feeding strategy in commercial pig production is to maximize profits, which does not necessarily imply maximal animal performance (Chiba, 2000). Compensatory growth in pigs subjected to a period of dietary restrictions has been observed (e.g., Robinson, 1964; Prince et al., 1983; Critser et al., 1995). However, the ability of pigs to exhibit compensatory growth and the magnitude of compensation may be influenced by several factors. These may include the age of the animal (Chiba, 1995), duration of dietary restrictions (Prince et al., 1983; Wahlstrom and Libal, 1983), and feed intake during the realimentation period (Ratcliffe and Fowler, 1980; Bikker et al., 1996b). Furthermore, the severity of dietary restrictions (Wahlstrom and Libal, 1983; Mersmann et al., 1987) and genotype (Hogberg and Zimmerman, 1978; Chiba et al., 2002) are likely to affect compensatory responses in pigs.

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A wide variation in the pig's potential for growth and protein accretion continue to exist in today's pig industry. If pigs have the ability to achieve compensatory growth regardless of their genetic potential, it can reduce feed costs, as well as excretion of unused nutrients, during the restriction phase. Furthermore, restricted pigs may grow faster and more efficiently during the realimentation phase, thus, reducing the excretion of unused nutrients further. Compensatory growth can, therefore, have a positive impact not only on the overall efficiency of pig production but also on the environment. The present study was conducted to investigate the effect of dietary lysine content or the degree of amino acid restrictions, during the grower phase on growth performance, serum urea nitrogen (N), internal organ weights, carcass traits, and meat quality traits in pigs selected for lean growth efficiency.

Experimental Procedures

Animals and Facilities. A line of Duroc pigs has been established at Auburn University by six generations of index selection for improved lean growth efficiency (Kuhlers et al., 1996). Selection was based on reduced real-time ultrasound 10th rib backfat and improved feed efficiency using the breeding values estimated from the pig performance test. A control line of contemporary, randomly selected pigs was also maintained.

A total of 32 control line and 32 select line pigs were used in two trials. In each trial, pigs weighing approximately 20 kg were assigned to 16 pens with two gilts or two castrated males per pen, and pens were randomly assigned within the genetic line to one of the four grower diets in a 2 × 4 factorial arrangement of treatments. After the grower phase, all pigs were fed common finisher 1 and finisher 2 diets. Diets were switched and pigs were slaughtered when the average pen weight reached the target weights. Pigs were allowed ad libitum access to feed and water throughout each trial. Pigs were housed in pens (8.9 m^2) with a solid concrete floor in an open-front, grower-finisher building. In the first trial, one pen was removed from the test because of the illness of a pig unrelated to the treatment. Therefore, an extra pen with the same treatment combination was added in the second trial. Pig weights and feed consumption data were collected weekly. The first trial was initiated in September and terminated in February, whereas the second trial was initiated in March and terminated in August. The protocol for animal care was approved by the Institutional Animal Care and Use Committee of Auburn University.

Experimental Diets. The purpose of using four grower diets with different amino acid contents was to create differences in growth performance and body composition during the grower phase. The grower diets were formulated to contain 5.0, 7.0, 9.0, or 11.0 g lysine/kg (Table 1). Corn and soybean meal were used as sources of amino acids and energy to formulate practical diets, and no effort was made to maintain a constant amino acid balance or DE content. The proportions of indispensable amino acids relative to lysine were, however, above that of balanced protein (NRC, 1998), and the DE content was relatively similar (14.4 to 14.6 MJ/kg) for all grower diets. The common corn-soybean meal finisher 1 and finisher 2 diets (Table 1) were formulated to meet the total lysine requirements (NRC, 1998). Minerals and vitamins for all diets were provided in amounts calculated to meet or exceed the NRC (1998) requirements. The grower diets were fed from 20.7 ± 2.0 to 50.2 ± 2.1 kg, the finisher 1 diet from 50.2 ± 2.1 to 80.5 ± 2.4 kg, and the finisher 2 diet from 80.5 ± 2.4 to 108.2 ± 3.6 kg. Feed samples from each batch of feed were pooled, and subsamples were analyzed for DM, CP (AOAC, 1990), and amino acids (Chiba et al., 1991). The results of the CP and amino acid analyses indicated that the dietary CP and lysine contents were generally similar to the intended values (Table 1).

Ultrasound Measurements and Blood Samples. Backfat thickness was measured 4 to 5 cm from the midline on the right side at the 10th rib at the end of grower phase and before slaughter using a real-time ultrasound instrument (SSD-500; Aloka Co., Ltd., Wallingford, CT). Blood samples were taken from each pig between 1000 and 1200 via vena cava puncture using a sterile needle and an evacuated tube at the beginning of the study, the end of the grower phase, and before slaughter. Serum was separated by centrifugation, and an aliquot was stored at −20°C until analyzed for urea nitrogen using a commercially available kit (Sigma Diagnostics, St. Louis, MO).

