EFFECT OF THE DEGREE AND DURATION OF EARLY DIETARY AMINO ACID

RESTRICTIONS ON GROWTH PERFORMANCE, CARCASS TRAITS, AND

SERUM METABOLITES OF PIGS, AND PHYSICAL AND SENSORY

CHARACTERISTICS OF PORK

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Rajesh Babu Kamalakar

A Thesis

Submitted to

the Graduate Faculty of

Auburn University

in Partial Fulfilment of the

Requirements for the

Degree of

Master of Science

Auburn University, Alabama
December 19, 2008

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Rajesh Babu Kamalakar, son of Gopal Rao Kamalakar and Veena Kamalakar, was born on September 5, 1981 in Hyderabad, India, where he was raised with his brother. In 1996, he graduated from St. George's Grammar School in Hyderabad, India. He attended Acharya N.G. Ranga Agricultural University in Rajendranagar, Andhra Pradesh, India and graduated with Bachelor of Veterinary Science Degree in February, 2004. He entered the Graduate School at Auburn University under the guidance of Dr. Lee I. Chiba. Upon completion of his degree, he plans to work in the feed industry.

THESIS ABSTRACT

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Master of Science, December 19, 2008
(B.V.Sc & A.H., ANGR Agricultural University, 2004)

103 Typed Pages

Directed by Lee I. Chiba

Satisfying the consumer by providing high quality pork is an integral part of successful and sustainable pig production. Unfortunately, the effort to satisfy consumer demands by producing leaner pigs in recent years has resulted in a reduction of marbling, which has adverse effects on eating quality of pork. It is possible that carcass fat can be reduced to satisfy today's consumer demands for leaner pork and marbling can be increased to enhance eating quality of pork simultaneously by taking advantage of compensatory growth. Furthermore, compensatory growth can increase the overall efficiency of nutrient utilization and minimize adverse impacts of pig production on the environment.

The objective of this study was to investigate the effect of degree and duration of early dietary amino acid restrictions on growth performance, serum metabolites, internal

organ weights, and carcass traits of pigs, and subjective quality scores and physical and sensory characteristics of pork. For the grower (G) and finisher 1 (F1) phases, 3 corn-soybean meal diets were formulated to contain 100, 80, or 60% of the 1998 NRC total lysine recommendation (100G, 80G, or 60G, and 100F1, 80F1, or 60F1, for the G and F1 phases, respectively). For the finisher 2 (F2) phase, a common corn-soybean meal diet was formulated to satisfy the 1998 NRC total lysine recommendation. Thirty gilts and 30 castrated males (2 gilts or 2 castrated males/pen) were randomly assigned to 5 dietary treatments [100G-100F1 (control), 80G-100F1, 80G-80F1, 60G-100F1, and 60G-60F1] when they weighed 22.7 ± 0.3 kg. Pigs were switched to F1 and F2 diets when they weighed 50.7 ± 0.4 and 79.9 ± 0.5 kg, respectively. Pigs had ad libitum access to feed and water throughout the study. Blood samples were collected at the end of the G, F1, and F2 phases. All pigs were slaughtered when they weighed 110.7 ± 0.5 kg, and standard carcass data and internal organ weight data were collected. The LM samples were collected for the assessment of physical and sensory characteristics of pork. Pigs fed the 60G diet had lower ($P < 0.05$) ADG during the G phase and greater ($P < 0.05$) ultrasound backfat (UBF) at the end of the G phase than those fed the 100G diet, and ADG decreased linearly ($R^2 = 0.70$; $P < 0.001$) as the degree of amino acid restrictions increased, indicating that the effort to depress growth performance and alter body composition by early dietary AA restrictions was successful. Although serum total protein (TP) and albumin in pigs fed the 60G-100F1 diets at the end of the G phase were lower ($P < 0.05$) than those fed the control G and F1 diets, TP was similar between the 2 groups at the end of the F1 phase. Their ADG during the F1 phase and UBF at the end of the F1 phase were, however, similar to those fed the control diets. Feeding the 80G diet

resulted in numerically depressed ADG during the G phase, but there was no difference in ADG during the F1 and F2 phases or UBF at the end of F1 and F2 phases between the pigs fed the 80G and 100G diets. Overall, pigs fed the 80G-80F1 diets had similar ADG, but they had less ($P < 0.05$) lean gain (LG) than those fed the control diets. They also had lower ($P < 0.05$) serum TP and albumin than pigs fed the control diets throughout the study. Pigs fed the 60G-60F1 diets had clearly lower ($P < 0.05$) overall ADG and G:F and less ($P < 0.05$) LM area and LG compared with those fed the control G and F1 diets. However, they had higher ($P < 0.05$) subjective marbling score than those fed the control diets. Dietary treatments had no clear effect on other serum metabolites, carcass backfat, subjective color and firmness scores, organ weights, or physical and sensory characteristics of pork.

The results of the present study indicated that pigs fed the 80G-80F1 diets may have exhibited compensatory growth in terms of weight gain but not in terms of lean accretion. On the other hand, growth performance and carcass traits of pigs fed the 60G-60F1 diets were clearly depressed, indicating that the amino acid restrictions may have been too severe or too long or both. Early dietary AA restrictions had no clear effect on physical and sensory characteristics of pork.

ACKNOWLEDGEMENTS

Style manual or journal used: <u>Journal of Animal Science</u>

Computer software used: <u>Microsoft Office Word, Excel, Statistical</u>

<u>Analysis System (SAS) Software</u>

<u>Package for Windows v. 9.1</u>

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I. INTRODUCTION

For successful pig production, as indicated by Chiba (2000, 2001), it is imperative to improve the overall efficiency of nutrient utilization, and this is especially true for protein sources because of their cost and their impact on the environment. The competition between humans and animals, particularly nonruminant species, for quality sources of nutrients is likely to increase continuously in the future because of the ever increasing world population. Efficient feed utilization, therefore, not only improves profitability of the pig enterprise, but it also has a positive impact on the environment by decreasing excretion of unused nutrients. Obviously, alleviating public concerns on environmental issues is imperative for sustainable pig production (Chiba, 2000). In addition, satisfying consumer demands by providing high quality pork is an integral part of successful and sustainable pig production.

Unfortunately, as pointed out (L. I. Chiba, Auburn University, AL, personal communication), the effort to satisfy consumer demands by providing leaner pigs in recent years has resulted in a reduction of intramuscular fat **(IMF)**, which has adverse effects on eating quality of pork (Cisneros et al., 1996; Gerbens et al., 2001). Because of a poor relationship between intramuscular fat and subcutaneous fat thickness (Jones et al., 1992), however, the IMF content can be increased while maintaining the leanness of pigs. Intramuscular fat has been often reported to have beneficial effects on nutritional as well as eating quality of pork (Bejerholm and Barton-Grade, 1986; Fernandez et al., 1999a;

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Wood et al., 2004). Hence, increasing IMF through a strategic feeding regimen would be a desirable tool in pork production.

Many studies have demonstrated an accelerated growth in pigs allowed ad libitum access to feed after a period of feed restriction (Robinson, 1964; Owen et al., 1971; Prince et al., 1983). Bohman (1955) called this accelerated growth phase "compensatory growth." Pigs subjected to early amino acid restrictions can exhibit improved leanness, via compensatory growth (e.g., Chiba, 1995; Chiba et al., 1999). It has also been shown that feeding protein deficient diets during the entire grower-finisher period can actually increase IMF (Castel et al., 1994; Kerr et al., 1995; Cisneros et al., 1996), but there was a negative effect on growth performance in those studies. It is possible that the growth depression can be avoided by taking advantage of compensatory growth.

It is reasonable to assume that compensatory responses in the efficiency of nutrient utilization are clearly a result of metabolic alterations (Valaja et al., 1992). Theories linking compensatory protein turnover prior to slaughter and post mortem tenderness of pork have been proposed (Oksbjerg et al., 2002; Therkildsen et al., 2002). However, there is a lack of information on the effect of degree and duration of early dietary amino acid restrictions and compensatory growth response on pork quality. Furthermore, the exact relationship between early dietary amino acid restrictions and IMF has not been elucidated.

If in fact, pigs can achieve compensatory growth, it can reduce feed costs, as well as excretion of unused nutrients during the restriction as well as realimentation phases. Furthermore, an increase in the IMF content (Fernandez et al., 1999a) and postmortem tenderization of pork because of increased protein turnover prior to slaughter

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(Therkildsen et al., 2002) can possibly have beneficial effects on the eating quality of pork. The compensatory growth response can, therefore, have a positive impact not only on overall efficiency of feed utilization, success of pig production, and the environment, but also possibly on the nutritional and eating quality of pork.

II. REVIEW OF LITERATURE

COMPENSATORY GROWTH IN SWINE

Historical Background

The occurrence of compensatory growth has been documented as far back as in 1908 when it was reported that nutritionally restricted cattle reached a mature height and weight when given access to a highly nutritious diet after a period of diet restriction (Wilson and Osbourne, 1960). Osbourne and Mendel (1916) first described how rats that had been restricted in growth exhibited a higher growth rate once the restriction was removed. Later, Bohman (1955) termed this faster rate of growth relative to age "Compensatory growth."

After these early reports, compensatory growth has been shown to occur in: cattle (Horton and Holmes, 1978; Rompala et al., 1985; Hayden et al., 1993), swine (McMeekan, 1940; Robinson, 1964; Wyllie et al., 1969; Zimmerman and Khajarern, 1973; Prince et al., 1983; Mersmann et al., 1987; Kyriazakis et al., 1991), and poultry (Wilson and Osbourne, 1960; Deaton et al., 1973; Moran, 1979; Plavnik and Hurwitz, 1985; Plavnik and Hurwitz, 1991; Zubair and Leeson, 1994). Some workers (Yu and Robinson, 1992) feel that catch-up growth is a more precise term because the word compensatory growth implies excessive growth of a body part in compensation for the loss of part or its function. Hence, depending on the author and their preference, these

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terms are used interchangeably. Reviews on the compensatory growth in pigs have been presented by Chiba (1999), Fabian (2001), and Mule (2005).

Early Dietary Restriction and Realimentation

A brief review of literature on compensatory growth in various species revealed that the findings have been very inconsistent. There are four possible responses that an animal can exhibit when realimented after a period of dietary restriction: complete compensation, partial compensation, no compensation, or a reduction in mature size.

Complete compensation occurs when an animal is able to attain the same weight for age as unrestricted counterparts. This has been observed in cattle (Ryan et al., 1993; Yambayamba et al., 1996), and sheep, pigs, and chickens (Plavnik and Hurwitz, 1985, 1991; de Greef et al., 1991; Ryan et al., 1993; Zubair and Leeson, 1994).

Partial compensation occurs when animals increase their rate of gain after realimentation, but are unable to attain the same weight as those as unrestricted animals (Hornick et al., 1998a). A less common response to early dietary restriction followed by realimentation is for restricted animals to grow at the same rate as unrestricted animals, thereby showing no compensation at all. This has been observed in various species and is usually seen when nutrient restriction has occurred at a very young age (Morgan, 1972; Tudor and O'Rourke, 1980).

In instances where dietary restriction, which was much more severe than what might occur due to some adverse conditions, has been imposed a reduction in mature size or permanent stunting has been observed (Taylor et al., 1981). In some other instances, compensatory response only in selected organ weights and(or) body composition has been observed (Pond and Mersmann, 1990).

Factors Affecting Compensatory Growth Response

The ability of the animal to compensate for prior undernutrition seems to be the result of possible interactions of nutritional, physiological, and genetic factors. Lawrence and Flower (1997) classified factors affecting compensatory growth into intrinsic features of the animal at the start of undernutrition and the dietary factors. The animal factors include: 1) the degree of maturity at the start of the undernutrition, 2) the proportion of body weight attributable to adipose depots at the start of undernutrition, 3) the genotype, 4) the gender, and 5) changes in metabolic rate. And the dietary factors include, 1) the severity of undernutrition, 2) the duration of the period of under nutrition, 3) the nutrient density of the food during undernutrition, and 4) feed intake during rehabilitation. Similarly, Wilson and Osbourne (1960) identified five factors that could affect compensatory growth and ultimate compensation: 1) the stage of development of the animal at the start of restriction, 2) the severity and duration of restriction, 3) genotype, 4) sex, and, 5) quality and duration of realimentation.

The Stage of Development of the Animal at the Start of Restriction. The most sensitive period of life, during which restriction could have a detrimental effect on future growth, is in the pre- and postnatal periods (Wilson and Osbourn, 1960; Tudor and O'Rourke, 1980). Mroz et al. (1987) reported that low-birth weight pigs grew slower than their heavier littermates regardless of lysine concentration during the starter as well as grower-finisher phases, indicating that lighter weight pigs were not making any compensatory growth for their birth weight. Gondret et al. (2006) observed a greater estimated lean content in high-birth weight pigs at market weight compared to low-birth weight pigs. Low-birth weight pigs exhibited a lower total number of muscle fibers, a

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characteristic that can be fixed before birth and determine the upper limit of protein accretion (Wigmore and Stickland, 1983), than heavier littermates but had larger myofibers at market weight (Kuhn et al., 2002). Fiber hypertrophy seems to be accelerated in muscle with a low number of fibers. These findings were also observed by Handel and Stickland (1988).

In studies with pigs, the body weight, at which the feed restriction is usually implemented, is around 15 to 25 kg (Prince et al., 1983). But, Stamataris et al. (1985) restricted pigs to 300 g of feed per day over the weight range 6 to 12 kg live weight. The pigs were then fed ad libitum, and they exhibited compensatory growth. The restricted pigs took 31.7 days to reach 12 kg, while those fed ad libitum took 12.6 days. Upon realimentation, however the restricted pigs took 5.5 days less to reach 24 kg (from 12 kg) than did those fed ad libitum. It was concluded that although there was compensatory growth, the time lost in growth during restriction could not be regained.

Wolter and Ellis (2001) studied the effect of weaning weight and rate of growth immediately after weaning on subsequent pig performance and carcass characteristics. Pigs were weaned at 18 to 22 days of age and the treatments were weaning weight (heavy vs. light) and post-weaning growth rate (accelerated vs. conventional), during the first 14 days post weaning. Pigs on accelerated treatment were housed in a specialized nursery and provided with liquid milk replacer and a dry diet, whereas pigs on conventional treatment were housed in a standard nursery and provided with a dry diet only. After the treatment period, all pigs were housed in the same building and provided the same dietary regimen up to slaughter weight (110 kg). Pigs on the accelerated growth treatment were heavier than pigs on the conventional treatments at the end of the treatment period and at

56 d of age. Early growth rate did not affect growth from 35 d of age to slaughter weight, or days to reach slaughter weight. Heavy pigs at weaning were heavier at birth and 56 d of age than light pigs, and reached slaughter weight 8.6 d earlier. In summary, weaning weight, but not growth rate during the first 2 weeks after weaning, influenced age at slaughter. In a recent study, Wolter et al. (2002) found that pigs exhibiting decreased early growth rate because of increased number of pigs per pen had a 4% increase in feed efficiency when provided adequate space in the subsequent grower-finisher period. Therefore, growth depression during very early stage of development seems to result in no compensatory growth to partial compensation in the subsequent phase, which may be somehow related to muscle tissue cellularity.

The Severity and Duration of Restriction. Growth depression is likely to be dependent on the severity and duration of dietary restriction relative to the stage of dietary restriction and the length of the realimentation period. Wilson and Osbourne (1960) suggested that the more severe the restriction, the greater the initial compensatory gains can be observed after realimentation. Carstens et al. (1991) followed this up by proposing that the severity of growth restriction would be greater when the growth restriction is imposed at an earlier stage of development when the impetus for lean tissue growth is higher. After examining a number of data sets, Wilson and Osbourne (1960) concluded that the nature of periods of growth restriction could be classified into three categories: 1) severe restriction that results in loss in live weight, 2) restriction resulting in maintenance of constant live weight, 3) mild restriction allowing small but subnormal increases in live weight.

Pond and Mersmann (1990) subjected weanling pigs to severe growth depression over a period of 21 days by providing high-fiber diets. There was no evidence of overt compensatory growth. However, pigs exhibited compensatory growth in the liver, kidneys, and backfat. These findings were supported by Bikker et al. (1996b). Prince et al., (1983) restricted pigs to 70 or 80% of ad libitum intake for either 2 or 4 weeks. Pigs restricted for 85% of ad libitum for 4 weeks performed better than pigs restricted for 70% of ad libitum for 4 weeks or control pigs, which were unable to fully compensate, indicating that the restriction was either too severe or too long. Robinson (1964) observed that the time taken to reach slaughter weight was delayed progressively with each increase in duration of restriction of feed. Fabian et al. (2002) reported that pigs subjected to dietary amino acid restrictions during the grower phase (as low as 5.0 g lysine/kg) compensated completely in terms of growth rate and body composition regardless of genotype. However, in an earlier study, Wahlstrom and Libal (1983) reported that pigs subjected to more severe restrictions failed to compensate fully compared to moderately restricted pigs. In summary, wide range in severity and duration of feed restrictions have been investigated, which produced variable compensatory growth responses. In many instances, a complete compensation has been observed, provided that the restriction was not too severe and there was enough time to exhibit compensatory response.

Effect of Genotype. A wide variation in the pig's potential for growth and protein accretion exists in today's pig industry. Not only the growth rates that are known to differ, but the body compensation can also be influenced by varying genetic factors within the species (Hogberg and Zimmerman, 1978; Plavnick and Hurwitz, 1985, 1991; Carstens at al., 1991; de Greef et al., 1992).