Slaughter Procedures. At the average pen weight of 108.2 ± 3.58 kg, all pigs were slaughtered at Auburn University's meat laboratory using conventional procedures. To make a gross assessment of metabolic and(or) physiological alterations, heart, liver, and kidneys were collected and weighed separately. The eviscerated carcass was split longitudinally through the vertebrae midline, and warm carcass weight was recorded. After chilling for 24 h at 2°C, the right side was weighed, and carcass length and midline backfat thicknesses at the first rib, last rib, and last lumbar vertebra were measured. To measure longissimus muscle area, the right side was exposed by a perpendicular cut between the 10th and 11th ribs and the longissimus muscle area was traced. Backfat thickness at the 10th rib (about 3/4 distance along the longissimus muscle toward the belly) was also measured. The trimmed weights of wholesale cuts (ham, loin, picnic shoulder, and Boston shoulder) were collected along with the subjective meat quality (color, firmness, and marbling) scores (NPPC, 1991). The rate of carcass lean accretion was estimated by the equation reported by NPPC (1991):

$$\text{Lean (kg/d)}=[(3.280+0.437\text{HCWT}+0.2726\text{LMA}\\ -0.3348\text{BF})-(0.418\text{IWT}-1.656)]/\text{Day}$$

where HCWT is hot carcass weight (kg), LMA is longissimus muscle area (cm^2), BF is 10th rib backfat thickness

Table 1. Composition of grower and finisher diets[a]

	Grower, g lysine/kg				Finisher	Finisher
Item	5.0	7.0	9.0	11.0	1	1
Ingredient, g/kg						
Corn	882.2	811.0	739.8	668.6	797.2	853.1
Soybean meal (48% CP)	89.6	162.0	234.4	306.7	179.7	125.2
Dicalcium phosphate	15.7	14.1	12.5	10.9	11.0	9.5
Limestone	7.0	7.4	7.8	8.3	6.6	6.7
Salt	3.5	3.5	3.5	3.5	3.5	3.5
Mineral-vitamin premix[b]	2.0	2.0	2.0	2.0	2.0	2.0
Calculated composition						
DE, MJ/kg	14.4	14.5	14.5	14.6	14.5	14.5
CP, g/kg	115.8	144.2	172.7	201.2	151.5	130.5
Lysine, g/kg	5.0	7.0	9.0	11.0	7.5	6.0
Calcium, g/kg	7.0	7.0	7.0	7.0	6.0	5.5
Phosphorus, g/kg	6.0	6.0	6.0	6.0	5.5	5.0
Analyzed composition, g/kg[c]						
CP	125.5	153.0	172.7	205.2	153.2	133.3
Lysine	5.2	6.9	8.7	10.6	7.3	5.7
Threonine	4.5	5.5	6.7	8.0	5.8	5.3
Isoleucine	4.1	5.5	6.4	7.9	5.5	4.5
Valine	4.8	6.1	7.3	8.7	6.5	5.4
Histidine	3.0	3.8	4.4	5.2	4.0	3.4

[a] Grower diets were formulated to contain 5.0, 7.0, 9.0, or 11.0 g lysine/kg, whereas finisher 1 and 2 diets were formulated to contain 7.5 and 6.0 g lysine/kg, respectively. Grower diets were offered from 20.7 ± 2.0 to 50.2 ± 2.1 kg, finisher 1 diet from 50.2 ± 2.1 to 80.5 ± 2.4 kg, and finisher 2 diet from 80.5 ± 2.4 to 108.2 ± 3.6 kg average pen weight.

[b] Provided the following (unit/kg diet): 90 mg of Zn, 80 mg of Fe, 32 mg of Mn, 10 mg of Cu, 0.4 mg of I, 0.3 mg of Se, 5,514 IU of vitamin A, 1,103 IU of vitamin D_3, 24 IU of vitamin E, 2 mg of vitamin K activity (menadione sodium bisulfite complex), 26 μg of vitamin B_{12}, 4 mg of riboflavin, 18 mg of pantothenic acid, 26 mg of niacin, and 66 mg of choline.

[c] No analysis for sulfur amino acids or tryptophan.

(mm), IWT is initial weight (kg), and Day is days on the study.

Statistical Analysis. Data were analyzed using the GLM procedure of SAS (SAS Inst. Inc., Cary, NC). The pen was considered as the experimental unit. The initial analysis of the data indicated the two-factor interactions with trial were not important sources of variation; thus, the two data sets were combined. The effects of genotype, grower diet, sex, trial, and the appropriate interactions were included in the model. The two-factor interactions with trial and all of the three-factor interactions were not important sources of variation; thus, they were deleted from the final model. Orthogonal polynomials were used to assess the effect of amino acid content of grower diets. The initial and final weights were included in the model as covariates for the analysis of the growth performance data, whereas only the final weight was used as a covariate for ultrasound, carcass, and internal organ weight data. For the serum urea N data, the initial urea N concentration was included in the model as a covariate.

Results

Grower Phase. There were no dietary amino acid content or grower diet × genotype interactions in any of the response criteria. During the grower phase, increasing the amino acid content resulted in a decrease in feed intake (linear, $P < 0.001$) and an increase in lysine intake (linear, $P < 0.001$; Table 2). Pigs grew faster (linear, $P < 0.05$) and more efficiently (linear, $P < 0.001$), but utilized lysine less efficiently (linear, $P < 0.001$) for weight gain as dietary amino acids increased. At the end of the grower phase, ultrasound backfat thickness decreased linearly ($P < 0.001$) with an increase in dietary lysine. On the other hand, serum urea N at the end of grower phase increased (linear and quadratic, $P < 0.01$] as dietary amino acids increased (11.6, 11.1, 12.6, and 16.7 mg/dL; Figure 1). The select line pigs grew faster ($P < 0.05$) and had less ultrasound backfat ($P < 0.001$; Table 2) and serum urea N (12.0 vs 14.1 mg/dL; $P < 0.05$; Figure 1) than the control line pigs.

Finisher 1 Phase. Similar to the grower phase, there were no grower diet × genotype interactions in any of the response criteria during the finisher 1 phase (Table 3). As the amino acid content of the grower diet increased, pigs grew more slowly (linear, $P < 0.01$; quadratic, $P < 0.05$), even though their feed and lysine intakes were relatively similar. Consequently, those pigs utilized feed and lysine less efficiently for weight gain (linear, $P < 0.05$). The select line pigs tended to consume more feed ($P = 0.08$) and lysine ($P = 0.07$) and grew faster ($P < 0.01$) than the control line pigs. The genotype had no effect on the efficiency of weight gain.

Finisher 2 Phase. There were grower diet × genotype interactions ($P < 0.05$) in the efficiency of feed and lysine utilization during the finisher 2 (Table 4). However, no

Table 2. Effect of the amino acid content of grower diets and genotype on growth performance and ultrasound backfat thickness of pigs during the grower phase[a,b]

Item	ADFI, g/d	ADLysI, g/d	ADG, g/d	G:F, g/kg	G:LysI, g/g	UBF, mm
Grower diet, g lysine/kg						
5.0	2,176	11.4	642	295	57.3	17.8
7.0	2,059	14.2	701	341	49.5	15.6
9.0	1,827	15.9	705	385	44.8	12.1
11.0	1,722	18.3	730	427	40.2	12.1
Genotype						
Control	1,909	14.6	669	357	47.3	16.4
Select	1,983	15.4	720	368	48.6	12.4
P-value[c,d]						
Grower diet:						
Linear	0.001	0.001	0.027	0.001	0.001	0.001
Quadratic	—	—	—	—	—	—
Cubic	—	—	—	—	—	—
Genotype	—	—	0.039	—	—	0.001
CV, %	11.2	11.4	9.1	8.1	9.0	17.2

[a] Grower diets were formulated to contain 5.0, 7.0, 9.0, or 11.0 g lysine/kg. ADLysI = average daily lysine intake; G:F = gain:feed ratio; G:LysI = gain:lysine intake ratio; and UBF = ultrasound backfat thickness.

[b] Least squares means were based on eight pens per grower diet or 16 pens per genotype; the initial (20.7 ± 2.0 kg) and final (50.2 ± 2.1 kg) weights were included in the model as covariates, whereas the final weight was used as a covariate for the ultrasound data.

[c] P-values ≤ 0.10 are reported.

[d] No grower diet × genotype interactions with $P \leq 0.10$.

clear trends were observed, and there were no grower diet × genotype interactions in other response criteria. As in the finisher 1 phase, pigs tended to grow more slowly (linear, $P = 0.07$) as the amino acid content of the grower diet increased. The grower diet had no effect on feed or lysine intake; thus, the efficiency of feed and lysine utilization seemed to decrease with the increase in dietary amino acids. There was a trend for quadratic ($P = 0.10$) effect of dietary lysine on ultrasound backfat thickness, but the grower diet had no effect on serum urea N at the end of the finisher 2 phase (Figure 1). The select line pigs grew faster ($P < 0.05$) and had less ultrasound backfat ($P < 0.001$) than the control line pigs (Table 4).

Grower-Finisher Phase. No grower diet × genotype interactions were observed in any of the response criteria during the grower-finisher phase (Table 5). Pigs consumed more lysine and utilized dietary lysine less efficiently (linear, $P < 0.001$) for weight gain as the amino acid content of the grower diet increased. The grower diet had no effect on feed intake, weight gain, or feed efficiency. The select line pigs tended to consume more feed ($P = 0.07$) and lysine ($P = 0.06$) and grew faster ($P < 0.01$) than the control line pigs. There were no effects of the genotype on the efficiency of overall feed or lysine utilization for weight gain.

Carcass, Internal Organs, and Meat Quality. Although there was a cubic ($P < 0.05$) effect of dietary amino acids on the weight of loin, other carcass measurements were not affected by the grower diet (Table 6). The select line pigs had a longer carcass ($P < 0.001$) and heavier ham ($P < 0.01$) and picnic shoulder ($P < 0.05$) than the control line pigs. Increasing the dietary amino acid content resulted in trends for quadratic ($P = 0.05$) and cubic ($P = 0.07$) effects on the weight of liver and kidneys, respectively. The select line pigs had heavier ($P < 0.01$) heart and liver, and tended to have heavier kidneys ($P = 0.06$) than the control line pigs.

Pigs utilized lysine less efficiently (linear, $P < 0.05$) for lean accretion as the amino acid content of the grower diet increased (Table 7). The grower diet had no effect on carcass traits or rate and feed efficiency of lean accretion. Similarly, subjective meat quality scores were not influenced by the amino acid content of grower diets. Pigs selected for lean growth efficiency had less 10th rib carcass backfat ($P < 0.001$) and tended to have a larger longissimus muscle area ($P = 0.09$) compared with the control line pigs. These were reflected in their greater rate of lean accretion ($P < 0.001$) and the efficiency of feed and lysine utilization for lean accretion ($P < 0.05$). The select line pigs tended to have a lower ($P = 0.07$) meat color score and had a lower ($P < 0.05$) marbling score compared with the control line pigs.