Pigs with distinct genotypes may respond differently to dietary manipulations. 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 (Fabian et al., 2002), activity of various lipogenic enzymes (Steele and Frobish, 1976), concentration of metabolites (Pond et al., 1981, 1988), activity of hormones (Buonomo and Klindt, 1993; Cameroon et al., 2000), and metabolism of adipose tissues (Steele et al., 1974) as summarized by (Chiba ,1999; Chiba et al., 2002). Those differences indicate the physiological and metabolic alterations that are taking place in pigs selected for specific traits, and they may affect nature of response to dietary manipulations in animals with distinct genotypes.

Hogberg and Zimmerman (1978) observed that a lean strain of pigs showed a very little compensation in comparison to a fat strain of pigs after being put on a severe protein restriction, during which the lean strain of pigs lost considerably more weight than the fat strain of pigs. In contrast, de Greef et al. (1992) found that when two strains of pigs with different rates of fat to lean deposition rates were restricted and subsequently realimented, they responded similarly and had similar body composition at the end of the realimentation phase. Chiba et al. (1999) also reported that two strains of pigs responded similarly to dietary restrictions, realimentation, and compensation. In a study conducted later (Chiba et al., 2002), genotype had no effect on growth performance, although there were some grower diet by genotype interactions that led them to conclude 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.

Thus, the published reports, with regard to the effect of genotype on compensatory growth, are conflicting and inconclusive. It is possible, that the effect of a genotype on compensatory response may depend on the difference in the potential for growth and protein accretion between the breeds/strains in question and the degree of protein or amino acid restrictions.

Effect of Sex. The findings on the effect of sex on compensatory growth have been inconsistent. The difference in responses between the sexes is likely the result of the higher innate rate of growth of intact males in comparison to females (Zubair and Leeson, 1996). Intact males, compared with females, have a greater propensity to exhibit compensatory growth (Plavnik and Hutwitz, 1991). Plavnik and Hurwitz (1985) found this to be true with broilers but Kyriazakis et al. (1991) failed to observe similar findings in pigs. However, Robinson (1964) observed that the compensatory growth response was greater in gilts. This observation is in agreement with another study (Christian et al., 1980), which showed that gilts responded to higher dietary protein concentrations. In female mammals that are beyond the stage of puberty and having regular estrous cycles, changes in hormonal status and related behavior could affect growth pathways (Lawrence and Flower, 1997).

Quality and Duration of Realimentation Diets. Numerous studies have pointed out the importance of the quality and duration of the realimentation diet and the effect that can have on the type of response. Kyriazakis et al. (1991) noted that pigs realimented with a diet high in protein grew substantially faster and laid down more lean tissue than pigs realimented on a low-protein diet and concluded that the severity of restriction

should be considered when formulating realimentation diets. This contention is supported by findings of Wahlstrom and Libal (1983).

Previous studies (Chiba 1994, 1995; Critser et al., 1995; Chiba et al., 1999, 2002) conducted in grower-finisher pigs to investigate the effect of the amino acid content of finisher diets on the performance of pigs subjected to early dietary restrictions did not provide any indication that pigs subjected to early amino acid restrictions have different amino acid requirement during the realimentation phase. In contrast, Fontana et al. (1992) indicated that protein might be a limiting nutrient during the recovery after a period of restriction. Whang et al. (2003) reported that during the period of compensatory growth, the requirement of crude protein for those pigs is higher than that of pigs previously fed an adequate diet. Similar findings have been obtained in other studies (Kyriazakis et al., 1991; Whang et al., 2000a). The period of time allowed for realimentation may also affect compensatory growth. Therkildsen et al. (2002) indicated that pigs provided an ad libitum feeding for about 42 days prior to slaughter after a period of restriction had similar carcass and muscle mass compared to pigs given ad libitum feed throughout the study.

In general, the quality of refeeding required for compensatory growth in various species has been quite variable and seems to be a reflection of the severity of the restriction, the maturity of the animal at the beginning of the restriction, and the duration of the realimentation diet. The varying results obtained in similar experiments on compensatory growth clearly points out the potential interaction among all the factors that have an effect on compensatory growth.

Dietary Restrictions and Compensatory Growth in Pigs

Various studies have been performed under different experimental conditions to investigate the possible effects of dietary restrictions during starter, grower, and early finisher phases on subsequent and overall growth performance of pigs. The results and interpretations of those studies have been quite varied.

Effect of Starter Diets. Sixty-four crossbred weanling pigs were assigned to two starter diets with four pens per diet, with each pen having 4 gilts or 4 castrated males (Chiba, 1995). The dietary treatments included a simple starter diet and complex starter diet. The lysine content of simple starter diet was less compared to complex starter diet. During the first two weeks, pigs offered the complex diet consumed more feed, grew faster, and were more efficient than those offered the simple starter diet. During the next two weeks, pigs offered the complex diets grew faster, but there was no difference in the feed intake or gain:feed. During the entire starter phase, pigs fed the complex diet consumed 14% more feed, grew 33% faster, and were 17% more efficient in the utilization of feed for weight gain than those offered the simple diet. However, the starter diet had no effect on the weight gain or average ultrasound backfat thickness measures at the end of the grower phase regardless of the amino acid content of the grower diets. That is, there was no evidence of compensatory growth during the grower phase in pigs fed the simple starter diet.

Whang et al. (2000b) concluded from his experiments with weanling pigs using different starter feeding programs, that the nutritional quality of the starter feeding program affected growth performance immediately after weaning but did not affect protein gain over the entire period. This conclusion was supported by findings of other

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research (Hancock et al., 1994; Tokach et al., 1995). However, one study has reported compensatory growth in pigs subjected to dietary restrictions during the starter phase (Zimmerman and Khajarern, 1973). Some reports have indicated that diet complexity during the starter phase had no effect on the length of required time needed for grower-finisher pigs to reach market weight (Whang et al., 2000b; Wolter et al., 2003), whereas one study has shown that lighter weight pigs at the end of the starter phase reach market weight at an older age (Chiba, 1995). The early dietary restrictions, however improved carcass traits in that study (Chiba, 1995).

Thus, the effect of varying the complexity of diets fed to nursery pigs on the subsequent responses to market weight has resulted in inconsistent responses. It is possible that the dietary restrictions during the very early stage of development may extend the time required to reach the market weight, and this must be weighed against any improvement in carcass quality that might be obtained through such restrictions (Chiba, 1995).

***Effect of Grower Diet*.** Wahlstrom and Libal (1983) investigated the effect of protein restriction during the early grower period on subsequent performance and carcass characteristics at slaughter. Protein restricted animals showed reduced rate and efficiency of growth during the initial restriction period, but showed improved gain and feed:gain ratio during the subsequent growth period. However, lighter weight pigs did not completely compensate for the decreased performance during the early four week period. Similar results have been obtained by Prince et al. (1983).

Experiments were designed to study the effect of dietary amino acid restrictions during the grower phase on subsequent and overall performance, and carcass traits

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(Chiba, 1994, 1995; Chiba et al., 1999, 2002). In each of the experiments, two grower diets were formulated to be either marginally deficient (0.423 g Lysine/ MJ DE or 80% of the 1998 NRC requirement) or adequate (0.765 g Lysine/ MJ DE; Chiba et al., 1991a,b) in lysine and other indispensable amino acid content. After the grower phase pigs were assigned to two or four finishing diets depending on the experiment. In earlier studies (Chiba, 1994, 1995), pigs fed the low amino acid grower diets grew faster and more efficiently during the finisher phase than those fed the high amino acid grower diets. Because of this turnaround, there was no difference in the overall growth performance and carcass quality of pigs fed the different types of grower diets. However, in later studies (Chiba et al., 1999; 2002), grower diet had no clear effect on weight gain during the finisher phase. Consequently, pigs fed the high amino acid grower diet had better overall weight gain than those fed the low amino acid diet.

In a later study, Fabian et al. (2002) investigated the effect of degree of amino acid restrictions during the grower phase on subsequent and overall growth performance in pigs selected for lean growth efficiency. During the grower phase, pigs consumed less feed and more lysine, grew faster, and utilized feed more and lysine less efficiently for weight gain as the amino acid content of the grower diet increased. Increasing amino acid content resulted in less ultrasound backfat at the end of the grower phase. However, during the F1 and F2 phases, pigs grew slowly, utilized feed and lysine less efficiently for weight gain as the amino acid content of the grower diets increase, indicating a complete compensation. Thus, it is possible that pigs subjected to marginal dietary amino acid restrictions during the grower phase can exhibit compensatory response during the subsequent phase without adversely affecting growth performance and(or) carcass traits.

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Effect of Finisher diets. The effects of finisher diets on the performance of pigs subjected to early dietary restrictions have been inconsistent. Chiba (1994) reported that pigs fed a high-amino acid combination of grower-finisher diets showed improved leanness and efficiency of growth performance than those fed other combinations, indicating that pigs fed high amino acid grower diets required high concentration of amino acids during the realimentation period because of the improved muscle growth during grower phase. There is increased protein accretion in skeletal muscles and metabolically active visceral organs in pigs fed high amino acid diets (e.g., Chiba et al., 1995). To sustain metabolical and(or) physiological alterations that might be associated with such periods of enhanced growth, pigs may need diets containing proportionally higher concentration of amino acids during the latter phase.

In an another study (Chiba et al., 2002), pigs fed a low-amino acid grower and finisher diet combination and high-amino acid grower and finisher diet combination grew faster and more efficiently than those fed other dietary combinations, which resulted in grower X finisher interactions. On the other hand, Critser et al. (1995) found no effect of increased dietary protein during the realimentation phase.

In summary, it seems that there is no compensatory response in pigs fed less nutrient dense starter diets, and the advantages obtained by feeding high nutrient dense starter diets were maintained throughout the grower-finisher period (Chiba, 1994). On the other hand pigs subjected to marginal dietary amino acid restrictions during the grower phase seemed to compensate completely during the subsequent phase. Thus, it seems that once pigs pass the early critical phase of their life, the degree of compensatory growth becomes an issue (Chiba, 1999).

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Possible Mechanisms of Compensatory Growth

Decreased maintenance costs, increased efficiency of growth, increased feed intake and digesta load, increased nitrogen retention, action of hormones, and expression of some genes associated with protein and lipid metabolism have been implicated as the key mechanisms in compensatory growth.

Reduced Maintenance Requirements. The theory of reduced maintenance requirements as a consequence of nutrient restriction has received a lot of attention. The reduction in maintenance requirements would, then, allow for comparatively more energy available for growth upon realimentation, thus, contributing to the compensatory growth (Ryan, 1990). Yambayamba et al. (1996) measured heat production as an indicator of basal metabolic rates in steers and noted a decline in heat production during the restriction. Following realimentation, there was a gradual increase in heat production, however, it remained lower than the control for the first two weeks post realimentation, and, then, slowly rose to levels similar to the control steers by 5 weeks post realimentation. Zubair and Leeson (1994) observed similar trends in broiler chickens. Thus, the decrease in maintenance requirement seems to be, at least, partially responsible for increased gains seen in animals exhibiting compensatory response.

It has been reported that pigs on a higher plane of nutrition had heavier metabolically active internal organs and gastrointestinal tract (Koong et al., 1983). This may affect heat loss associated with maintenance (Ferrell, 1988), thus, the nutrient needs for growth. This contention is supported by an earlier experiment (Campbell et al., 1983).

In addition, undernourished animals are likely to be younger in physiological age than those with a similar chronological age, and they tend to grow at a rate appropriate to

their physiological age rather than their chronological age (Robinson, 1964). Therefore, in animals previously restricted, the synthesis of muscle tissues rather than the deposition of fatty tissues would be the more active metabolic process at a given weight during realimentation.

Increased Efficiency of Growth and N Retention. Another mechanism involved in compensatory growth seems to be an alteration in energy deposition. Because of concomitant water deposition that results in more gain per gram of protein deposited than lipid deposited, higher rates of protein deposition during the realimentation would have an impact on the overall growth rate. Previous experiments involving the compensatory growth response showed increase in protein deposition rate and decrease in lipid deposition rate (Ryan, 1990; Carstens et al., 1991; de Greef et al., 1992; Zubair and Leeson, 1996). Bikker at al., (1996a,b) indicated that compensatory growth was mainly due to an increase in organ weights. However, Whang et al. (2000b) indicated that organ growth was not the major component for the compensatory growth. Zimmerman and Khajarern (1973) indicated that compensatory growth responses are not due to an increased appetite, but reflect a change in metabolism. Others have also reported that pigs subjected to a period of dietary restrictions utilized feed more efficiently during the realimentation phase than unrestricted pigs (Campbell et al., 1983; Prince et al., 1983; Kyriazakis et al., 1991; Chiba, 1994; Whang et al., 2003).

Compensatory nitrogen retention following nitrogen deprivation in pigs has been demonstrated (Whittemore et al., 1978). Fabian et al. (2004) observed some carry over effects of early amino acid restrictions on the nitrogen metabolism during the realimentation phase. They observed that the pigs given low-amino acid grower diets had

a greater net nitrogen utilization and numerically greater nitrogen retention and consequently decreased urinary excretion in the subsequent phase. Wykes et al. (1996) suggested that the adaptation to a low-protein diet may involve a decrease in the rate of protein synthesis in most body tissues, with the most marked changes occurring in skin and intestine. Vaughan et al. (1962) reported that pigs fed a high-protein diet during the early phase of growth had a higher rate of protein turnover in the subsequent phase than pigs fed a low-protein diet. Conversely, an inadequate protein or lysine intake has been shown to reduce amino acid oxidation, as well as whole body protein turnover, or spare amino acids as noted by Chiba et al. (1991), which may persist into the realimentation phase.

Increased Feed Intake and Digestive Load. In his study, Ratcliffe and Flower (1980) reported that the compensatory response following severe nutritional restrictions was mainly due to a greater feed intake relative to body weight. The amount of feed consumed during realimentation may have an effect on compensatory growth (Owen et al., 1971; Donker et al., 1986; Ryan et al., 1993). However, Wahlstrom and Libal (1983) and Pond and Mersmann (1990) found no evidence of increased feed intake in previously restricted pigs fed ad libitum during realimentation. This contention was further supported by de Greef et al. (1992). In a later study, Lovatto et al. (2006) indicated that the compensatory growth after a period of feed restriction does not seem to be related to a change in metabolic utilization of energy for gain but more likely is due to gain in water and gut contents.

Increase in digesta load due to increased feed intake as a contributing factor to compensatory growth has been implicated by some researchers (Carstens et al., 1991;

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Hornick et al., 1998a). However, Ryan (1990) indicated that it is usually only true when animals have been restricted in quantity of feed. Stamataris et al. (1991) found that pigs restricted in the amount of feed offered exhibited a decrease in organ weight. Upon the onset of realimentation to ad libitum intake, there was an increase in organ size to accommodate the greater feed intake. Therefore, more gut fill has resulted in the increase in subsequent live weight gain.

A possibility of the increased digestibility as one of the contributing mechanism of compensatory growth was explored by various scientists. Hicks (1990) suggested that feed digestibility and feed intake are inversely related, i.e., with an increase in feed intake, digestibility would decrease due to accelerated rate of passage. However, Santra and Pathak (1999) reported that, with an increase in feed intake, digestibility did not differ from the control group. Thus, it is possible that digestibility plays an important role in nutrient utilization, but its role as one of the mechanisms contributing to compensatory growth seems to be still unclear.

Action of Hormones. The action of various hormones are probably an integral part of compensatory response. The effect of growth hormone **(GH)**, insulin-like growth factor-1 **(IGF-1)**, and insulin during restrictions and realimentation has undergone the most intensive research to date, although the role of myostatin and leptin in growth has captured the attention of researchers very recently.

Hayden et al. (1993) indicated that plasma levels of IGF-1, GH, insulin, and thyroid hormones, but not insulin-like growth factor-2, are markedly affected by alteration of energy intake and are highly correlated with empty body gain and protein deposition in compensating late maturing steers. Hornick et al. (1998b) observed an

increase in plasma thyroxine (T_4) and IGF-1 during the realimentation period, whereas

GH and triiodothyroxine (T_3) concentration decreased during the same period. They

concluded that higher nutrient supply improved the functionality of the somatotropic axis

and increased the concentration of anabolic hormones, allowing rapid muscle deposition

in Belgian bulls.

In heifers, feed intake restriction was associated with a higher plasma

concentration of GH and lower concentrations of IGF-1, T_4, T_3, and insulin

(Yambayamba et al., 1996). During the early realimentation period, differences in the

hormonal profile between the restricted and control animals were maintained, but

gradually diminished thereafter. This led them to the conclusion that the uncoupling of

the GH-IGF-1 axis as one of the possible factors of compensatory growth. Atinmo et al.

(1978) reported that GH concentration was considerably greater in protein restricted pigs

and other species, which may have been responsible for compensatory response

observed. Dietary restriction causes dampening of insulin/IGF-1 axis via reduced

circulating insulin and down regulation of insulin sensitivity during subsequent refeeding

(Hamdy et al., 2001).