Discussion

Pigs selected for or against subcutaneous fat and(or) growth rate have shown differences in the mass of metabolically active organs (Koong et al., 1983; Pond et al., 1988), feed intake (Woltmann et al., 1992), N retention (Yen et al., 1983), activity of various lipogenic enzymes (Steele and Frobish, 1976), concentrations of metabolites (Pond et al., 1981, 1988), hormones (Buonomo and Klindt, 1993; Ramsay et al., 1998; Cameron et al., 2000), and metabolism of adipose tissues (Standal et al., 1973; Steele et al., 1974). Those reported differences indicate the physiological and metabolic alterations taking place in pigs selected for specific traits, and they may affect a nature

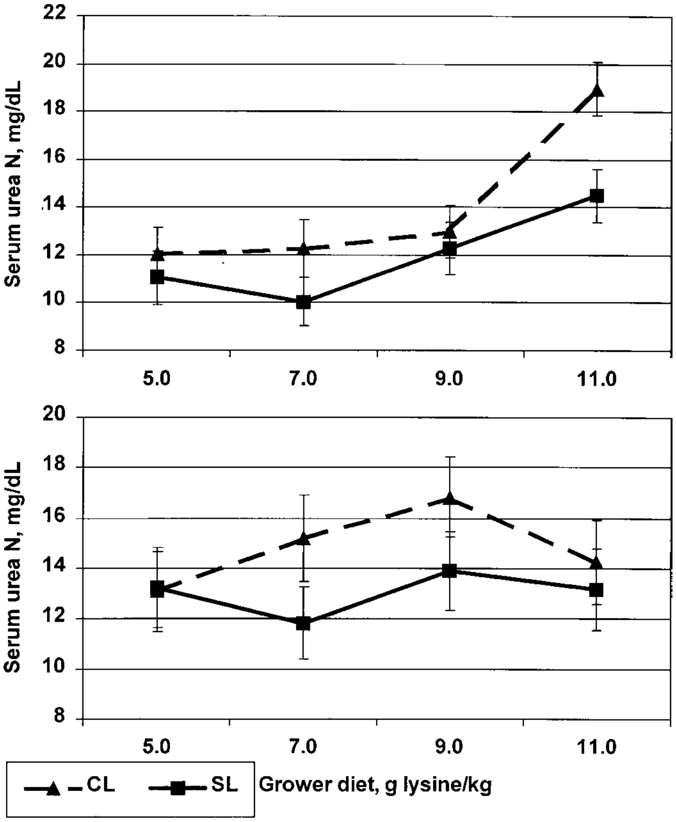

Figure 1. Effect of the amino acid content of grower diet on serum urea nitrogen (N) concentrations in the control line (CL) and select line (SL) pigs at the end of the grower (top; 50.2 ± 2.1 kg) and finisher 2 (bottom; 108.2 ± 3.6 kg) phases. Grower diets were formulated to contain 5.0, 7.0, 9.0 or 11.0 g lysine/kg. The initial serum urea N concentration was used as a covariate, and least squares means are based on four pens per treatment. At the end of the grower phase: linear ($P < 0.001$) and quadratic ($P < 0.01$) effects of the grower diet, and genotype effect ($P < 0.05$).

of response to dietary manipulations in animals with distinct genotypes.

In the present study, the select line pigs grew faster and had less ultrasound and carcass backfat and a greater rate of lean accretion than the control line pigs. Although the select line pigs tended to consume more feed and lysine, they had a more efficient overall lean growth than the control line pigs, indicating that the selection for lean growth efficiency was successful. The lower serum urea N concentration at the end of the grower phase may be a further indication that the select line pigs utilized amino acids more efficiently for growth than did the control line pigs (Berschauer et al., 1983; Chiba et al., 1991).

The select line pigs seemed to have heavier metabolically active organs than the control line pigs. Similar results have been reported by Pond et al. (1988) and Cliplef and McKay (1993). Heavier metabolically active organs can be a reflection of a more intense protein turnover, which may result in better carcass quality. As mentioned before, the selection has resulted in improved carcass quality and lean growth efficiency in the present study. On the other hand, the select line pigs had a lower marbling score and had a tendency for a lower meat color score than the control line pigs. Although the relationships between lean growth and meat quality traits have not been defined well, the results of the present study indicate that the ultimate product quality may have declined. Using the previous generations of the same two lines of pigs at this station, Huff-Lonergan et al. (1997, 1998) reached a similar conclusion. Nevertheless, these results indicate that the genotype had clear effects on growth performance and carcass and meat quality traits.

Hogberg and Zimmerman (1978) found that a fat-strain of pigs fed a low-CP diet during the early phase of development exhibited partial or complete compensation in growth rate and carcass composition during the realimentation phase. However, a lean-strain of pigs failed to compensate, implying that the early protein restriction may have been too severe for pigs with a higher genetic potential for lean growth. Using the same two genotypes as in the present study, Chiba et al. (2002) observed some grower diet × genotype interactions and concluded that pigs selected for lean growth efficiency may have to be offered a grower diet containing adequate amino acid concentrations to optimize overall growth performance. These findings clearly indicate that compensatory responses can be influenced by the genotype.

In the present study, although there were grower diet × genotype interactions in the efficiency of feed and lysine utilization for weight gain during the finisher 2 phase, no clear trends were observed. Furthermore, there were no interactions in any other response criteria during the finisher 2 phase or in any response criteria during the grower, finisher 1, or overall phase. These results indicate that both genotypes responded similarly to the dietary manipulations during the grower and finisher phases. Likewise, Pond and Yen (1984) reported that obese and lean pigs responded similarly to a protein restriction during the realimentation phase, even though lean pigs were affected more severely by the restriction compared with the obese pigs. Similar results have been reported by de Greef et al. (1992).