Gene Expression. Little is known about molecular mechanisms of dietary

restrictions in young, growing animals, and even less in large animal models. For an

organism to survive during nutritional deprivation, it must be able to regulate the genes

involved in energy metabolism. White adipose tissue is an energy source during fasting

conditions. McNeel and Mersmann (2000) investigated the transcript concentrations of

two key transcription factors, as well as the transcript concentrations of several

adipocyte-charcteristic proteins and genes involved in adipocyte energy metabolism in

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the adipose tissue of pigs fasted for 72 hours. Nutritional deprivation resulted in decreased concentrations of the transcript factors. They observed that transcript concentrations of several adipocyte-charcteristic proteins, fatty acid synthase, glucose transporter 4, lipoprotein lipase, leptin, and adipocyte fatty acid binding protein were also reduced. This led them to conclude that the transcript concentration changes are aimed at adjusting energy partitioning to conserve energy during nutritional deprivation.

da Costa et al. (2004) conducted experiments to profile the molecular changes and gain insights into the signaling molecules that mediate the effects of dietary restriction, including candidate genes that could be involved in compensatory growth. Their findings indicate that the cellular response to dietary restriction is an actively driven process. They found a gene, P311, which was not only responsive to dietary restrictions, but was most highly expressed in skeletal muscles. In that study, moderately reduced energy and protein diet in growing pigs led to reduced growth and it was accompanied by increased intramuscular lipid, and increased potentials for substrate (protein, glycogen, and lipid) turnover and mitochondrial function.

COMPENSATORY GROWTH AND EATING QUALITY OF PORK

Introduction

Traditionally, growing-finishing pig diets have been formulated to meet the animal's requirement for energy and proteins to optimize growth performance and carcass lean content. But, in recent times, the focus has been on improving eating quality of pork. A vast amount of scientific literature is now available on the effect of nutrition on pork quality attributes such as muscle color, tenderness, water holding capacity and

pork palatability. Another important consumer demand pertinent to the pork industry has been the increased desire for healthy, more nutritious meat products.

The important aspect of pork quality is sensory quality, usually defined as scores given by taste panelists for tenderness, juiciness, flavor, and overall acceptability. Today, technological quality and eating quality of pork have become important factors in pork production if repeat purchase is desired. Feeding strategy has proved to be important for controlling overall meat quality in pork production (Anderson et al., 2005). Breed (van Laack et al., 2001), intramuscular fat content (DeVol et al,. 1988; Goransson et al., 1992), halothane gene status (Leach et al., 1996), antemortem handling (Asghar and Pearson, 1980), rate of pH decline (Gardner et al., 2005), and muscle fiber type as determined by the proportion of different muscle fibers (Aberle et al., 1999; Karlssen et al., 1999) are the other factors contributing to eating quality of pork.

Compensatory Growth and Pork Tenderness

The compensatory growth is interesting from a meat quality standpoint, especially meat tenderness, which is generally rated by the consumers as one of the most important quality traits. Several studies have been conducted to establish the relationship between compensatory growth and pork tenderness by estimating concentrations of nucleic acids (RNA and DNA) as indicators of muscle protein synthetic capacity, Elongation Factor-2 (eEf-2) concentrations, Myofibrillar Fragmentation Index (**MFI**), activity of calpain system at time of slaughter, collagen content and solubility, and muscle fiber type characteristics (Kristensen et al., 2002, 2004; Oksbjerg et al., 2002; Therkildsen et al., 2002, 2004) in pigs subjected to restriction and realimentation strategy.

The difference between the rate of protein synthesis and the rate of protein degradation is reflected as postnatal muscle growth, and it has been suggested that both the rates of protein synthesis and degradation are elevated during periods of compensatory growth response (Jones et al., 1990). Muscle growth is dependent on at least two mechanisms, satellite cell proliferation and protein accretion rate (Allen et al., 1979). Satellite cell proliferation increases the total amount of DNA in a muscle cell, and the protein synthetic capacity is a reflection of the RNA levels (Oksbjerg et al., 2002).

It has been hypothesized that the improved tenderness is a result of increased postmortem protein degradation as a consequence of elevated protein turnover during compensatory growth (Kristensen et al., 2002). Also, it was found that the length of the compensatory growth influenced the degree of postmortem tenderness, and an ad libitum feeding period of above 42 days was required to observe an increase in tenderness (Therkildsen et al., 2002). Furthermore, it was also suggested that the growth rate increased at a faster rate after change to ad libitum feeding and reached the same level of growth rate as in control pigs. In a later study (Kristensen et al., 2004), it was found that refed gilts exhibited improved tenderness compared with controls, where as meat from castrated males was not affected. Several scientists suggested that the link between the rate of protein degradation in living muscles and tenderness development postmortem may be through proteolytic system of calpains (Wheeler and Koohmarie, 1992; Shackelford et al., 1994).

Effect on Calpain System. The primary proteolytic enzyme system, which is responsible for the tenderization process, is the calpain system as proposed by Koohmarie (1996) and Huff-Lonergan et al. (1996). In living animals, calpains are suggested to be

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involved in muscle growth by initiating myofibrillar protein degradation (Goll et al., 1998). It is, therefore, likely that an increased muscle growth rate in vivo may affect the tenderization rate by increasing a proteolytic potential. The rate at which a muscle may tenderize postmortem is indicated by the proteolytic potential, which can be measured by the ratio between μ-calpain activity and the calpastatin activity at slaughter. The rationale behind this is that μ-calpain is suggested to be the primary proteolytic enzyme that causes tenderness development and the calpastatin is an inhibitor of μ-calpain. In the study conducted by Kristensen et al. (2002), the ratio between μ-calpain activity and calpastatin activity was higher in pigs that were fed ad libitum after a period of nutritional restriction compared to other treatment groups, indicating a higher protein turnover, thus, a higher protein degradation in that group compared to other groups. Therkildsen et al. (2002) also observed a similar finding in their study. However, such a tendency was not observed in either barrows or gilts in the study conducted by Kristensen et al. (2004).

   Effect on Myofibrillar Fragmentation Index. The MFI indicates degree of proteolysis in muscle proteins at a given time (Wheeler and Koohmarie, 1992). Several studies (Anderson and Parrish, 1989; Huff-Lonergan et al., 1996) reported that postmortem tenderization is due to proteolytic degradation of structural proteins (desmin, vinculin, titin, and nebulin), and fragmentation of myofibrils. In one study (Kristensen et al., 2002), MFI values increased in pigs which were fed ad libitum after a period of restriction from day 0 to day 1 postmortem compared to control pigs or pigs restricted throughout. Consequently, the meat from pigs subjected to compensatory growth was more tender compared to control pigs or pigs restricted throughout. However, in a later study conducted by Kristensen et al. (2004), there was no effect of compensatory growth

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or gender on MFI values of either *biceps femoris* or *longissimus dorsi* muscle of pork, but MFI values increased with increasing duration of storage. This increase in MFI values is believed to reflect the proteolytic degradation that occurs during the storage.

Effect on Collagen Content and Solubility. Pork tenderness has been associated with the amount of total collagen and its solubility. The amount of heat soluble collagen gives an indication of the amount of newly synthesized collagen in the muscle and the turnover of the collagen component, and, in general the amount of heat soluble collagen decreases with age (Therkildsen et al., 2002). Therkildsen et al. (2002) reported in their study that the compensatory growth increases collagen solubility and stimulates the turnover of collagen component, which is in agreement with Allingham et al. (1998), who suggested alterations in the collagen component in response to compensatory growth in steers.

Compensatory Growth and Muscle Fiber Type

Growth rate may affect muscle fiber type characteristics (Johnston et al., 1981; Seideman and Crouse, 1986), and these characteristics have been associated with the final tenderness of the meat (Seideman et al., 1987). It has been suggested that skeletal muscle fiber types influence pork quality (Kerth et al., 2001). Because many of the factors which describe muscle fiber types, deal with characteristics of metabolism, it makes sense that fiber type then, could be related to pork quality. However, the relationship between nutritionally induced changes in fiber type characteristics and meat quality is not well established.

The myofiber number in porcine muscle is determined prenatally (Wigmore and Stickland, 1983), and, therefore, the postnatal increase in muscle mass depends mainly on

myofiber hypertrophy. However, differentiation of myofibers occurs during postnatal development. Quantitative and qualitative aspects of postnatal nutrition have a major effect on muscle development by affecting the growth rate and body composition. Gondret et al. (2007) reported that feed restriction and subsequent ad libitum feeding caused incomplete lipid recovery in the glycolytic *biceps femoris* muscle, whereas there was a full recovery in the lipid content in the oxidative *rhomboideus* muscle, indicating metabolic activities in response to restriction and re-feeding differed according to the muscle metabolic type. With respect to pork quality, greater drip losses, lower tenderness, and reduced intramuscular lipid and collagen were reported after feed restriction (Kristensen et al., 2002). Thus, there is a possibility that restriction and realimentation response of animals is manifested by changes in muscle histochemical and metabolic properties, which in turn may have an effect on eating quality of pork.

Compensatory Growth and Development of Intramuscular Fat

Many studies have revealed that compensatory growth might modify carcass composition at market weight by influencing the deposition rates of lean and adipose tissues (Campbell et al., 1983c; Donker et al., 1986). Heyer and Lebret (2007) reported that compensatory growth increased deposition of carcass adipose tissue but not lean tissue, but had no effect on the muscle level.

Intramuscular fat **(IMF)** is often reported to have beneficial effects on pork quality (Bejerholm and Barton-Grade, 1986; Fernandez et al., 1999a; Wood et al., 2004), although some authors showed only weak correlations between IMF and pork quality (Eikelenboom et al., 1996). Hence, an elevated intramuscular fat content in the muscle through appropriate production strategies would improve pork quality. It has been

suggested that raising the number of intramuscular adipocytes (Essen-Gustavsson et al., 1994), increases IMF, because more than 80% of muscle lipids are stored in intramuscular adipocytes. In addition, Gondret and Lebret (2002) showed an increase in the number of intramuscular adipocytes with age independently of IMF, whereas the size of the adipocytes increased with average daily feed intake. Thus IMF might increase simultaneously with the number and size of intramuscular adipocytes because of greater final age and feed intake. It is possible to increase both the age at slaughter as well as feed intake during realimentation through compensatory growth.

The metabolism of ketogenic branched-chain amino acids (Cisneros et al., 1996; Hyun et al., 2002) or the rate of lean tissue growth (Warkup and Kempster, 1991; Blanchard et al., 1999) or both may be responsible for the increase in the intramuscular fat content in pigs subjected to the dietary restrictions. In addition, many data in pigs now support the idea of the capacity of skeletal muscle to have de novo lipogenesis (e.g., Gondret and Lebret, 2002). After a period of feed restriction, free fatty acids are released in enhanced amounts by adipose tissue (Brockman and Laarveld, 1986) that may be used by skeletal muscles as energy substrates and excess fatty acids, in turn, may be stored as intra myocellular lipids.

The rate of protein to fat deposition in the pig is determined by the protein to energy ratio of a diet, and feeding a diet containing reduced protein to energy ratio diets to pigs decreases the protein to fat deposition, resulting in increased overall fatness of the pig and increased IMF levels (Castell et al., 1994). This was consistent with studies reported by Kerr et al. (1995) and Cisneros et al. (1996), but there was a negative impact

on growth performance in those studies. However, the exact relationship between dietary protein restrictions and intramuscular fat has not been elucidated.

Some studies have reported that supplementation of dietary fats in pig diets may be a better strategy to increase IMF in pork (Moser, 1977; Maynard et al., 1979; Mayes, 2000). In addition to enhancing eating quality of pork, IMF may have beneficial effects on human health (Baghurst, 2004), and this potential can be enhanced even further if the increase in the intramuscular fat content can be achieved by dietary supplementation of omega (ω)-3 fatty acids because dietary fatty acids are incorporated directly into tissue lipids in pigs (Wood et al., 2003). Therefore, it may be possible to decrease carcass fat by taking advantage of compensatory growth strategy and increase intramuscular fat high in ω-3 fatty acids simultaneously by supplementing diets with ω-3 fatty acids.

Intramuscular Fat and Pork Quality

Marbling is a true adipose tissue, in that it is comprised of adipocytes embedded in a connective tissue matrix. Intramuscular fat is usually chemically quantified, while marbling is usually assessed subjectively by meat graders. In the literature, the term 'intramuscular' is used synonymously with 'marbling fat'. Traditionally, it has been believed that higher degrees of carcass fatness was coincidental with marbling. However, researchers with beef and pork have shown only 1 to 3% of the variation in marbling is accounted for by subcutaneous fat thickness, and there is also a low correlation between carcass lean and intramuscular fat (Jones et al., 1992).

Effect on Consumer Acceptability of Pork. For the pork industry to be success, meat products must satisfy the consumer at the point of purchase as well as at the point of consumption. Fernandez et al. (1999b) observed that consumers opted for loin chops with

moderate amounts of marbling and were reluctant to buy loin chops with high amounts of marbling. The major factor influencing their choice being the health concerns associated with high-fat meat (Resurreccion, 2004). On the contrary, consumption frequency is influenced by the sensory experience during consumption of pork (Bryhni et al., 2003), and it has been accepted that IMF has a positive influence on the sensory attributes of pork like tenderness, texture, juiciness, and flavor (Bejerholm and Barton-Grade., 1986; De Vol et al., 1988; Fortin et al., 2005). For repeat purchase, the industry has to produce pork with minimum amount of visible fat to alleviate the health concern of the consumer and simultaneously produce pork with sufficient IMF to satisfy the eating experience of the same consumer.

Effect on Eating Quality of Pork. The literature concerning the effects of IMF on the sensory quality of meat is controversial. Some studies indicate a positive effect of IMF content on the sensory attributes of pork (Candek-Potokar et al., 1998; Lonergan et al., 2001). On the other hand, some others show minor influence (Wood et al., 1996; Fernandez et al., 1999a), or even a negative influence of IMF content (Lan et al., 1993). Some authors are of the view that a minimum level of IMF is required for a satisfactory eating experience. Bejerholm and Barton-Grade (1986) proposed a minimum of 2% IMF to ensure satisfactory eating experience. DeVol et al. (1988) reported that a minimum of 2.5 to 3.0% of IMF was necessary to avoid any negative response for tenderness. In a recent study, Fortin et al. (2005) proposed that the threshold level of IMF that will ensure a pleasing eating experience is 1.5%. Lonergan and Prusa (2002) demonstrated negative relationships between IMF content and objective measures of textural integrity.

Other reports have demonstrated no relationship between IMF content and objective measures of meat quality. Blanchard et al. (2000) found no effect of IMF content on sensory juiciness, tenderness, or overall acceptability. However, Fernandez et al. (1999a) demonstrated that increasing IMF content above approximately 2.5% enhanced flavor and juiciness significantly. The effect of IMF content on the sensory quality of pork is not consistent, even when other known sources of sensory quality variation are under control (Goransson et al., 1992).

SUMMARY

Many studies have demonstrated compensatory growth in pigs allowed ad libitum access to feed after a period of feed restriction. There are four possible responses that an animal can exhibit when realimented after a period of dietary restriction: complete compensation, partial compensation, no compensation, or a reduction in mature size. Some of the factors that could affect compensatory growth and ultimate compensation are: 1) the stage of development of the animal at the start of restriction, 2) the severity and duration of restriction, 3) genotype, 4) sex, and, 5) quality and duration of realimentation

Many studies investigated the possible effects of dietary restrictions during the starter, grower, and early finisher phases on subsequent and overall growth performance of pigs. The results and interpretations of those studies have been quite varied. In general, growth depression during very early stage of development seems to result in no compensatory growth to partial compensation in the subsequent phase, which may be somehow related to muscle tissue cellularity. Once pigs pass the early critical phase of their life, the degree of compensatory growth becomes an issue. On the other hand, pigs

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subjected to marginal dietary amino acid restrictions during the grower phase seemed to compensate completely during the subsequent phase. Although the mechanisms underlying compensatory growth are not clear, the decreased maintenance costs, increased efficiency of growth, increased feed intake and digesta load, increased nitrogen retention, action of hormones, and expression of some genes associated with protein and lipid metabolism have been implicated as the key mechanisms in compensatory growth.

Recently, the focus has been on improving eating quality of pork. A vast amount of scientific literature is now available on the effect of nutrition on pork quality attributes such as muscle color, tenderness, water holding capacity, and pork palatability. The important aspect of pork quality is sensory quality, which is usually defined as scores given by taste panelists for tenderness, juiciness, flavor, and overall acceptability. It has been hypothesized that the improved tenderness is a result of increased postmortem protein degradation as a consequence of elevated protein turnover during compensatory growth. In addition, many studies have revealed that compensatory growth might modify carcass composition at market weight by influencing the deposition rates of lean and adipose tissues. Intramuscular fat is often reported to have beneficial effects on pork quality, although some authors showed only weak correlations or even a negative influence of IMF on pork quality. For the pork industry to be successful, meat products must satisfy the consumer at the point of purchase as well as at the point of consumption. The compensatory growth response can, therefore, have a positive impact not only on overall efficiency of feed utilization, success of pig production, and the environment, but also possibly on the nutritional and eating quality of pork.

III. EFFECT OF THE DEGREE AND DURATION OF EARLY DIETARY AMINO ACID RESTRICTIONS ON GROWTH PERFORMANCE, CARCASS TRAITS, AND SERUM METABOLITES OF PIGS, AND PHYSICAL AND SENSORY CHARACTERISTICS OF PORK

Effect of the degree and duration of early dietary amino acid restrictions on growth performance, carcass traits, and serum metabolites of pigs, and physical and sensory characteristics of pork[1]

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ABSTRACT

The objective of this study was to investigate the effect of the degree and duration of early dietary amino acid restrictions on growth performance, serum metabolites, internal organ weights, and carcass traits of pigs, and subjective meat quality scores and physical and sensory characteristics of pork. For the grower (G) and finisher 1 (F1) phases, 3 corn-soybean meal diets were formulated to contain 100, 80, or 60% of the 1998 NRC total lysine recommendation (100G, 80G, or 60G, and 100F1, 80F1, or 60F1, for the G and F1 phases, respectively). For the finisher 2 (F2) phase, a common corn-soybean meal diet was formulated to satisfy the 1998 NRC total lysine recommendation. Thirty gilts and 30 castrated males (2 gilts or 2 castrated males/pen) were randomly assigned to 5 dietary treatments [100G-100F1 (control), 80G-100F1, 80G-80F1, 60G-100F1, and 60G-60F1] when they weighed 22.7 ± 0.3 kg. Pigs were switched to F1 and F2 diets when they weighed 50.7 ± 0.4 and 79.9 ± 0.5 kg, respectively. Pigs had ad libitum access to feed and water throughout the study. Blood samples were collected at the end of the G, F1, and F2 phases. All pigs were slaughtered when they weighed 110.7 ± 0.5 kg, and standard carcass data and internal organ weight data were collected. The LM samples were collected for the assessment of physical and sensory characteristics of pork. Pigs fed the 60G diet had lower ($P < 0.05$) ADG during the G phase and greater ($P < 0.05$) ultrasound backfat (UBF) at the end of the G phase than those fed the 100G diet, and ADG decreased linearly ($R^2 = 0.70$; $P < 0.001$) as the degree of amino acid restrictions increased, indicating that the effort to depress growth performance and alter body composition by early dietary AA restrictions was successful. Although serum total protein (TP) and albumin in pigs fed the 60G-100F1 diets at the end of the G phase were

lower ($P < 0.05$) than those fed the control G and F1 diets, TP was similar between the 2 groups at the end of the F1 phase. Their ADG during the F1 phase and UBF at the end of the F1 phase were, however, similar to those fed the control diets. Feeding the 80G diet resulted in numerically depressed ADG during the G phase, but there was no difference in ADG during the F1 and F2 phases or UBF at the end of F1 and F2 phases between the pigs fed the 80G and 100G diets. Overall, pigs fed the 80G-80F1 diets had similar ADG, but they had less ($P < 0.05$) lean gain (LG) than those fed the control diets. They also had lower ($P < 0.05$) serum TP and albumin than pigs fed the control diets throughout the study. Pigs fed the 60G-60F1 diets had clearly lower ($P < 0.05$) overall ADG and G:F and less ($P < 0.05$) LM area and LG compared with those fed the control G and F1 diets. However, they had higher ($P < 0.05$) subjective marbling score than those fed the control diets. Dietary treatments had no clear effect on other serum metabolites, carcass backfat, subjective color and firmness scores, organ weights, or physical and sensory characteristics of pork. The results of the present study indicated that pigs fed the 80G-80F1 diets may have exhibited compensatory growth in terms of weight gain but not in terms of lean accretion. On the other hand, growth performance and carcass traits of pigs fed the 60G-60F1 diets were clearly depressed, indicating that the amino acid restrictions may have been too severe or too long or both. Early dietary AA restrictions had no clear effect on physical and sensory characteristics of pork.

Key words: carcass traits, early amino acid restrictions, growth performance, physical and sensory pork characteristics, pigs, serum metabolites

INTRODUCTION

Satisfying the consumer by providing high quality pork is an integral part of successful and sustainable pig production. Unfortunately, the effort to satisfy consumer demands by producing leaner pigs in recent years has resulted in a reduction of marbling, which has adverse effects on eating quality of pork (Cisneros et al., 1996; Gerbens et al., 2001). Because of a poor relationship between marbling and subcutaneous fat thickness (Jones et al., 1992), however, marbling can be increased while maintaining the leanness of pigs. Also, it is possible that marbling has some beneficial attributes on human health (Baghurst, 2004).

The leanness of pigs can be improved by early dietary restrictions (e.g., Chiba, 1995; Chiba et al., 1999), implying that compensatory growth may have a negative effect on eating quality of pork. On the other hand, it has been shown that feeding protein-deficient diets can actually increase marbling (Castel et al., 1994; Cisneros et al., 1996; Blanchard et al., 1999). Unfortunately, growth performance was reduced in those studies because pigs were fed protein-deficient diets during the entire grower-finisher phase. It is possible that growth depression can be avoided by taking advantage of compensatory growth.

The results of our previous studies have indicated that pigs subjected to early dietary amino acid restrictions can exhibit compensatory growth (Chiba, 1994, 1995; Chiba et al., 1999, 2002; Fabian et al., 2002, 2004), utilize nutrients more efficiently (Chiba et al., 2002; Fabian et al., 2004), have better carcass traits (Chiba, 1995; Chiba et al., 1999), and reduce N excretion (Fabian et al., 2004). Obviously, alleviating public concerns on the environmental issue is imperative for sustainable pig production (Chiba,

2000). Compensatory growth, therefore, can have a positive impact on the overall efficiency of pig production, carcass quality of pigs, eating quality of pork, and beneficial effects on the environment.

Recently, there have been reports indicating that pork tenderness may be improved by early limit-feeding and realimentation (Oksbjerg et al., 2002; Therkildsen et al., 2002; Lametsch et al., 2006). However, there is a lack of information on the effect of early dietary amino acid restrictions on physical and sensory characteristics of pork. The objective of this study was, therefore, to investigate the effect of degree and duration of early dietary amino acid restrictions on growth performance, serum metabolites, internal organ weights, and carcass traits of pigs, and subjective quality scores and physical and sensory characteristics of pork.

EXPERIMENTAL PROCEDURES

General

A total of 60 (30 gilts and 30 castrated males) purebred Yorkshire grower-finisher pigs were used in the study. The protocol for animal care was approved by the Institutional Animal Care and Use Committee of Auburn University. Corn and soybean meal **(SBM)** diets were used in this study, and the chemical composition of corn and SBM is presented in Table 1. The results of crude protein analysis indicated that dietary CP contents were generally similar to the calculated values (Tables 2 and 3).

Animals and Facilities

Pigs approaching approximately 20 kg were selected and moved into open-sided grower-finisher unit. Pigs were allocated to 30 pens (1.35 m^2/pig) based on their BW, sex, and ancestry with 2 gilts or 2 castrated males per pen, and pens were assigned

randomly to 5 dietary treatments. Because of the availability of pigs, the study was

conducted in 2 trials. The first trial used 10 gilts and 10 castrated males, whereas the

second trial used 20 gilts and 20 castrated males. Two trials were approximately 4 wk

apart, and the average minimum and maximum daily temperatures during the study were

3.4 and 17.8°C, respectively. When the average pen weight reached 22.7 ± 0.3 kg, pigs

were offered the 3 grower **(G)** diets, and they were switched to finisher 1 **(F1)** and

finisher 2 **(F2)** diets when they weighed 50.7 ± 0.4 kg and 79.9 ± 0.5 kg, respectively. Pig

weights and feed consumption data were collected weekly. One pig was removed from

the study because of rectal prolapse.

Dietary Treatments

A fundamental assumption of the dietary treatments was that lysine is the first-

limiting amino acid in all diets, and all other indispensable amino acid needs would be

satisfied when diets are formulated to meet the lysine requirement. As the dietary lysine

content increases, there would be concomitant increases in other amino acids and vice

versa. Therefore, although experimental diets were formulated and identified based on

the lysine content, all amino acids were manipulated in the present study. The effort was

not made to maintain a constant amino acid balance, but a proportion of each amino acid

relative to lysine in each diet was above the balanced protein (NRC, 1998). For the G and

F1 phases, 3 corn-SBM diets were formulated to contain 100, 80, or 60% of the total

lysine recommendation (100G, 80G, or 60G and 100F1, 80F1, or 60F1 for the G and F1

phases, respectively; NRC, 1998), whereas the corn-SBM F2 diet was formulated to

satisfy the total lysine recommendation during the F2 phase (NRC, 1998). Five dietary

treatments or 5 combinations of the G and F1 diets offered were: 100G-100F1 (control),

80G-100F1, 80G-80F1, 60G-100F1, and 60G-60F1. The energy content was similar for all diets, and minerals and vitamins were provided in amounts calculated to meet or exceed the recommendations (NRC, 1998). Feed samples were taken from every batch of feed mixed and were stored frozen until they were pooled, subsampled, and analyzed for CP (AOAC, 1995).

Ultrasound Measurements and Blood Samples

For gross assessment of alterations in body composition during the restriction and realimentation phases, backfat thickness of each pig was measured 4 to 5 cm from the midline on the right side at the 10th rib at the end of the G, F-1, and F-2 phases using an ultrasound instrument (Lean-Meater, Renco; Minneapolis, MN). To assess metabolite profile, 10 mL of blood samples was taken from each pig via vena cava puncture using a sterile needle and syringe at the end of the G, F1, and F2 phases. All blood samples were collected in the morning between 1000 to 1200. Serum were separated by centrifugation at 1,500 x g for 15 min to obtain cleaner samples, and an aliquot was stored frozen at −20°C until analyzed for urea N, total protein, albumin, glucose, triglycerides, and cholesterol using the auto analyzer (Boehringer Mannheim/Hitachi 911; Boehringer Manheim Corp, Indianapolis, IN) at the Clinical Pathology Laboratory, Auburn University (Chiba et al., 2002; Mule et al., 2006).

Slaughter Procedures and Assessment of Physical and Sensory Characteristics of Pork

At an average pen weight of 110.7 ± 0.5 kg, pigs were slaughtered at Auburn University Meat Laboratory using conventional procedures after 24-h fast. The eviscerated carcass was split longitudinally through the vertebrae midline, and warm carcass weight was recorded. For gross assessment of metabolic alterations, heart, liver,

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and kidneys were collected and weighed separately. After chilling for 48 h at 2°C, the carcass was weighed and backfat thicknesses at the first rib, last rib, and last lumbar vertebra were measured. Longissimus muscle of the right side was exposed by a perpendicular cut between the 10th and 11th rib, and LM area was traced. Backfat thickness at the 10th rib (about ¾ distance along the LM toward the belly) was also measured. The exposed LM was used to determine subjective color, firmness, marbling, and muscling scores (NPPC, 1991). The proportion of carcass lean and the rate of carcass lean accretion were estimated by equations reported by NPPC (2000).

A section of LM from the 10th to 12th rib was removed from each pig, two 2.54-cm chops were used for sensory evaluation and 2 chops for shear force determination. Samples were vaccum packaged and frozen for later analysis. Chops were thawed in vaccum package bags at 4°C for 24 h, removed from the bags, weighed, and cooked to an internal temperature of 70°C on a grill (Model No. GRV120; George Foreman grilling machine, Lake Forest, IL). Chops were removed from the grill and weighed to estimate cook loss. For the assessment of sensory evaluation of pork, cooked chops were cut into 1 × 1 cm thickness pieces and held in metal double stack poachers filled with sand and placed in warming oven for a minimal period of time prior to the evaluation. Each sample was evaluated in duplicate (AMSA, 1995) by a minimum of 6 experienced sensory panelists. Each sample was evaluated on an 8 point scale for initial and sustained juiciness, initial and sustained tenderness, flavor intensity and pork flavor (1 being extremely dry, extremely tough, extremely bland, and extremely uncharacteristic of pork, respectively; 8 being extremely juicy, extremely tender, extremely intense, and extremely characteristic of pork, respectively).

For shear force determination, chops were prepared and cooked as previously described. Chops were removed from the grill, weighed, and stored at 4°C for 24 h on a metal pan covered with PVC wrap. Three 1.27-cm cores were taken from each of 2 chops parallel to the orientation of muscle fibers and sheared once perpendicular to the length of the core using a Warner-Bratzler shear force (Model No. 1955; G-R Electric Manufacturing Co., Manhattan, KS). Peak force from each core was recorded in kg, and 6 core readings per sample were averaged (AMSA, 1995).

Statistical Analysis

The data were analyzed using GLM procedure of SAS (SAS Inst. Inc., Cary, NC). Initially, the data for the 2 trials were tested for homogeneity of variance (Steele and Torrie, 1980). The results indicated that the variances for 2 trials were homogenous, thus, the data were combined and analyzed accordingly. The treatment, sex, trial, and appropriate covariates were included in the statistical models initially, and the covariates that did not reach a statistically significant trend (i.e., $P > 0.10$) were deleted from the final models. The initial and final BW for the growth performance data, the final BW for serum metabolite data, and the hot carcass weight for the carcass, internal organ weight, and physical and sensory characteristics were initially considered as a covariate(s). The effect of dietary treatments was assessed using PDIFF option of SAS when the overall F-ratio was statistically significant ($P \leq 0.05$). The pen was considered as the experimental unit in the statistical analysis. In addition, regressions were developed to describe the relationship between growth performance and the degree of early dietary amino acid restrictions.

RESULTS

Growth Performance during the Grower Phase

There were no differences in feed intake of pigs fed different diets. Pigs fed the 60G diet grew slower ($P \leq 0.05$) than those fed the 80G or 100G diet (Table 4). Pigs fed the 100G diet utilized feed more efficiently ($P \leq 0.05$) for weight gain compared with those fed the 60G diet, but ADG and G:F did not differ between pigs fed the 100G and 80G diets. As expected, the lysine intake **(LysI)** was greater ($P \leq 0.05$) for the pigs fed 100G diet than those fed the 80G or 60G diet, and they utilized lysine less efficiently ($P \leq 0.05$) for weight gain compared with those fed the 80G or 60G diet. The ultrasound backfat thickness at the end of the G phase was greater ($P \leq 0.05$) for the pigs fed the 60G diet compared with those pigs fed the 100G diet.

Growth Performance during the Finisher 1 Phase

The feed intake of pigs subjected to different dietary treatments did not differ during the F1 phase. Pigs fed the 60G-60F1 diets grew ($P \leq 0.05$) slower than those fed the other diet combinations. Pigs fed the 60G-100F1 diets had similar growth rate as those fed the control G and F1 diets, and also tended to grow faster than those fed the 80G-100F1 diets ($P = 0.087$) and the 80G-80F1 diets ($P = 0.072$). Although there was no difference in ADG, pigs fed the 80G-80F1 diets had better feed efficiency ($P \leq 0.05$) compared with those fed the 80G-100F1 diets. The G:F in pigs fed the 60G-100F1 diets was greater ($P \leq 0.05$) compared with those fed the 80G-100F1 diets but did not differ with those fed the control diets. The gain to LysI **(G:LysI)** in pigs fed the 80G-80F1 treatment pigs was similar to those fed the 60G-60F1 diets, but was greater ($P \leq 0.05$) than those fed the control, 80G-100F1, or 60G-100F1 diets. There were no differences in

the ultrasound backfat thickness at the end of the F1 phase among pigs subjected to various dietary treatments.

Growth Performance during the Finisher 2 Phase

There were no differences among different dietary treatments in any of the growth performance criteria. Similarly, UBF at the end of the F2 phase was not affected by dietary treatments.

Growth Performance during the Grower-Finisher Phase

There were no differences in feed intake of pigs subjected to different dietary treatments. There were no differences in the overall ADG of pigs fed the 80G-80F1 diets and those fed the control G and F1 diets. The lysine intake of pigs fed the control diets was greater ($P \leq 0.05$) than those fed the 80G-100F1, 80G-80F1, 60G-100F1, or 60G-60F1 diets. The G:F did not differ among pigs fed the control, 80G-80F1, 60G-100F1 diets, whereas G:LysI was greater ($P \leq 0.05$) for pigs fed the 60G-100F1 and 60G-60F1 diets compared with those fed the control diets.

Carcass Characteristics and Organ Weights

The LM area was similar among the different treatment groups, except pigs fed the 60G-60F1 diets had considerably less ($P \leq 0.05$) LM area compared with those fed other diet combinations. The fat-free lean gain (**LG**) was greater ($P \leq 0.05$) for pigs fed the control diets compared with those fed the 80G-100F1, 80G-80F1, or 60G-100F1 diets. There were no differences in LG among pigs fed the 80G-100F1, 80G-80F1, and 60G-100F1 diets. Dietary treatments had no effect on fat-free lean percentage, 10th rib backfat, or average backfat thickness. The LG to Lys intake (**LG:LysI**) was similar for pigs fed the 80G-80F1 and 60G-100F1 diets compared with those fed the control diets.

There were no differences in subjective color and firmness scores among different dietary treatments, but subjective marbling score was higher ($P \leq 0.05$) in pigs fed the 60G-60F1 diets compared with those fed the control diets and 80G-80F1 diets. No clear difference in the subjective muscling score was observed. Similarly, there were no differences in internal organ weights among pigs subjected to different degrees and durations of early dietary amino acid restrictions.

Serum Metabolites

At the end of the G phase, serum total protein and albumin concentrations were greater ($P \leq 0.05$) in pigs fed the control diets compared with those fed the 60G-100F1 and 60G-60F1 diets. Similarly, pigs fed the control diets had greater ($P \leq 0.05$) serum urea N concentration compared with those fed the 80G-100F1, 80G-80F1, 60G-100F1, or 60G-60F1 diets. Serum cholesterol concentration was greater ($P \leq 0.05$) in pigs fed the 60G-100F1 and 60G-60F1 diets compared with those pigs fed the 80G-80F1 diets. At the end of the F1 phase, there was no difference in the serum total protein concentration in pigs fed the 60G-100F1 diets compared with those fed the control diets. Similarly, there were no differences in urea N, glucose, and cholesterol concentrations among different treatment groups, however, serum triglyceride concentration was higher ($P \leq 0.05$) in pigs fed the 60G-60F1 diets compared with those fed the control diets at the end of the F1 phase. At the end of the F2 phase, pigs fed the 60G-100F1 diets had similar total protein and albumin concentrations compared with those fed the control diets, but pigs fed the 80G-80F1 diets had lower ($P \leq 0.05$) total protein and albumin concentrations compared with those fed the control diets.