During the grower phase, the decrease in dietary amino acid content resulted in reductions in the rate and efficiency of growth. In addition, ultrasound backfat thickness increased as the dietary amino acid content decreased. These results are in agreement with previous reports (Chiba, 1994, 1995; Chiba et al., 1999, 2002), and the effort to reduce growth performance of pigs through amino acid restrictions was, therefore, successful.

The results also indicate that pigs responded positively to higher concentrations of amino acids than those recommended by the NRC (1998). In terms of weight gain and feed efficiency, pigs responded linearly to the increase in dietary amino acids or the increase in lysine from 5.0 to 11.0 g/kg. On the other hand, pigs consumed less lysine and utilized it more efficiently for weight gain as dietary

Table 3. Effect of the amino acid content of grower diets and genotype on growth performance during the finisher 1 phase[a,b]

Item	ADFI g/d	ADLysI g/d	ADG g/d	G:F g/kg	G:LysI g/g
Grower diet, g lysine/kg					
5.0	2,761	20.2	898	326	44.5
7.0	2,709	19.8	810	299	40.7
9.0	2,683	19.6	745	280	38.2
11.0	2,686	19.7	772	287	39.4
Genotype					
Control	2,623	19.2	762	292	39.8
Select	2,796	20.5	850	304	41.6
P-value[c,d]					
Grower diet:					
Linear	—	—	0.004	0.027	0.028
Quadratic	—	—	0.051	—	—
Cubic	—	—	—	—	—
Genotype	0.076	0.070	0.004	—	—
CV, %	9.1	9.1	8.9	10.2	10.2

[a] Grower diets were formulated to contain 5.0, 7.0, 9.0, or 11.0 g lysine/kg. ADLysI = average daily lysine intake; G:F = gain:feed ratio; and G:LysI = gain:lysine intake ratio.

[b] Least squares means were based on eight pens per grower diet or 16 pens per genotype; the initial (50.2 ± 2.1 kg) and final (80.5 ± 2.4 kg) weights were included in the model as covariates.

[c] *P*-values ≤ 0.10 are reported.

[d] No grower diet × genotype interactions with $P \leq 0.10$.

amino acids decreased. Similar results have been reported previously (Chiba et al., 1991; Chiba, 1994). A decrease in blood urea N may be associated with an increase in the efficiency of N (Berschauer et al., 1983) or lysine (Chiba et al., 1991) utilization. In the present research, serum urea N concentrations at the end of the grower phase decreased as the dietary amino acid content decreased. Because of their total protein consumption, pigs fed the low-amino acid diets were expected to eliminate less N compared with those fed the high-amino acid

Table 4. Effect of the amino acid content of grower diets and genotype on growth performance and ultrasound backfat thickness of pigs during the finisher 2 phase[a,b]

Item	ADFI, g/d	ADLysI, g/d	ADG, g/d	G:F, g/kg[c]	G:LysI, g/g[d]	UBF, mm
Grower diet, g lysine/kg						
5.0	3,124	17.8	816	261	46.0	25.6
7.0	3,221	18.3	772	241	42.4	26.3
9.0	3,233	18.4	759	237	41.7	31.3
11.0	3,206	18.2	737	231	40.6	23.1
Genotype						
Control	3,137	17.8	741	238	41.8	32.0
Select	3,255	18.5	801	248	43.5	21.1
P-value[e]						
Grower diet:						
Linear	—	—	0.066	0.029	0.027	—
Quadratic	—	—	—	—	—	0.099
Cubic	—	—	—	—	—	—
Genotype	—	—	0.048	—	—	0.001
Grower diet × genotype	—	—	—	0.036	0.036	—
CV, %	7.2	7.2	10.1	9.9	9.9	26.8

[a] Grower diets were formulated to contain 5.0, 7.0, 9.0, or 11.0 g lysine/kg. ADLysI = average daily lysine intake; G:F = gain:feed ratio; G:LysI = gain:lysine intake ratio; and UBF = ultrasound backfat thickness.

[b] Least squares means were based on eight pens per grower diet or 16 pens per genotype; the initial (80.5 ± 2.4 kg) and final (108.2 ± 3.6 kg) weights were included in the model as covariates, whereas the final weight was used as a covariate for the ultrasound data.

[c] G:F = 241, 258, 218, and 233 g/kg in the control line pigs and 281, 224, 257, and 229 g/kg in the select line pigs fed diets containing 5.0, 7.0, 9.0, and 11.0 g lysine/kg, respectively.

[d] G:LysI = 42.4, 45.4, 38.4, and 40.9 g/g in the control line pigs and 49.5, 39.3, 45.1, and 40.3 g/g in the select line pigs fed diets containing 5.0, 7.0, 9.0, and 11.0 g lysine/kg, respectively.

[e] *P*-values ≤ 0.10 are reported.

Table 5. Effect of the amino acid content of grower diets and genotype on growth performance during the grower-finisher phase[a,b]

Item	ADFI g/d	ADLysI g/d	ADG g/d	G:F g/kg	G:LysI g/g
Grower diet, g lysine/kg					
5.0	2,616	15.9	764	293	48.3
7.0	2,612	17.2	756	291	44.1
9.0	2,527	17.8	731	291	41.3
11.0	2,547	19.0	749	293	39.2
Genotype					
Control	2,519	17.0	719	287	42.5
Select	2,632	17.9	781	297	44.0
P-value[c,d]					
Grower diet:					
Linear	—	0.001	—	—	0.001
Quadratic	—	—	—	—	—
Cubic	—	—	—	—	—
Genotype	0.070	0.057	0.004	—	—
CV, %	6.2	6.6	6.7	6.9	6.8

[a] Grower diets were formulated to contain 5.0, 7.0, 9.0, or 11.0 g lysine/kg. ADLysI = average daily lysine intake; G:F = gain:feed ratio; and G:LysI = gain:lysine intake ratio.