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Physical and Sensory Characteristics of Pork

The dietary treatment did not affect physical characteristics of pork such as Warner-Bratzler Shear force and cook loss. Cook loss seemed to be greater for the pigs fed 60G-60F1 diets compared with those fed the 80G-80F1 ($P = 0.021$) and 100G-100F1 ($P = 0.028$) diets (F- ratio; $P = 0.096$). Sensory scores for initial juiciness, sustained juiciness, initial tenderness, sustained tenderness, flavor intensity, and off flavor were not affected by the dietary treatment.

DISCUSSION

During the G phase, as the degree of dietary amino acid restrictions increased, the weight gain decreased linearly ($R^2 = 0.70$; $P < 0.001$). In addition, ultrasound backfat was greater for pigs fed the 60G diet compared with those fed the 100G or 80G diet, indicating that the effort to depress growth performance and alter the body composition of pigs by the early dietary restriction was successful. The results also indicated that the improved growth performance in pigs fed high-amino acid diets was associated with a greater accretion of lean and less fat, which is in agreement with previous reports (Chiba, 1994, 1995; Chiba et al., 1999, 2002). As would be expected, pigs fed diets with the higher amino acid content had better feed efficiency than those fed diets with the lower amino acid content. On the other hand, as the dietary amino acid restriction increased, pigs consumed less lysine (and other amino acids) and utilized it more efficiently for weight gain, which can be attributed to the amino acid sparing effect associated with pigs fed a diet deficient in lysine and other amino acids as mentioned by Chiba et al. (1991).

During the F1 phase, ADG in pigs fed the 60G diet increased when they were fed the 100F1 diet, and they seemed to grow faster than those fed the control diets or other

combinations of the G and F1 diets. The results indicated that the more severe the dietary restriction, the greater the initial weight gain after realimentation, as pointed out earlier by Wilson and Osbourne (1960). The ADG in pigs fed the 60G-100F1 was, however, not statistically different from those fed the control G and F1 diets. As expected, pigs fed the restricted diets continuously (80G-80F1 and 60G-60F1) had less lysine intake and greater efficiency of lysine utilization for weight gain compared with those fed other combinations of diets.

During the F2 phase, there were no differences in growth performance among pigs subjected to different dietary treatments. Pigs fed the 60G-100F1 diets, which showed numerically greater ADG during the F1 phase, had similar weight gain, even though they had numerically higher G:F compared with pigs fed other combinations of diets. Consequently, after suffering severe amino acid restrictions earlier, pigs fed the 60G-100F1 diets were unable to attain the same weight for the age as those fed the control diets, which is in agreement with a previous finding in restricted sheep (Ryan, 1990).

Although there were no statistically significant differences, pigs subjected to dietary amino acid restrictions during both the G and F1 phases (80G-80F1) seemed to increase their feed intake (3,942 g/d) compared with those on other dietary treatments (average, 3,472 g/d). Such an increased feed intake after realimentation phase was observed in other studies (Owen et al., 1971; Bikker et al., 1996; Whang et al., 2000). On the other hand, instead of increasing their feed intake, pigs fed the 60G-60F1 diets had, numerically, the lowest feed intake (3,282 g/d) during the F2 phase. The ADG of those pigs subjected to amino acid restrictions during both the G and F1 phases was, however,

similar to those fed the other combinations of diets during the F2 phase. Similarly, although some differences were observed at the end of the G phase, there were no differences in ultrasound backfat thickness among pigs fed various combinations of G and F1 diets at the end of the F2 phase.

During the entire grower-finisher period, pigs fed the diets containing 60% of the total lysine recommendation (NRC, 1998) during both the G and F1 phases consumed less lysine and utilized it more efficiently for weight gain. However, they had lower ADG, G:F, LM area, and LG than those fed other combinations of the G and F1 diets, indicating that the early dietary amino acid restrictions may have been simply too severe or too long or both. On the other hand, overall ADG for the pigs fed the 80G-80F1 diets was similar to those fed the control diets, and they utilized feed and lysine for weight gain and LG as efficiently as those fed the control G and F1 diets. However, pigs fed the control diets had greater LG than those fed the 80G-80F1 diets. Thus, those pigs fed the 80G-80F1 diets may have exhibited compensatory growth response in terms of rate and efficiency of weight gain, but not in terms of lean accretion. On the other hand, other researchers reported that the differences in body composition associated with early protein or amino acid restrictions were almost completely disappeared by the time pigs reached market weight (Zimmerman and Khajarern, 1973; Campbell and Biden, 1978; Chiba, 1994, 1995; Fabian et al., 2002), indicating that pigs subjected to early amino acid restrictions compensated completely in those studies.

The diets used in this study were formulated to satisfy the needs of pigs with 325 g of carcass fat-free lean per day during the grower-finisher phase (NRC, 1998). However, considering the lean gain potential of genotype used in this study (as high as

377 g/d for the control group), it is likely that the NRC (1998) estimates were, perhaps, still inadequate in supplying necessary amino acids. Therefore, it is possible that realimentation diets used in this study may not have contained sufficient amino acids. Previous studies have indicated the importance of amino acid content of realimenting diets on the ability of the pigs to exhibit compensatory growth (Kyriazakis et al., 1991; Kyriazakis and Emmans, 1991). Those studies, however, dealt with pigs weighing up to only about 30 kg. Furthermore, other studies conducted with grower-finisher pigs indicated that there was no beneficial effect of dietary protein or amino acid content of realimention diets on compensatory growth response (Critser et al., 1995; Chiba et al., 1999).

Hogberg and Zimmerman (1978) reported that lean-strain of pigs did not make compensatory weight gain and had a smaller LM areas after protein restriction, whereas obese-strain pigs made partial or complete compensation in the rate and efficiency of weight gain and body composition. Their results indicated that genotypes may have some implications on compensatory growth. Chiba et al. (2002) also reported that pigs with lean genotype may be less tolerant of early dietary amino acid restrictions. It seems that pigs used in the present study may be considered as a lean genotype, thus, they may not have exhibited compensatory responses. There are, however, some reports indicating that the pigs with distinct genotypes responded similarly to early dietary restrictions during the realimentation phase (de Greef et al. 1992; Chiba et al., 1999; Fabian et al., 2002).

There were no differences in the subjective color and firmness scores among pigs fed different combinations of G and F1 diets. Subjective marbling score was, however, higher for pigs fed the 60G-60F1 diets compared with those fed other combinations of

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diets, which agree with the findings of other researchers (Castell et al., 1994; Cisneros et al., 1996; Blanchard et al., 1999) who reported that feeding protein deficient diets can increase marbling. The metabolism of branched chain amino acids (Cisneros et al., 1996; Hyun et al., 2002) in pigs fed the amino acid-deficient diet during the restriction phases may have been responsible for the increased marbling score in the present study.

It is well known that the mass of metabolically active internal organs can be affected by the protein or amino acid content of the diets (e.g., Koong et al., 1983; Chiba, 1994), and it has been suggested that compensatory growth response can be explained by alterations in internal organs (Bikker et al., 1996). In the present study, however, dietary treatments had no effect on the weight of metabolically active organs, which is in agreement with some earlier reports (Critser et al., 1995; Chiba et al., 1999; Whang et al., 2003). It is possible that the compensatory growth response in organ weights may have occurred during the initial realimentation period, but organ weights were determined only at the end of F2 phase in the present study.

Serum metabolite status may be a reflection of changes in metabolic and physiological activities in response to dietary manipulations. Dietary manipulations are likely to affect the metabolic profile possibly through the modulation of enzymes associated with N and lipid metabolism (Clarke and Abraham, 1992; McNeel and Mersmann, 2000). However, the effect of early dietary restrictions on various metabolites has not been elucidated fully. It has been suggested that serum total protein and albumin can be used as an indicator of the adequacy of dietary protein content (Lowrey et al., 1962). At the end of the G phase, serum total protein and albumin concentrations decreased as the dietary amino acid restrictions increased, which agrees with the previous

reports (Atinmo et al., 1976; Pond et al., 1980). As expected, serum urea N concentration was lower in pigs fed the 60G diet, and it could be a reflection of simply a reduced N intake. There were no differences in the serum glucose and triglycerides concentrations at the end of the G phase, but serum cholesterol concentration was, however, higher for the pigs fed 60G diet, and it may be due to the changes in the lipoprotein composition or transport or both that may be taking place in lipid metabolism causing hypercholesteromic effect in pigs (Pond et al., 1986).

Serum total protein and albumin concentrations in pigs fed the 60G-100F1 diets were clearly lower at the end of the G phase compared with those fed the control diets, however, total protein concentration was similar between the 2 groups at the end of the F1 and F2 phases. Although it was still depressed, serum albumin concentration in pigs fed the 60G-100F1 diets seemed to be relatively similar to those fed the control diets at the end of the F1 phase (4.76 vs. 4.46 g/dL). Mule et al. (2006) implied that pigs exhibiting compensatory growth after a period of dietary restrictions may show some indications of positive protein metabolism such as greater serum protein and albumin concentrations. During the G phase, ADG in pigs fed the 60G diet was clearly depressed, but when offered the 100F1 diet, those pigs had the greatest ADG during the F1 phase, even though it was statistically similar to those fed the control diets.

At the end of the F1 phase, pigs fed the 60G diet had a greater triglyceride concentration, especially those fed the 60G-100F1 diets, but there were no differences in UBF at the end of F1 phase or carcass backfat at the end of the F2 phase. As indicated before, there were no differences in overall rate and efficiency of weight gain between pigs fed the 80G-80F1 diets and control diets, however, those restricted during both the G

and F1 phases had lower concentrations of total protein and albumin at the end of G, F1, and F2 phases. These results, along with the LG data, may indicate that pigs fed the 80G-80F1 diets did not achieve apparent compensatory growth in weight gain through lean or protein accretion.

In the present study, the early dietary restriction had no effect on the physical and sensory characteristics of pork, which agrees with one report (Candek-Potokar et al., 1998) but contradicts with some other reports (Ellis et al., 1990; Warkup et al., 1990). Cook loss seemed to be greater in the 60G-60F1 dietary treatment compared with other dietary treatments, even though, again, the F-test was not statistically significant. It is possible that the reduced collagen in the muscles of pigs subjected to dietary restrictions (Candek-Potokar et al., 1998) may have lead to a greater cook loss. Pigs fed the 60G-60F1 diets, which had higher subjective marbling scores compared with others, seemed to have, numerically, least shear force values (3.56 vs. 3.63 to 3.88). Such a negative relationship between marbling and shear force values is in agreement with previous reports (DeVol et al., 1988; Ramsey et al., 1990), implying that marbling is positively related to pork tenderness. Although sustained tenderness seemed to be, numerically, the greatest in the 60G-60F1 treatment, no clear trend in initial or sustained tenderness was found in the present study. Similarly, there was no effect of dietary treatment on juiciness or flavor of pork in the present study, which agrees with a previous study (Blanchard et al., 2000). Other studies, however, showed a positive correlation between marbling and juiciness (Fernandez et al., 1999; Heyer and Lebret, 2007), indicating that beneficial effect of marbling on the sensory quality of pork is still rather controversial (Goransson et al., 1992).

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In conclusion, the results of the present study indicated that pigs fed the 80G-80F1 diets may have exhibited compensatory growth in terms of weight gain but not in terms of lean accretion. On the other hand, growth performance and carcass traits of pigs fed the 60G-60F1 diets were considerably depressed, indicating that the amino acid restrictions may have been too severe or too long or both. Early dietary AA restrictions did not have any clear effect on physical and sensory characteristics of pork.

LITERATURE CITED

AMSA. 1995. Research guidelines for cookery, sensory evaluation, and instrumental tenderness measurements of meat. Am. Meat Sci. Assoc., Chicago, IL.

AOAC. 1995. Official Methods of Analysis, 16th ed. Assoc. Off. Anal. Chem., Washington, DC.

Atinmo, T., C. Baldijao. W. G. Pond, and R. H. Barnes. 1976. Plasma insulin levels in weaned pigs fed protein or energy restricted diets. J. Nutr. 106:1654-1658.

Baghurst, K. 2004. Dietary fats, marbling and human health. Aust. J. Exp. Agric. 44:635-644.

Bejerholm, C., and P. Barton-Grade. 1986. Effect of intramuscular fat level on eating quality of pig meat. Page 389-391 in Proc. 32nd Eur. Meeting. Meat Res. Workers, Ghent, Belgium.

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

Blanchard, P. J., M. Willis, C. C. Warkup, and M. Ellis. 2000. The influence of carcass backfat and intramuscular fat level on pork eating quality. J. Sci. Food. Agric. 80:145-151.

Blanchard, P. J., M. Ellis, C. C. Warkup, B. Hardy, J. P. Chadwick, and G. A. Deans. 1999. The influence of rate of lean and fat tissue development on pork eating quality. Anim. Sci. 68:477-485.

Campbell, R. G., and R. S. Bidden. 1978. The effect of protein malnutrition between 5.5 and 20 kg live weight on the subsequent performance and carcass quality of pigs. Anim. Prod. 27:223-228.

Candek-Potokar, M., B. Zlender, L. Lefoucher, and M. Bonneau. 1998. Effects of age and/ or slaughter weight at slaughter on LM:Biochemical and sensory quality in pigs. Meat Sci. 48:287-300.

Castell, A. G., R. L. Cliplef, L. M. Poste-Flynn, and G. Butler. 1994. Performance, carcass and pork characteristics of castrates and gilts self-fed diets differing in protein content and lysine: energy ratio. Can. J. Anim. Sci. 74:519-528.

Chiba, L. I. 1994. Effects of dietary amino acid content between 20 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. Pages 181-209 in Feeding Systems and Feed Evaluation Models. M. K. Theodorou, and J. France, ed. CABI Publishing, Wallingford.

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. Dietary restrictions and growth performance and carcass traits 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: I. Rate and efficiency of weight gain. J. Anim. Sci. 69:694-707.

Cisneros, F., M. Ellis, D. H. Baker, R. A. Easter, and F. K. McKeith. 1996. The influence of short-term feeding of amino acid-deficient diets and high dietary leucine levels on the intramuscular fat content of pig muscle. Anim. Sci. 63:517-522.

Clarke, S. D., and S. Abraham. 1992. Gene expression: nutrient control of pre- and posttranscriptional events. FASEB J. 6:3146-3152.

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.

De Vol, D. L., F. K. McKeith, P. J. Bechtel, J. Novakofski, R. D. Shanks, and T. R. Carr. 1988. Variations in composition and palatability traits and relationships between

muscle characteristics and palatability in a random sample of pork carcasses. J. Anim. Sci. 66:385-395.

Ellis, M., A. J. Webb, P. Avery, R. Smithard, and I. Brown. 1990. Sex and feeding level effects on the eating quality of fresh pork. Anim. Prod. 50:551.

Fabian, J., L. I. Chiba, L. T. Frobish, W. H. McElhenny, D. L. Kuhlers, and K. Nadarajah. 2004. Compensatory growth and nitrogen balance in grower-finisher pigs. J. Anim. Sci. 82:2579-2587.

Fabian, J., L. I. Chiba, D. L. Kuhlers, L. T. Frobish, K. Nadarajah, C. R. Kerth, W. H. McElhenney, and A. J. Lewis. 2002. Degree of amino acid restrictions during the grower phase and compensatory growth in pigs selected for lean growth efficiency. J. Anim. Sci. 80:2610-2618.

Fernandez, X., G. Monin, A. Talmont, J. Mourot, and B. Lebret. 1999. Influence of intramuscular fat content on the quality of pig meat - 1. Composition of the lipid fraction and sensory characteristics of m. longissimus lumborum. Meat. Sci. 53:59-65.

Gerbens, F., F. J. Verburg, H. T. B. Van Moerkerk, B. Engel, W. Buist, J. H. Veerkamp, and M. F. W. te Pas. 2001. Associations of heart and adipocyte fatty acid-binding protein gene expression with intramuscular fat content in pigs. J. Anim. Sci. 79:347-354.

Goransson, A., G. von Seth, and E. Tornberg. 1992. The influence of intramuscular fat content on the eating quality of pork. Pages 245-248 in Proc. 38th Int. Congr. Meat Sci. Technol., Clermont-Ferrand, France.

Heyer, A., and B. Lebret. 2007. Compensatory growth response in pigs: Effects on
growth performance, composition of weight gain at carcass and muscle levels,
and meat quality. J. Anim. Sci. 85:769-778.

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.

Hyun, Y., M. Ellis, G. Bressner, and D. Baker. 2002. Effect of dietary leucine levels on
carcass composition, meat quality, and growth performance in finishing pigs.
http://www.traill.uiuc.edu/porknet/paperDisplay.cfm?ContentID=126 Accessed
Nov. 1, 2007.

Jones, S. D. M., W. M. Robertson, and S. Talbot. 1992. Marbling standards for beef and
pork. Agric. and Agri-Food Canada Pub. No. 1879/E, Ottawa, ON.

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

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.

Kyriazakis, I., and G. C. Emmans. 1991. Diet selection in pigs: dietary choices made by
growing pigs following a period of underfeeding with protein. Anim. Prod.
52:337-346.