[b] Least squares means were based on eight pens per grower diet and 16 pens per genotype; the initial (20.7 ± 2.0 kg) and final (108.2 ± 3.6 kg) weights were included in the model as covariates.

[c] *P*-values ≤ 0.10 are reported.

[d] No grower diet × genotype interactions with *P* ≤ 0.10.

diets, but it is possible that pigs subjected to early amino acid restrictions may have utilized lysine more efficiently for growth.

The grower diet had clear effects on growth performance in the subsequent phases, even though there were some aforementioned interactions. Previously restricted pigs grew faster and more efficiently during the finisher 1 and finisher 2 phases than the unrestricted pigs, and their responses were essentially linear as dietary amino acids or dietary lysine content decreased from 11.0 to 5.0 g/kg. Because of this turnaround, there was no difference in overall growth performance due to the amino acid content of the grower diet. The results indicate that the restricted pigs exhibited compensatory responses in growth performance during the realimentation phase. Similar results have been reported earlier (Wahlstrom and Libal, 1983; Chiba, 1994, 1995).

Furthermore, the grower diet had no effect on carcass traits, estimated rate and efficiency of lean accretion, or meat quality. Similarly, other investigators reported no effect of grower diets on carcass traits or lean accretion (Chiba, 1995; Chiba et al., 1999). Although the pigs' responses may be dependent on the degree of dietary restrictions (Mersmann et al., 1987), these results indicate that pigs subjected to amino acid restrictions during the grower phase (as low as 5.0 g lysine/kg in the present study) can compensate completely in terms of growth performance and body composition by the time they reach the slaughter weight.

It has been reported that pigs on a higher plane of nutrition had heavier metabolically active internal organs and some components of the gastrointestinal tract (Koong et al., 1983). This may affect heat loss associated with maintenance (Ferrell, 1988), thus, the nutrient needs for growth. Specific organs may exhibit compensatory growth (Bikker et al., 1996b; Lu et al., 1996), as evidenced by an increased rate of protein accretion in organs after a period of dietary restrictions (Bikker et al., 1996a). In the present study, no clear effect of the grower diet on the weight of internal organs was observed, even though there were some differences (Table 6). Similar results have been reported previously (Chiba, 1995; Chiba et al., 1999).

Ratcliffe and Fowler (1980) indicated that a compensatory growth response, which persisted for several weeks following severe nutritional restrictions, was mainly due to an increase in feed intake relative to the body weight. On the other hand, Zimmerman and Khajarern (1973) suggested that compensatory responses in growth performance are not due to an increased appetite, but reflect a change in metabolism. This contention was supported by findings of several other researchers (e.g., Campbell et al., 1983; Valaja et al., 1992; Chiba et al., 2002), who reported that pigs subjected to dietary restrictions utilized feed more efficiently during the realimentation phase than the unrestricted pigs. In the present study, although the dietary restriction resulted in improved efficiency of feed utilization in the subsequent phases, it had no effect on overall feed efficiency. The reduced intake during the grower phase and enhanced utilization throughout the study in pigs subjected to dietary restrictions were reflected, however, in an overall decrease in lysine intake and a more efficient overall utilization of lysine for weight gain and also for lean growth compared with unrestricted pigs.

Implications

Although pigs selected for lean growth efficiency had superior growth performance and body composition com-

Table 6. Effect of the amino acid content of grower diets and genotype on carcass measurements and internal organ weights[a,b]

	Carcass					Internal organ		
Item	Length, cm	Ham, kg	Loin, kg	Picnic, kg	Boston, kg	Heart, g	Liver, g	Kidneys, g
Grower diet, g lysine/kg								
5.0	78.4	8.34	7.24	4.01	2.90	386	1,571	327
7.0	78.3	8.46	7.43	3.88	2.98	377	1,589	317
9.0	78.0	8.34	6.92	3.69	2.88	396	1,638	341
11.0	77.9	8.37	7.29	4.03	3.00	380	1,460	324
Genotype								
Control	77.1	8.15	7.22	3.72	2.91	366	1,492	318
Select	79.2	8.60	7.22	4.09	2.97	403	1,637	337
P-value[c,d]								
Grower diet:								
Linear	—	—	—	—	—	—	—	—
Quadratic	—	—	—	—	—	—	0.054	—
Cubic	—	—	0.046	—	—	—	—	0.066
Genotype	0.001	0.004	—	0.020	—	0.005	0.006	0.060
CV, %	1.7	4.3	6.3	10.0	11.1	8.1	8.1	8.1

[a] Grower diets were formulated to contain 5.0, 7.0, 9.0, or 11.0 g lysine/kg. Picnic = picnic shoulder and Boston = Boston shoulder.

[b] Least squares means were based on eight pens per grower diet or 16 pens per genotype; the final (108.2 ± 3.6 kg) weight was included in the model as a covariate.

[c] *P*-values ≤ 0.10 are reported.

[d] No grower diet × genotype interactions with P ≤ 0.10.

pared with the control line pigs, both lines of pigs compensated completely in terms of growth rate and body composition after a period of dietary amino acid restrictions. Furthermore, the overall efficiency of lysine utilization for weight gain and lean accretion was improved by amino acid restrictions during the grower phase regardless of the genotype. Compensatory growth can have a positive impact not only on the overall efficiency of pig production but also on the environment by reducing excretion of unused nutrients.

Literature Cited

AOAC. 1990. Official Methods of Analysis. 15th ed. Association of Official Analytical Chemists, Arlington, VA.

Table 7. Effect of the amino acid content of grower diet and genotype on carcass traits, rate and efficiency of lean accretion, and meat quality scores[a,b]

	Carcass		Lean			Meat quality		
Item	Backfat, mm	LMA, cm^2	ADLG, g/d	LG:F, g/kg	LG:LysI, g/g	Color	Marbling	Firmness
Grower diet, g lysine/kg								
5.0	27.9	29.4	236	89.8	14.7	2.43	3.08	3.36
7.0	28.5	30.7	238	91.8	13.9	2.45	2.70	2.95
9.0	28.1	30.0	222	89.6	12.8	2.49	2.63	2.99
11.0	28.3	31.3	235	92.7	12.2	2.33	2.74	2.90
Genotype								
Control	33.4	29.2	209	84.4	12.4	2.53	2.99	3.15
Select	23.0	31.5	257	97.5	14.4	2.32	2.57	2.95
P-value[c,d]								
Grower diet:								
Linear	—	—	—	—	0.014	—	—	—
Quadratic	—	—	—	—	—	—	—	—
Cubic	—	—	—	—	—	—	—	—
Genotype	0.001	0.093	0.001	0.011	0.013	0.068	0.030	—
CV, %	21.3	12.0	12.3	14.0	14.1	12.2	18.0	16.0

[a] Grower diets were formulated to contain 5.0, 7.0, 9.0, or 11.0 g lysine/kg. Backfat = 10th rib backfat; LMA = longissimus muscle area; ADLG = average daily lean gain; LG:F = lean gain:feed ratio; and LG:LysI = lean gain:lysine intake ratio.

[b] Least squares means were based on eight pens per grower diet or 16 pens per genotype; the final (108.2 ± 3.6 kg) weight was included in the model as a covariate for the backfat and longissimus muscle area data.

[c] *P*-values ≤ 0.10 are reported.

[d] No grower diet × genotype interactions with *P* ≤ 0.10.

Berschauer, F., W. H. Close, and D. B. Stephens. 1983. 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. Br. J. Nutr. 49: 271–283

Bikker, P., M. W. A. Verstegen, and R. G. Campbell. 1996a. Performance and body composition of finishing gilts (45 to 85 kilograms) as affected by energy intake and nutrition in earlier life: II. Protein and lipid accretion in body components. J. Anim. Sci. 74:817–826.

Bikker, P., M. W. A. Verstegen, B. Kemp, and M. W. Bosch. 1996b. Performance and body composition of finishing gilts (45 to 85 kilograms) as affected by energy intake and nutrition in earlier life: I. Growth of the body and body components. J. Anim. Sci. 74:806–816.

Buonomo, F. C., and J. Klindt. 1993. Ontogeny of growth hormone(GH), insulin like growth factors (IGF-I and IGF-II) and IGF binding protein-2 (IGFBP-2) in genetically lean and obese swine. Domest. Anim. Edocrinol. 10:257–265.

Cameron, N. D., J. C. Penman, and E. McCullough. 2000. Serum leptin concentration in pigs selected for high or low daily food intake. Genet. Res. 75:209–213.

Campbell, R. G., M. R. Taverner, and D. M. Curic. 1983. Effects of feeding level from 20 to 45 kg on the performance and carcass composition of pigs grown to 90 kg live weight. Livest. Prod. Sci. 10:265–272.

Chiba, L. I. 1994. Effects of dietary amino acid content between 20 and 50 and 50 and 100 kg live weight on the subsequent and overall growth performance of pigs. Livest. Prod. Sci. 39:213–221.

Chiba, L. I. 1995. Effects of nutritional history on the subsequent and overall growth performance and carcass traits of pigs. Livest. Prod. Sci. 41:151–161.

Chiba, L. I. 2000. Feeding systems for pigs. In: M. K. Theodorou, and J. France (ed.) Feeding Systems and Feed Evaluation Models. pp 181–209. CABI Publishing, Wallingford, UK.

Chiba, L. I., H. W. Ivey, K. A. Cummins, and B. E. Gamble. 1999. Growth performance and carcass traits of pigs subjected to marginal dietary restrictions during the grower phase. J. Anim. Sci. 77:1769–1776.

Chiba, L. I., D. L. Kuhlers, L. T. Frobish, S. B. Jungst, E. J. Huff-Lonergan, S. M. Lonergan, and K. A. Cummins. 2002. Effect of dietary restrictions on growth performance and carcass quality of pigs selected for lean growth efficiency. Livest. Prod. Sci. 74:93–102.

Chiba, L. I., A. J. Lewis, and E. R. Peo, Jr. 1991. Amino acid and energy interrelationships in pigs weighing 20 to 50 kilograms: 1. Rate and efficiency of weight gain. J. Anim. Sci. 69:694–707.

Cliplef, R. L., and R. M. McKay. 1993. Visceral organ weights of swine selected for reduced backfat thickness and increased growth rate. Can. J. Anim. Sci. 73:201–206.