Kyriazakis, I., C. Statmaris, G. C. Emmans, and C. T. Whittemore. 1991. The effects of
food protein content on the performance of pigs previously given foods with low
or moderate protein content. Anim. Prod. 52:165-172.

Lametsch, R., L. Kristensen, M. R. Larsen, M. Therkildsen, N. Oksbjerg, and P. Ertbjerg. 2006. Changes in the muscle proteome after compensatory growth in pigs. J. Anim. Sci. 84:918-924.

Lawrence, T. L. J., and V. R. Flower. 1997. Growth of Farm Animals. CAB International, Wallingford.

Lonergan, S. M., and K. J. Prussa. 2002. Sensory and instrumental analysis of the textural parameters of pork. Pages 33-38 in Recip. Meat Conf. Post Conf. Symp.: Pork Quality Measurement Systems. Am. Meat Sci. Assoc., Savoy, IL

Lowrey, R. S., W. G. Pond, R. H. Barnes, L. Krook, and J. K. Loosli. 1962. Influence of caloric level and protein deficiency in the young pig. J. Nutr. 78:245-252.

McNeel, R. L., and H. J. Mersmann. 2000. Nutritional deprivation reduces the transcripts for transcription factors and adipocyte-characteristic proteins in porcine adipocytes. J. Nutr. Biochem. 11:139-146.

Mule, H. R., L. I. Chiba, J. Fabian, D. L. Kuhlers, S. B. Jungst, L. T. Frobish, K. Nadarajah, W. G. Bergen, and E. G. Welles. 2006. Effect of early dietary amino acid restrictions on serum metabolites in pigs selected for lean growth efficiency. Can. J. Anim. Sci. 86:489-500.

NPPC. 2000. Pork Composition and Quality Assessment Procedures. Natl. Pork Prod. Council, Des Moines, IA.

NRC. 1998. Nutrient Requirements of Swine. 10th rev. ed. Natl. Acad. Press, Washington, DC.

Oksbjerg, N., M. T. Sorensen, and M. Vestergaard. 2002. Compensatory growth and its effects on muscularity and technological meat quality in growing pigs. Acta Agric. Scand. Sect. A-Anim. Sci. 52:85-90.

Owen, J. B., W. F. Ridgman, and D. Wyllie. 1971. The effect of food restriction on subsequent voluntary intake of pigs. Anim. Prod.13:537-543.

Pond, E. G., J. T. Yen, and R. N. Lindvall. 1980. Early protein deficiency: Effects on later growth and carcass composition of lean or obese swine. J. Nutr. 110:2506-2513.

Pond, W. G., H. J. Mersmann, and L. D. Young. 1986. Heritability of plasma cholesterol and triglyceride concentration in swine. Proc. Soc. Exp. Biol. Med. 182:221-224.

Ramsey, C. B., L. F. Tribble, C. Wu, and K. D. Lind. 1990. Effects of grains, marbling and sex on pork tenderness and composition. J. Anim. Sci. 68:148-154.

Ryan, W. J. 1990. Compensatory growth in cattle and sheep. Nutr. Abstr. Rev. 60:653-664.

Steel, R. G. D., and J. H. Torrie. 1980. Principles and Procedures of Statistics: A Biometrical Approach. 2nd ed. McGraw-Hill Book Co., New York.

Therkildsen, M., B. Riis, A. Karlsson, L. Kristensen, P. Ertbjerg, P. P. Purslow, M. D. Aaslyng, and N. Oksbjerg. 2002. Compensatory growth response in pigs, muscle protein turnover and meat texture: Effects of restriction/realimentation period. Anim. Sci. 75:367-377.

Warkup, C. C., and A. J. Kempster. 1991. A possible explanation of the variation in tenderness and juiciness of pig meat. Anim. Prod. 52:559. (Abstr.)

Warkup, C. C., A. W. Dilworth, A. J. Kempster, and J. D. Wood. 1990. The effects of sire type, company source, feeding regimen and sex on eating quality of pig meat. Anim. Prod. 50:550.

Whang, K. Y., S. M. Donovan, and R. A. Easter. 2000. Effect of protein deprivation on subsequent efficiency of dietary protein utilization in finishing pigs. Asian -Aust. J. Anim. Sci. 13:659-665.

Whang, K. Y., S. W. Kim, S. M. Donovan, F. K. McKeith, and R. A. Easter. 2003. Effects of protein deprivation on subsequent growth performance, gain of body components, and protein requirements in growing pigs. J. Anim. Sci. 81:705-716.

Wilson, P. N. and D. F. Osbourn, 1960. Compensatory growth after undernutrition in mammals and birds. Biol. Rev. 35:324.

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

Table 1. Composition of soybean meal and corn (as-fed basis)[1,2]

Item	Soybean meal	Corn
Ingredient, g/kg		
DM	885.3	865.1
CP	473.2	81.9
Arg	34.9	3.9
His	12.8	2.3
Ile	21.4	2.7
Leu	36.0	9.8
Lys	29.2	2.5
Met	6.4	1.6
Cys	7.2	1.7
Met + Cys	13.7	3.4
Phe	24.1	4.1
Thr	18.4	2.9
Trp	6.4	0.6
Val	22.6	3.8

[1]Corn and soybean meal were analyzed by a commercial laboratory (Evonik-Degussa Corp., Kennesaw, GA).

[2]Reported the values of a single batch of samples; some AA values were not reported.

Table 2. Composition of grower diets (as-fed basis)[1]

Item	100G	80G	60G
Ingredient, g/kg			
Corn	707.96	778.58	849.21
Soybean meal (47.3% CP)	266.39	194.79	123.20
Dicalcium phosphate	12.67	14.15	15.60
Limestone	6.98	6.48	5.99
Salt	3.50	3.50	3.50
Vitamin-trace mineral premix[2]	2.50	2.50	2.50
Calculated composition			
DE, Mcal/kg	3.43	3.43	3.43
CP, g/kg	177.40	151.90	126.40
Ca, g/kg	7.00	7.00	7.00
P, g/kg	6.00	6.00	6.00
Ca:P	1.17	1.17	1.17
Lys, g/kg	9.50	7.60	5.70
Lys:DE, g/Mcal	2.77	2.22	1.66
Trp, g/kg	2.34	1.95	1.55
Thr, g/kg	7.08	6.11	5.15
His, g/kg	4.90	4.28	3.67
Ile, g/kg	7.81	6.62	5.44
Analyzed composition			
CP, g/kg	169.50	149.30	121.10

[1]100G, 80G, and 60G: diets formulated to contain 100, 80, and 60% of total lysine recommendation during the grower phase (NRC, 1998).

[2]Provided the following (unit/kg diet): Fe (ferrous sulphate), 150 mg; Zn (zinc oxide), 150 mg; Mn (manganous oxide), 37.5 mg; Cu (copper sulfate), 150 ppm; I (ethylenediamine dihydroiodide), 5 ppm; Se (sodium selenite), 3 ppm; vitamin A, 6,614 IU; vitamin D_3, 1,102 IU; vitamin E, 26 IU; vitamin B_{12}, 0.03 mg; menadione (menadione Na bisulfite complex), 1 mg; riboflavin, 6 mg; D-pantothenic acid (D-Ca pantothenate), 45 mg; niacin, 28 mg; and choline (choline chloride), 110 mg.

Table 3. Composition of finisher 1 and finisher 2 diets (as-fed basis)[1]

Item	100F1	80F1	60F1	F2
Ingredient, g/kg				
Corn	786.02	841.84	897.60	844.24
Soybean meal (47.3% CP)	190.80	134.23	77.70	134.00
Dicalcium phosphate	11.40	12.54	13.73	9.76
Limestone	5.78	5.39	4.97	6.00
Salt	3.50	3.50	3.50	3.50
Vitamin-trace mineral premix[2]	2.50	2.50	2.50	2.50
Calculated composition				
DE, Mcal/kg	3.44	3.44	3.44	3.45
CP, g/kg	150.80	130.60	110.50	130.70
Ca, g/kg	6.00	6.00	6.00	5.50
P, g/kg	5.50	5.50	5.50	5.00
Ca:P	1.09	1.09	1.09	1.10
Lys, g/kg	7.50	6.00	4.50	6.00
Lys:DE, g/Mcal	2.18	1.74	1.31	1.74
Trp, g/kg	1.93	1.62	1.31	1.62
Thr, g/kg	6.07	5.31	4.55	5.32
His, g/kg	4.26	3.78	3.29	3.78
Ile, g/kg	6.57	5.63	4.70	5.63
Analyzed composition				
CP, g/kg	148.30	129.80	106.90	125.10

[1]100F1, 80F1, and 60F1: diets formulated to contain 100, 80, and 60% of total lysine recommendation during the F1 phase (NRC, 1998). F2: diet formulated to satisfy total lysine recommendation during the finisher 2 phase (NRC, 1998).

[2]Provided the following (unit/kg diet): Fe (ferrous sulphate), 150 mg; Zn (zinc oxide), 150 mg; Mn (manganous oxide), 37.5 mg; Cu (copper sulfate), 150 ppm; I (ethylenediamine dihydroiodide), 5 ppm; Se (sodium selenite), 3 ppm; vitamin A, 6,614 IU; vitamin D_3, 1,102 IU; vitamin E, 26 IU; vitamin B_{12}, 0.03 mg; menadione (menadione Na bisulfite complex), 1 mg; riboflavin, 6 mg; D-pantothenic acid (D-Ca pantothenate), 45 mg; niacin, 28 mg; and choline (choline chloride), 110 mg.

Table 4. Effect of the degree and duration of dietary amino acid restrictions on growth performance of pigs during the grower, finisher 1, finisher 2 phases, and overall, and ultrasound backfat thickness of pigs at the end of the grower, finisher 1, and finisher 2 phases[1,2]

Item	100G-100F1 (Control)	80G-100F1	80G-80F1	60G-100F1	60G-60F1	SEM[3]	*P*-value
Grower phase							
ADFI, g/d	2,272	2,199	2,170	2,229	2,124	53	0.418
Avg daily Lys intake, g/d	21.1[a]	16.8[b]	16.5[b]	12.8[c]	12.0[c]	0.4	< 0.001
ADG, g/d	931[a]	881[a]	890[a]	753[b]	752[b]	18	< 0.001
G:F, g/kg	411[a]	399[a]	413[a]	337[b]	354[b]	8	< 0.001
Gain:Lys intake, g/g	43[a]	53[b]	54[b]	59[c]	62[c]	1	< 0.001
Ultrasound backfat, mm	7.0[a]	7.5[a]	7.2[a]	7.6[b]	8.0[bc]	0.2	0.009
Finisher 1 phase							
ADFI, g/d	2,699	3,065	2,493	2,784	2,623	165	0.189
Avg daily Lys intake, g/d	20.3[a]	23.0[a]	14.9[bc]	20.9[ab]	11.6[c]	1.2	< 0.001
ADG, g/d	987[a]	931[a]	926[a]	1019[a]	759[b]	34	< 0.001
G:F, g/kg	375[a]	315[b]	371[a]	372[a]	286[b]	17	0.004
Gain:Lys intake, g/g	50[a]	42[b]	62[c]	50[ab]	63[c]	3	< 0.001
Ultrasound backfat, mm	10.0	9.9	9.9	10.0	10.3	0.5	0.976
Finisher 2 phase							
ADFI, g/d	3,736	3,506	3,942	3,364	3,282	213	0.205
Avg daily Lys intake, g/d	22.4	21.0	23.7	20.2	19.7	1.3	0.203
ADG, g/d	1,171	997	1139	1117	1078	69	0.488
G:F, g/kg	312	285	288	339	329	19	0.193
Gain:Lys intake, g/g	52	47	48	57	55	3	0.182
Ultrasound backfat, mm	12.3	12.5	12.6	12.3	12.2	0.3	0.932

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Item	100G-100F1 (Control)	80G-100F1	80G-80F1	60G-100F1	60G-60F1	SEM[3]	P-value
Overall							
ADFI, g/d	2,840	2,914	2,815	2,716	2,638	80	0.153
Avg daily Lys intake, g/d	21.1[a]	20.2[a]	18.1[bc]	17.3[c]	14.1[d]	0.6	< 0.001
ADG, g/d	1018[a]	935[b]	978[ab]	930[b]	834[c]	26	0.001
G:F, g/kg	359[a]	322[b]	347[a]	344[a]	316[b]	9	0.014
Gain:Lys intake, g/g	49[a]	46[a]	54[b]	54[b]	59[c]	1	< 0.001

[a-d]Within a row, means with different superscripts differ ($P \leq 0.05$).

[1]Least squares means based on 6 pens containing 2 gilts or 2 castrated males/pen. Grower: 22.7 ± 0.3 to 50.6 ± 0.4 kg; finisher 1: 50.6 ± 0.4 to 79.9 ± 0.5 kg; and finisher 2: 79.9 ± 0.5 to 110.7 ± 0.5 kg; The initial and final BW for the growth performance data, and the final BW for the ultrasound backfat thickness were initially considered as a covariate(s), and the covariate(s) that did not reach a statistically significant trend (i.e., $P > 0.10$) were deleted from the final models.

[2]100G, 80G, or 60G and 100F1, 100F1, or 60F1: diets formulated to contain 100, 80, or 60% of total lysine recommendation (NRC, 1998) during the G and F1 phases, respectively. Pigs were fed a common diet during the F2 phase.

[3]Pooled SEM.

Table 5. Effect of the degree and duration of dietary amino acid restrictions on carcass traits, subjective meat quality scores, and internal organ weights at the end of the finisher phase[1,2]

Item	100G-100F1 (Control)	80G-100F1	80G-80F1	60G-100F1	60G-60F1	SEM[3]	*P*-value
Carcass traits							
Average backfat, mm	27.6	27.4	28.0	29.0	28.7	1.0	0.778
10th rib backfat, mm	20.0	20.5	19.6	21.0	20.3	1.1	0.921
LM area, cm^2	45.9^a	46.4^a	44.1^a	43.8^a	40.3^b	1.4	0.041
Fat-free lean, %	53.6	53.2	53.1	52.1	51.4	0.6	0.212
Fat-free lean gain, g/d	376.7^a	332.3^b	344.6^b	324.4^b	286.5^c	9.3	< 0.001
Fat-free lean gain:feed intake, g/kg	132.6^a	114.4^{bc}	122.4^{ab}	119.5^b	108.6^c	3.7	0.002
Fat-free lean gain: Lys intake, g/g	17.9^{ab}	16.5^a	19.1^{bc}	18.8^{bc}	20.3^c	0.5	0.001
Subjective meat quality scores							
Color	3.14	3.22	2.96	3.19	3.50	0.16	0.275
Firmness	2.96	2.89	2.76	2.97	3.41	0.15	0.102
Marbling	2.06^a	1.93^a	2.09^a	2.41^{ab}	2.92^b	0.19	0.008
Muscling	2.37^{ab}	2.38^a	2.37^{ab}	2.43^a	2.30^b	0.03	0.122
Internal organ weights							
Liver, g	1,426	1,477	1,472	1,499	1,391	73	0.852
Kidney, g	342	347	356	362	341	23	0.973
Heart, g	357	357	397	371	376	24	0.886

[a-c]Within a row, means with different superscripts differ ($P \leq 0.05$).

[1]Least squares means based on 6 pens containing 2 gilts or 2 castrated males/pen. Grower diets were fed from: 22.7 ± 0.3 to 50.6 ± 0.4 kg; finisher 1 diets were fed from: 50.6 ± 0.4 to 79.9 ± 0.5 kg; and finisher 2 diets were fed from: 79.9 ± 0.5 to 110.7 ± 0.5 kg. The hot carcass weight was initially included in the model as a covariate, and it was deleted from the final model if P > 0.10.

[2]100G, 80G, or 60G and 100F1, 100F1, or 60F1: diets formulated to contain 100, 80, or 60% of total lysine recommendation (NRC, 1998) during the G and F1 phases, respectively. Pigs were fed a common diet during the F2 phase.
[3]Pooled SEM.

Table 6. Effect of the degree and duration of dietary amino acid restrictions on serum metabolites of pigs at the end of the grower, finisher 1, and finisher 2 phases[1,2]

Item	100G-100F1 (Control)	80G-100F1	80G-80F1	60G-100F1	60G-60F1	SEM[3]	*P*-value
Grower phase							
Total protein, g/dL	5.97[a]	5.79[ab]	5.57[bc]	5.18[c]	5.06[d]	0.13	< 0.001
Albumin, g/dL	4.59[a]	4.42[ab]	4.13[b]	3.53[c]	3.44[c]	0.11	< 0.001
Urea nitrogen, mg/dL	17.0[a]	13.7[bc]	14.3[c]	14.4[bc]	12.3[d]	0.6	< 0.001
Cholesterol, mg/dL	113.6[ab]	107.6[a]	106.9[a]	125.6[b]	124.2[b]	4.7	0.020
Triglycerides, mg/dL	30.4	27.0	35.1	39.4	27.8	4.7	0.338
Glucose, mg/dL	115.0	112.3	118.9	118.3	108.8	3.4	0.255
Finisher 1 phase							
Total protein, g/dL	6.23[a]	6.18[ab]	5.88[b]	6.02[ab]	5.30[c]	0.11	< 0.001
Albumin, g/dL	4.76[a]	4.68[ab]	4.38[b]	4.46[b]	3.42[c]	0.10	< 0.001
Blood urea nitrogen, mg/dL	15.5	15.1	13.8	14.2	12.4	0.8	0.083
Cholesterol, mg/dL	108.4	113.0	109.9	109.6	141.7	4.7	< 0.001
Triglycerides, mg/dL	18.0[a]	19.7[ab]	21.3[ab]	25.5[bc]	29.6[c]	2.6	0.023
Glucose, mg/dL	101.7	106.5	106.3	113.0	108.1	2.5	0.062
Finisher 2 phase							
Total protein, g/dL	6.19[ac]	6.1[a]	5.61[b]	6.25[a]	5.50[b]	0.12	< 0.001
Albumin, g/dL	4.75[a]	4.6[a]	4.24[b]	4.45[a]	4.03[c]	0.10	< 0.001
Blood urea nitrogen, mg/dL	13.9	13.4	12.6	13.3	11.4	0.7	0.102
Cholesterol, mg/dL	106.2	100.5	101	104	106.1	3.6	0.676
Triglycerides, mg/dL	22.7	31.4	47.5	26.6	38.1	5.9	0.059
Glucose, mg/dL	100.0	99.6	101.0	99.7	104.9	3.7	0.838

[a-d]Within a row, means with different superscripts differ (*P* ≤ 0.05).

[1]Least squares means based on 6 pens containing 2 gilts or 2 castrated males/pen. Grower diets were fed from: 22.7 ± 0.3 to 50.6 ± 0.4 kg; finisher 1 diets were fed from: 50.6 ± 0.4 to 79.9 ± 0.5 kg; and finisher 2 diets were fed from: 79.9 ± 0.5 to 110.7 ± 0.5 kg. The final BW was included in the model as a covariate, and it was deleted from the final model if *P* > 0.10.

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[2]100G, 80G, or 60G and 100F1, 100F1, or 60F1: diets formulated to contain 100, 80, or 60% of total lysine recommendation (NRC, 1998) during the G and F1 phases, respectively. Pigs were fed a common diet during the F2 phase.

[3]Pooled SEM.

Table 7. Effect of the degree and duration of dietary amino acid restrictions on physical and sensory characteristics of pork chops[1,2]

Item	100G-100F1 (Control)	80G-100F1	80G-80F1	60G-100F1	60G-60F1	SEM[3]	*P*-value
Warner-Bratzler shear force, kg	4.01	3.96	3.66	3.62	3.63	0.26	0.710
Cook loss, %	20.19	22.66	20.05	21.64	23.66	1.02	0.096
Sensory scores							
Initial juiciness	4.90	4.33	5.13	4.71	4.30	0.23	0.090
Sustained juiciness	4.86	4.08	5.17	4.63	4.44	0.25	0.063
Initial tenderness	5.51	5.16	5.54	5.39	5.25	0.12	0.146
Sustained tenderness	5.39	4.99	5.46	5.39	5.57	0.13	0.099
Flavor intensity	4.85	4.39	4.98	4.56	4.62	0.18	0.207
Off flavor	1.14	1.07	1.20	1.10	1.24	0.07	0.488

[1]Least squares means based on 6 pens containing 2 gilts or 2 castrated males/pen. Grower diets were fed from: 22.7 ± 0.3 to 50.6 ± 0.4 kg; finisher 1 diets were fed from: 50.6 ± 0.4 to 79.9 ± 0.5 kg; and finisher 2 diets were fed from: 79.9 ± 0.5 to 110.7 ± 0.5 kg. The hot carcass weight was initially included in the model as covariate, and it was deleted from the final model if *P* > 0.10.

[2]100G, 80G, or 60G and 100F1, 100F1, or 60F1: diets formulated to contain 100, 80, or 60% of total lysine recommendation (NRC, 1998) during the G and F1 phases, respectively. Pigs were fed a common diet during the F2 phase.

[3]Pooled SEM.

IV. SUMMARY AND CONCLUSIONS

Satisfying the consumer by providing high quality pork is an integral part of successful and sustainable pig production. Unfortunately, the effort to satisfy consumer demands by producing leaner pigs in recent years has resulted in a reduction of marbling, which has adverse effects on eating quality of pork. It is possible that carcass fat can be reduced to satisfy today's consumer demands for leaner pork and marbling can be increased to enhance eating quality of pork simultaneously by taking advantage of compensatory growth. Furthermore, compensatory growth can increase the overall efficiency of nutrient utilization and minimize adverse impacts of pig production on the environment.

The objective of this study was to investigate the effect of degree and duration of early dietary amino acid restrictions on growth performance, serum metabolites, internal organ weights, and carcass traits of pigs, and subjective quality scores and physical and sensory characteristics of pork. For the grower (G) and finisher 1 (F1) phases, 3 corn-soybean meal diets were formulated to contain 100, 80, or 60% of the 1998 NRC total lysine recommendation (100G, 80G, or 60G, and 100F1, 80F1, or 60F1, for the G and F1 phases, respectively). For the finisher 2 (F2) phase, a common corn-soybean meal diet was formulated to satisfy the 1998 NRC total lysine recommendation. Thirty gilts and 30 castrated males (2 gilts or 2 castrated males/pen) were randomly assigned to 5 dietary treatments [100G-100F1 (control), 80G-100F1, 80G-80F1, 60G-100F1, and 60G-60F1]

when they weighed 22.7 ± 0.3 kg. Pigs were switched to F1 and F2 diets when they

weighed 50.7 ± 0.4 and 79.9 ± 0.5 kg, respectively. Pigs had ad libitum access to feed

and water throughout the study. Blood samples were collected at the end of the G, F1,

and F2 phases. All pigs were slaughtered when they weighed 110.7 ± 0.5 kg, and

standard carcass data and internal organ weight data were collected. The LM samples

were collected for the assessment of physical and sensory characteristics of pork. Pigs fed

the 60G diet had lower ($P < 0.05$) ADG during the G phase and greater ($P < 0.05$)

ultrasound backfat (UBF) at the end of the G phase than those fed the 100G diet, and

ADG decreased linearly ($R^2 = 0.70$; $P < 0.001$) as the degree of amino acid restrictions

increased, indicating that the effort to depress growth performance and alter body

composition by early dietary AA restrictions was successful. Although serum total

protein (TP) and albumin in pigs fed the 60G-100F1 diets at the end of the G phase were

lower ($P < 0.05$) than those fed the control G and F1 diets, TP was similar between the 2

groups at the end of the F1 phase. Their ADG during the F1 phase and UBF at the end of

the F1 phase were, however, similar to those fed the control diets. Feeding the 80G diet

resulted in numerically depressed ADG during the G phase, but there was no difference

in ADG during the F1 and F2 phases or UBF at the end of F1 and F2 phases between the

pigs fed the 80G and 100G diets. Overall, pigs fed the 80G-80F1 diets had similar ADG,

but they had less ($P < 0.05$) lean gain (LG) than those fed the control diets. They also had

lower ($P < 0.05$) serum TP and albumin than pigs fed the control diets throughout the

study. Pigs fed the 60G-60F1 diets had clearly lower ($P < 0.05$) overall ADG and G:F

and less ($P < 0.05$) LM area and LG compared with those fed the control G and F1 diets.

However, they had higher ($P < 0.05$) subjective marbling score than those fed the control

diets. Dietary treatments had no clear effect on other serum metabolites, carcass backfat, subjective color and firmness scores, organ weights, or physical and sensory characteristics of pork.

The results of the present study indicated that pigs fed the 80G-80F1 diets may have exhibited compensatory growth in terms of weight gain but not in terms of lean accretion. On the other hand, growth performance and carcass traits of pigs fed the 60G-60F1 diets were clearly depressed, indicating that the amino acid restrictions may have been too severe or too long or both. Early dietary AA restrictions had no clear effect on physical and sensory characteristics of pork.

CUMULATIVE BIBLIOGRAPHY

AMSA. 1995. Research guidelines for cookery, sensory evaluation, and instrumental tenderness measurements of meat. Am. Meat Sci. Assoc., Chicago, IL.

AOAC. 1995. Official Methods of Analysis, 16th ed. Assoc. Off. Anal. Chem., Washington, DC.

Aberle, E. D., J. C. Forrest, D. E. Gerrard, E. W. Mills. 2001. Principles of meat science 4th ed. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Allen, R. E., R. A. Merkel, and R. B. Young. 1979. Cellular aspect of muscle growth: Myogenic cell proliferation. J. Anim. Sci. 49:115-127.

Anderson, T. J., and F. C. Parrish. 1989. Postmortem degradation of titin and nebulin of beef steaks varying in tenderness. J. Food Sci. 54:748-749.

Andersen, H. J., N. Oksbjerg, J. F. Young, and M. Therkildsen. 2005. Feeding and meat quality – A future approach. Meat Sci. 70:543-554.

Alingham, P. G., G. S. Harper, and R. A. Hunter. 1998. Effect of growth path on the tenderness of the semitendinosus muscle of Brahman-cross steers. Meat Sci. 48:65-73.

Asghar, A., and A. M. Pearson. 1980. Influence of ante- and post-mortem treatments on muscle composition and Meat quality. Adv. Food. Res 26:53-61.

Atinmo, T., C. Baldijao. W.G. Pond, and R.H. Barnes. 1976. Plasma insulin levels in weaned pigs fed protein or energy restricted diets. J. Nutr. 106:1654-1658.

Baghurst, K. 2004. Dietary fats, marbling and human health. Aust. J. Exp. Agric. 44:635-644.

Bejerholm, C., and P. Barton-Grade. 1986. Effect of intramuscular fat level on eating quality of pig meat. Page 389-391 in Proc. 32nd European Meeting. Meat Res. Workers, Ghent, Belgium.

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

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: II. Protein and lipid accretion in body components. J. Anim. Sci. 74:817-826.

Blanchard, P. J., M. Willis, C. C. Warkup, and M. Ellis. 2000. The influence of carcass backfat and intramuscular fat level on pork eating quality. J. Sci. Food. Agric. 80:145-151.

Blanchard, P. J., M. Ellis, C. C. Warkup, B. Hardy, J. P. Chadwick, and G. A. Deans. 1999. The influence of rate of lean and fat tissue development on pork eating quality. Anim. Sci. 68:477-485.

Bohman, V. R. 1955. Compensatory growth of beef cattle: The effect of hay maturity. J. Anim. Sci. 14:249-255.

Brockman, R. P., and B. Laarveld. 1986. Hormonal regulation of metabolism in ruminants: a review. Livest. Prod. Sci. 14, pp 313-334. (Abstr)

Bryhni, E. A., D. V., Byrne, M. Rodbotten, S. Moller, C. Claudi-Magnussen, and A. Karlsson. 2003. Consumer and sensory investigations in relation to physical/chemical aspects of cooked pork in Scandinavia. Meat Sci. 65:737-748.

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. Endocrinol. 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. Gent. Res. 75:209-213.

Campbell, R. G., and R. S. Bidden. 1978. The effect of protein malnutrition between 5.5 and 20 kg live weight on the subsequent performance and carcass quality of pigs. Anim. Prod. 27:223-228.

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.

Candek-Potokar, M., B. Zlender, L. Lefoucher, and M. Bonneau. 1998. Effects of age and/ or slaughter weight at slaughter on LM:Biochemical and sensory quality in pigs. Meat Sci. 48:287-300.

Carstens, G. E., D. E. Johnson, M. A. Ellenberger and J. D. Tatum. 1991. Physical and chemical components of the empty body during compensatory growth in beef steers. J. Anim. Sci. 69:3251-3264.

Castell, A. G., R. L. Cliplef, L. M. Poste-Flynn, and G. Butler. 1994. Performance, carcass and pork characteristics of castrates and gilts self-fed diets differing in protein content and lysine: energy ratio. Can. J. Anim. Sci. 74:519-528.

Chiba, L. I. 1994. Effects of dietary amino acid content between 20 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. 1999. Compensatory growth in swine: fact or fiction. Proc. The 16th Annual Biokyowa Amino Acid Council Meeting, October 7, St. Louis, MO.

Chiba, L. I. 2000. Feeding systems for pigs. Pages 181-209 in M. K. Theodorou, and J. France, Feeding Systems and Feed Evaluation Models. CABI Publishing, Wallingford.

Chiba, L. I. 2001. Protein supplements. Pages 803-837 in Swine Nutrition. 2nd ed. A. J. Lewis, and L. L. Southern, ed. CRC Press, Boca Raton.

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: I. Rate and efficiency of weight gain. J. Anim. Sci. 69:694-707.

Christian, L. L., K. L. Strock, and J. P. Carlson. 1980. Effects of protein, breed cross, sex, and slaughter weight on swine performance and carcass traits. J. Anim. Sci. 51: 51-58.

Cisneros, F., M. Ellis, D. H. Baker, R. A. Easter, and F. K. McKeith. 1996. The influence of short-term feeding of amino acid-deficient diets and high dietary leucine levels on the intramuscular fat content of pig muscle. Anim. Sci. 63:517-522.

Clarke, S. D., and S. Abraham. 1992. Gene expression: nutrient control of pre- and posttranscriptional events. FASEB J. 6:3146-3152.

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.

da Costa, N., C. McGillivray, Q. Bai, J. D. Wood, G. Evans, and K. C. Chang. 2004. Restriction of dietary energy and protein induces molecular changes in young porcine skeletal muscles. J. Nutr. 134:2191-2199.

Deaton, J. W., F. N. Reece, L. F. Kubena, B. D. Colt, and J. D. May. 1973. The ability of the broiler to compensate for early growth depression. Poult. Sci. 52:262-265.

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.

De Vol, D. L., F. K. McKeith, P. J. Bechtel, J. Novakofski, R. D. Shanks, and T. R. Carr. 1988. Variations in composition and palatability traits and relationships between muscle characteristics and palatability in a random sample of pork carcasses. J. Anim. Sci. 66:385-395.

Donker, R. A., L. A. denHartog, E. W. Brascamp, J. W. M. Merks, G. J. Noordewier, and G. A. J. Buitting. 1986. Restriction of feed intake to optimize overall performance and composition of pigs. Livest. Prod. Sci. 15:353-365.

Eikelenboom, G., A. H. Hoving-Bolink, and P. G. van der Wal. 1996. The eating quality of pork. 2. The influence of intramuscular fat. Fleischwirtschaft 76:517-518.

Ellis, M., A. J. Webb, P. Avery, R. Smithard, and I. Brown. 1990. Sex and feeding level effects on the eating quality of fresh pork. Anim. Prod. 50:551.

Essen-Gustavsson, B., A. Karlsson, K. Lundstrom, and A. C. Enfalt. 1994. Intramuscular fat and muscle fiber lipid contents in halothane-gene-free pigs fed high or low protein diets and its relation to meat quality. Meat Sci. 53:59-65.

Fabian, J., L. I. Chiba, L. T. Frobish, W. H. McElhenny, D. L. Kuhlers, and K. Nadarajah. 2004. Compensatory growth and nitrogen balance in grower-finisher pigs. J. Anim. Sci. 82:2579-2587.

Fabian, J., L. I. Chiba, D. L. Kuhlers, L.T. Frobish, K. Nadarajah, C. R. Kerth, W. H. McElhenny, and A. J. Lewis. 2002. Degree of amino acid restrictions during the grower phase and compensatory growth in pigs selected for lean growth efficiency. J. Anim. Sci. 80:2610-2618.

Fabian, J. 2001. Compensatory growth and pigs selected for lean growth efficiency. M. S. Thesis, Auburn Univ., Auburn University, AL.

Ferrell, C. L. 1988. Contribution of visceral organs to animal energy expenditure. J. Anim. Sci. 66(Suppl. 3):23-33.

Fernandez, X., G. Monin, A. Talmont, J. Mourot, and B. Lebret. 1999a. Influence of intramuscular fat content on the quality of pig meat- 1. Composition of the lipid

fraction and sensory characteristics of m. longissimus lumborum. Meat. Sci. 53:59-65.

Fernandez, X., G. Monin, A. Talmont, J. Mourot, and B. Lebret. 1999b. Influence of intramuscular fat content on the quality of pig meat- 2. Consumer acceptability of m. longissimus lumborum. Meat. Sci. 53: 67-72.

Fontana, E. A., W. D. Weaver Jr., B. A. Watkins and D. M. Denbow. 1992. Effect of early feed restriction on growth, feed conversion and mortality in broiler chickens. Poult. Sci. 71:1296-1305.

Fortin, A., W. M. Robertson, and A. K. W. Tong. 2005. The eating quality of Canadian pork and its relationship with intramuscular fat. Meat Sci. 69:297-305.

Gardener, M., E. Huff-Lonergan, and S. M. Lonergan. 2005. Prediction of fresh pork quality using indicators of protein degradation and calpain activation. 51st Int. Congr. Meat Sci. Technol. No. 51:1428-1434. Am. Meat Sci. Assoc., Baltimore, MD.

Gerbens, F., F. J. Verburg, H. T. B. Van Moerkerk, B. Engel, W. Buist, J. H. Veerkamp, and M. F. W. te Pas. 2001. Associations of heart and adipocyte fatty acid-binding protein gene expression with intramuscular fat content in pigs. J. Anim. Sci. 79:347-354.

Goll, D. E., V. F. Thompson, R. G. Taylor, and A. Ouali. 1992. The capain system and muscle growth. Can. J. Anim. Sci. 78:503-517.

Gondret, F., and B. Lebret. 2002. Feeding intensity and dietary protein level affect adipocyte cellularity and lipogenic capacity of muscle homogenates in growing

pigs, without modification of the expression of sterol regulatory element binding protein. J. Anim. Sci. 80:3184-3193.