Critser, D. J., P. S. Miller, and A. J. Lewis. 1995. The effects of dietary protein concentration on compensatory growth in barrows and gilts. J. Anim. Sci. 73:3376–3383.

de Greef, K. H., B. Kemp, and M. W. A. Verstegen. 1992. Performance and body composition of fattening pigs of two strains during protein deficiency and subsequent realimentation. Livest. Prod. Sci. 30:141–153.

Ferrell, C. L. 1988. Contribution of visceral organs to animal energy expenditures. J. Anim. Sci. 66(Suppl. 3):23–34.

Hogberg, M. G., and D. R. Zimmerman. 1978. Compensatory responses to dietary protein, length of starter period and strain of pig. J. Anim. Sci. 47:893–899.

Huff-Lonergan, E., D. L. Kuhlers, S. M. Lonergan, and S. B. Jungst. 1998. Characterization of pork quality in response to five generation of selection for lean growth efficiency. J. Anim. Sci. 76(Suppl. 1):151 (Abstr.).

Huff-Lonergan, E., D. L. Kuhlers, S. M. Lonergan, W. B. Mikel, S. B. Jungst, S. Dale, and V. D. Reed. 1997. Pork quality decline in response to selection for lean growth efficiency in absence of the halothane gene. J. Anim. Sci. 75(Suppl. 1):176 (Abstr.).

Koong, L. J., J. A. Nienaber, and H. J. Mersmann. 1983. Effects of plane of nutrition on organ size and fasting heat production in genetically obese and lean pigs. J. Nutr. 113:1626–1631.

Kuhlers, D. L., S. B Jungst, and B. E., Gamble. 1996. Indirect selection for lean feed conversion in Duroc swine. J. Anim. Sci. 74(Suppl. 1):119 (Abstr).

Lu, C. D., P. A. Schoknecht, K. J. Ellis, R. Shypailo, D-R. Su, and W. G. Pond. 1996. Differential compensatory organ growth in young pigs after short-term rehabilitation from protein deficiency. Nutr. Res. 16:627–637.

Mersmann, H. J., M. D. MacNeil, S. C. Seideman, and W. G. Pond. 1987. Compensatory growth in finishing pigs after feed restriction. J. Anim. Sci. 64:752–764.

NPPC. 1991. Procedures to Evaluate Market Hogs. National Pork Producers Council, Des Moines, IA.

NRC. 1998. Nutrient Requirements of Swine. 10th ed. National Academic Press, Washington, DC.

Pond, W. G., H. G. Jung, and V. H. Varel. 1988. Effect of dietary fiber on young adult genetically lean, obese and contemporary pigs: body weight, carcass measurements, organ weights and digesta content. J. Anim. Sci. 66:699–706.

Pond, W. G., and J. T. Yen. 1984. Effect of protein deficiency on growth and plasma zinc concentration in genetically lean and obese swine. J. Anim. Sci. 59:710–716.

Pond, W. G., J. T. Yen, R. N. Lindvall, and D. Hill. 1981. Dietary alfalfa meal for genetically obese and lean growing pigs: effect on body weight gain and on carcass and gastrointestinal tract measurements and blood metabolites. J. Anim. Sci. 51:367–373.

Prince, T. J., S. B. Jungst, and D. L. Kuhlers. 1983. Compensatory responses to short-term feed restriction during the growing period in swine. J. Anim. Sci. 56:846–852.

Ramsay, T. G., X. Yan, and C. Morrison. 1998. The obesity gene in swine: Sequence and expression of porcine leptin. J. Anim. Sci. 76:484–490.

Ratcliffe, B., and V. R. Fowler. 1980. The effect of low birth weight and early undernutrition on subsequent development in pigs. Anim. Prod. 30:470 (Abstr.).

Robinson, D. W. 1964. The plane of nutrition and compensatory growth in pigs. Anim. Prod. 6:227–236.

Standal, N., E. Vold, O. Trygstadand, and I. Foss. 1973. Lipid mobilization in pigs selected for leanness or fatness. Anim. Prod. 16:37–42.

Steele, N. C., and L. T. Frobish. 1976. Selected lipogenic enzyme activities of swine adipose tissue as influenced by genetic phenotype, age, feeding frequency and dietary energy source. Growth 40:369–378.

Steele, N. C., L. T. Frobish, and M. Keeney. 1974. Lipogenesis and cellularity of adipose tissue from genetically lean and obese swine. J. Anim. Sci. 39:712–719.

Valaja, J., T. Alaviuhkola, K. Suomi, and I. Immonen. 1992. Compensatory growth after feed restriction during the rearing period in pigs. Agric. Sci. 1:15–20.

Wahlstrom, R. C., and G. W. Libal. 1983. Compensatory responses of swine following protein insufficiency in grower diets. J. Anim. Sci. 56:118–124.

Woltmann, M. D., A. C. Clutter, D. S. Buchanan, and H. G. Dolezal. 1992. Growth and carcass characteristics of pigs selected for fast or slow gain in relation to feed intake and efficiency. J. Anim. Sci. 70:1049–1059.

Yen, J. T., M. W. Tess, W. G. Pond, and G. E. Dickerson. 1983. Digestibility and metabolism of dietary nitrogen and energy in contemporary, genetically lean and obese pigs as estimated by total fecal collection and acid insoluble ash. J. Anim. Sci. 56:426–430.

Zimmerman, D. R., and S. Khajarern. 1973. Starter protein nutrition and compensatory responses in swine. J. Anim. Sci. 36:189–194.