Gondret, F., and L. Lefaucheur, H. Juin, I. Louveau, and B. Lebret. 2006. Low birth weight is associated with enlarged muscle fiber area and impaired meat tenderness of the longissimus muscle in pigs. J. Anim. Sci. 84:93-103.

Goransson, A., G. von Seth, and E. Tornberg. 1992. The influence of intramuscular fat content on the eating quality of pork. Pages 245-248 Proc. 38th Int. Congr. Meat Sci. Technol., Clermont-Ferrand, France.

Hancock, J. D., R. H. Hines, C. G. Mills, and D. A. Nichols. 1994. Effect of nursery diets on growth of pigs to market weight. J. Anim. Sci. 72(Suppl. 2):64 (Abstr.)

Hayden, J. M., J. E. Williams, and R. J. Collier. 1993. Plasma growth hormone, insulin-like growth factor, insulin, and thyroid hormone association with body protein and fat accretion in steers undergoing compensatory gain after dietary energy restriction. J. Anim. Sci. 71:3327-3338.

Hendel, S. E., and N. C. Stickland. 1988. Catch-up growth in pigs: A relationship with muscle cellularity. Anim. Prod. 47:291-295.

Heyer, A., and B. Lebret. 2007. Compensatory growth response in pigs: Effects on growth performance, composition of weight gain at carcass and muscle levels, and meat quality. J. Anim. Sci. 85:769-778.

Hicks, R. B., F. N. Owens, D. R. Gill, J. J. Martin and C. A. Strasia. 1990. Effects of controlled feed intake on performance and carcass characteristics of feedlot steers and heifers. J. Anim. Sci. 68:233-244.

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.

Hornick, J. L., C. Van Eenaeme, A. Clinquart, M. Diex and L. Istasse. 1998a. Different periods of feed restriction before compensatory growth in Belgian Blue bulls: I. Animal performance, nitrogen balance, meat characteristics and fat composition. J. Anim. Sci. 76:249-259.

Hornick, J. L., C. Van Eenaeme, A. Clinquart, M. Diex and L. Istasse. 1998b. Different periods of feed restriction before compensatory growth in Belgian Blue bulls: I. Plasma metabolites and hormones. J. Anim. Sci. 76:260-271.

Horton, G. M. J., and W. Holmes. 1978. Compensatory growth by beef cattle at grassland or on an alfalfa-based diet. J. Anim. Sci. 46:297-303.

Huff-Lonergan, E., T. Mitsuhashi, D. D. Beekman, F. C. Parrish, Jr., D. G. Olson, and R. M. Robson. 1996. Proteolysis of specific muscle structural proteins by micro-calpain at low pH and temperature is similar to degradation in postmortem bovine muscle. J. Anim. Sci. 74:993-1008.

Hyun, Y., M. Ellis, G. Bressner, and D. Baker. 2002. Effect of dietary leucine levels on carcass composition, meat quality, and growth performance in finishing pigs. Available: http://www.traill.uiuc.edu/porknet/paperDisplay.cfm?ContentID=126. Accessed Nov. 1, 2007.

Johnston, J. D., Moody, W. G., Boling, J. A. and Bradley, N. W. 1981. Influence of breed type, sex, feeding systems, and muscle bundle size on bovine fiber type characteristics. J. Food Sci. 46: 1760-1765.

Jones, S. J., D. L. Starkey, C. R. Calkins, and J. D. Crouse. 1990. Myofibrillar protein-turnover in feed-restricted and realimented beef-cattle. J. Anim. Sci. 68:2707-2715.

Jones, S. D. M., W. M. Robertson, and S. Talbot. 1992. Marbling standards for beef and pork. Agric. and Agri-Food Canada Pub. No. 1879/E, Ottawa, ON.

Karlsson, A. H., R. E. Klont, X. Fernandez. 1999. Skeletal muscle fibres as factors of pork quality. Livestock Production Science. 60:255-269.

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

Kerth, C. R., A. A. Helm, D. L. Kuhlers, L. B. Cagle, L. K. Blair-Kerth, W. R. Jones. 2001. Relationship between muscle fiber type and pork quality traits of pigs selected for leanness and growth efficiency. J. Anim. Sci. 79(Suppl. 1):18. (Abstr.)

Koohmaraie, M. 1996. Biochemical factors regulating the toughening and tenderization processes of meat. Meat Sci. 43:193-201.

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.

Kuhn, G., C. Rehfeldt, M. Hartung, and K. Edner. 2002. Heavy new-born piglets develop a high carcass quality. Fleichwirtsch. 82:128-129.

Kyriazakis, I., and G.C. Emmans. 1991. Diet selection in pigs: dietary choices made by growing pigs following a period of underfeeding with protein. Anim. Prod. 52:337-346.

Kyriazakis, I., C. Statmaris, G.C. Emmans, and C. T. Whittemore. 1991. The effects of food protein content on the performance of pigs previously given foods with low or moderate protein content. Anim. Prod. 52:165-172.

Kristensen, L., M. Therkildsen, M. D. Aaslyng, N. Oksbjerg, and P. Ertbjerg. 2004. Compensatory growth improves meat tenderness in gilts but not in barrows. J. Anim. Sci. 82:3617-3624.

Kristensen, L., M. Therkildsen, B. Riis, M. T. Sorensen, N. Oksbjerg, P. P. Purslow, and P. Ertbjerg. 2002. Dietary-induced changes of muscle growth rate in pigs: Effects on in vivo and post-mortem muscle proteolysis and meat quality. J. Anim. Sci. 80:2862-2871.

Lametsch, R., L. Kristensen, M. R. Larsen, M. Therkildsen, N. Oksbjerg, and P. Ertbjerg. 2006. Changes in the muscle proteome after compensatory growth in pigs. J. Anim. Sci. 84:918-924.

Lawrence, T. L. J., and V. R. Flower. 1997. Growth of Farm Animals. CAB International, Wallingford.

Lan, Y. H.., F. K. Mckeith, J. Novakofski, and T. R.Carr. 1993. Carcass and Muscle characteristics of Yorkshire, Meishan, Yorkshire×Meishan, Meishan×Yorkshire, Fengjing×Yorkshire, and Minzhu×Yorkshire pigs. J. Anim. Sci. 71:3344-3349.

Leach, L., M. Ellis, D. S. Sutton, F. K. McKeith, E. R. Wilson. 1996. The growth performance, carcass characteristics, and meat quality of Halothane carrier and negative pigs. J. Anim. Sci. 74, 934-943.

Lovatto, P. A., and D. Sauvant, J. Noblet, S. Dubois and J. van Milgen. 2006. Effects of feed restriction and subsequent refeeding on energy utilization in growing pigs. J. Anim. Sci. 84:3329-3336.

Lowrey, R. S., W. G. Pond, R. H. Barnes, L. Krook, and J. K. Loosli. 1962. Influence of caloric level and protein deficiency in the young pig. J. Nutr. 78:245-252.

Lonergan, S. M., E. Huff-Lonergan, L. J. Rowe, D. L. Kuhlers, and S. B. Jungst. 2001. Selection for lean growth efficiency in Duroc pigs influences pork quality. J. Anim. Sci. 79:2075-2085.

Lonergan, S. M., and K. J. Prussa. 2002. Sensory and instrumental analysis of the textural parameters of pork. Pages 33-38 in Recip. Meat Conf. Post Conf. Symp.: Pork Quality Measurement Systems. Am. Meat Sci. Assoc., Savoy, IL.

Mayes, P. A. 2000. Biosynthesis of fatty acids. Pages 230-237 in Harper's Biochemistry. 25th ed. R. K. Murray, D. K. Granner, P. A. Mayes, and V. W. Rodwell, ed. McGraw-Hill, New York.

Maynard, L.A., J. K. Loosli, H. F. Hintz, and R. G. Warner. 1979. Animal Nutrition. 7th ed. McGraw-Hill Book Company, New York.

Mc Meekan, C. P. 1940. Growth and development in the pig, with special reference to carcass quality characters. III. Effect of plane of nutrition on the form and composition of the bacon pig. J. Agr. Sci. (Camb.) 30:511-516.

McNeel, R. L., and H. J. Mersmann. 2000. Nutritional deprivation reduces the transcripts for transcription factors and adipocyte-characteristic proteins in porcine adipocytes. J. Nutr. Biochem. 11:139-146.

Mersmann, H. J., W. G. Pond, and J. T. Yen. 1982. Plasma glucose, insulin and lipids
during growth of genetically lean and obsess swine. Growth 46:189-198.

Morgan, J. H. L. 1972. Effect of plane of nutrition in early life on subsequent live-weight
gain, carcass and muscle characteristics and eating quality of meat in cattle. J.
Agri. Sci. (Camb). 78:417-423.

Moser, B. D. 1977. Feeding animal fat to growing and finishing pigs. Feedstuffs
49(15):20-39.

Mróz, Z., A. Lipiec, C. Wenk, and M. Kronauer. 1987. The effects of birth weight and
dietary lysine between 21 and 84 days of age on the subsequent performance of
pigs to 225 days of age. Livest. Prod. Sci. 17:351-363.

Mule, H. R., L. I. Chiba, J. Fabian, D. L. Kuhlers, S. B. Jungst, L. T. Frobish, K.
Nadarajah, W. G. Bergen, and E. G. Welles. 2006. Effect of early dietary amino
acid restrictions on serum metabolites in pigs selected for lean growth efficiency.
Can. J. Anim. Sci. 86:489-500.

Mule, H. R. 2001. The effect of early dietary amino acid restrictions on serum
metabolites in pigs selected for lean growth efficiency. M. S. Thesis, Auburn
Univ., Auburn University, AL.

NRC. 1998. Nutrient Requirements of Swine. 10th ed. Natl. Acad. Press, Washington, DC.

NPPC, 1991. Procedures to Evaluate Market Hogs. 3rd ed. Natl. Pork Prod. Council, Des
Moines, IA.

NPPC. 2000. Pork Composition and Quality Assessment Procedures. Natl. Pork Prod.
Council, Des Moines, IA.

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Oksbjerg, N., M. T. Sorensen, and M. Vestergaard. 2002. Compensatory growth and its effects on muscularity and technological meat quality in growing pigs. Acta Agric. Scand. Sect. A-Anim. Sci. 52:85-90.

Osborne, T. B. and Mendel. L. B. 1916. Acceleration of growth after retardation. Am. J. Physiol. 40:16.

Owen, J. B., W. F. Ridgman, and D. Wyllie. 1971. The effect of food restriction on subsequent voluntary intake of pigs. Anim. Prod.13:537-543.

Plavnik, I., and S. Hurwitz. 1985. The performance of broiler chicks during and following a severe feed restriction at an early age. Poult. Sci. 64:348.

Plavnik, I., and S. Hurwitz. 1991. Response of broiler chickens and turkey pouts to food restriction of varied severity during early life. Br. Poul. Sci. 32:343.

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.

Pond, W. G., H. J. Mersmann, and L. D. Young. 1986. Heritability of plasma cholesterol and triglyceride concentration in swine. Proc. Soc. Exp. Biol. Med. 182:221-224.

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 H. J. Mersmann. 1990. Differential compensatory growth in swine following control of feed intake by a high-alfalfa diet fed ad libitum or by limited feed. J. Anim. Sci. 68:352-362.

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.

Ramsey, C. B., L. F. Tribble, C. Wu, and K. D. Lind. 1990. Effects of grains, marbling and sex on pork tenderness and composition. J. Anim. Sci. 68:148-154.

Resurreccion, A. V. A. 2004. Sensory properties and preferences. Meat Sci. 36:67-77.

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

Rompala, R. E., S. D. M. Jones, J. G. Buchanan-Smith, and H. S. Bayley. 1985. Feedlot performance and composition of gain in late-maturing steers exhibiting normal and compensatory growth. J. Anim. Sci. 61:637-646.

Ryan, W. J. 1990. Compensatory growth in cattle and sheep. Nutr. Abstr. Rev. 60:653-664.

Santra, A., and N. N. Pathak. 1999. Nutrient utilization and compensatory in crossbred (Bos indicus×Bos taurus) calves. J. Anim. Sci. 73:2971-2979.

Seideman, S. C. and J. D. Crouse. 1986. The effects of sex condition, genotype and diet on bovine muscle fiber characteristics. Meat Sci. 17: 55-72.

Seideman, S. C., M. Koohmaraie, and J. D. Crouse. 1987. Factors associated with tenderness in young beef. Meat Sci. 21: 281-291.

Shackelford, S. D., M. Koohmaraie, L. V. Cundiff, K. E. Gregory, G. A. Rohrer, and J. W. Savell. 1994. Heritabilities and phenotypic and genetic correlations for bovine postrigor calpastatin activity, intramuscular fat content, Warner-bratzler shear force, retail product yield, and growth rate. J. Anim. Sci. 72:857-863.

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Stamataris, C., G. M. Hillyer, C. T. Whittemore, G. C. Emmans, A. G. Taylor, and P. Phillips. 1985. Performance and body composition of young pigs following a period of growth retardation by food restriction. Anim. Prod. 40:536. (Abstr.)

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. 39:712-718.

Steel, R. G. D., and J. H. Torrie. 1980. Principles and Procedures of Statistics: A Biometrical Approach. (2nd Ed.). McGraw-Hill Book Co., New York.

Taylor, St. C. S., H. G. Turner and G. B. Young. 1981. Genetic control of equilibrium maintenance efficiency in cattle. Anim. Prod. 33:170-194.

Therkildsen, M., B. Riis, A. Karlsson, L. Kristensen, P. Ertbjerg, P. P. Purslow, M. D. Aaslyng, and N. Oksbjerg. 2002. Compensatory growth response in pigs, muscle protein turnover and meat texture: Effects of restriction/realimentation period. Anim. Sci. 75:367-377.

Therkildsen, M., M. Vestergard, H. Busk, M. Jensen, B. Riis, A. Karlsson, L. Kristensen, P. Ertbjerg, and N. Oksbjerg. 2004. Compensatory growth in slaughter pigs-In vitro muscle protein turnover at slaughter, circulating IGF-I, performance and carcass quality. Livest. Prod. Sci. 88:63-75.

Tokach, M. D., J. E. Pettigrew, L. J. Johnston, M. Overland, J. W. Rust, S. G. Cornelius. 1995. Effect of adding fat and(or) milk products to the weanling pig diet on

performance in the nursery and subsequent grow-finish stages. J. Anim. Sci. 73:3358-3368.

Tudor, G. D., and P. K. O' Rourke. 1980. The effect of pre and post-natal nutrition on the growth of beef cattle. II. The effect of severe restriction in early post-natal life on growth and feed efficiency during recovery. Aust. J. Agric. Res. 31:179-189.

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

van Laack, R. L. J. M., S. G. Stevens, and K. J. Stalder. 2001. The influence of ultimate pH and intramuscular fat content on pork tenderness and tenderization. J. Anim. Sci. 79:392-397.

Vaughan, O. W., L. J. Filer, and H. Churella. 1962. Influence of prior dietary protein levels on resistance to stress of protein depletion. Pediatrics 29:90-96.

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

Warkup, C. C., and A. J. Kempster. 1991. A possible explanation of the variation in tenderness and juiciness of pig meat. Anim. Prod. 52:559. (Abstr.).

Warkup, C. C., A. W. Dilworth, A. J. Kempster and J. D. Wood. 1990. The effects of sire type, company source, feeding regimen and sex on eating quality of pig meat. Anim. Prod. 50:550.

Whang, K. Y., S. M. Donovan, and R. A. Easter. 2000a. Effect of protein deprivation on subsequent efficiency of dietary protein utilization in finishing pigs. Asian Austr. J. Anim. Sci. 13:659-665.

Whang, K. Y., F. K. McKeith, S. W. Kim, and R. A. Easter. 2000b. Effect of starter

    feeding program on growth performance and gains of body components from

    weaning to market weight in swine. J. Anim. Sci. 78:2885-2895.

Whang, K. Y., S. W. Kim, S. M. Donovan, F. K. McKeith, and R. A. Easter. 2003.

    Effects of protein deprivation on subsequent growth performance, gain of body

    components, and protein requirements in growing pigs. J. Anim. Sci. 81:705-716.

Wheeler, T. L., and M. Koohmaraie. 1992. Effects of the b-adrenergic agonist $L_{644, 969}$ on

    muscle protein turnover, endogenous proteinases activities, and meat tenderness

    in steers. J. Anim. Sci. 70:3035-3043.

Whittemore, C. T., J. B. Tullis, and S. W. Hastie. 1978. Efficiency of use of nitrogen

    from dried microbial cells after a period of N deprivation in growing pigs. Br. J.

    Nutr. 39:193-200.

Wigmore, P. M. C., and N. C. Stickland. 1983. Muscle development in small and large

    pig fetuses. J. Anat. 137:235-245.

Wilson, P. N. and D. F. Osbourn, 1960. Compensatory growth after undernutrition in

    mammals and birds. Biol. Rev. 35:324.

Wolter, B. F., and M. Ellis. 2001. The effects of weaning weight and rate on growth

    immediately after weaning on subsequent pig growth performance and carcass

    characteristics. Can. J. Anim. Sci. 81:363-369.

Wolter, B. F., and M. Ellis, B. P. Corrigan, and J. M. DeDecker. 2002. The effect of birth

    weight and feeding of supplemental milk replacer to piglets during lactation on

    pre-weaning and post weaning growth performance and carcass characteristics. J.

    Anim. Sci. 80:301-308.

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 growth in relation to feed intake and efficiency. J. Anim. Sci. 70:1049-1059.

Wood, J. D., G. R. Nute, R. I. Richardson, F. M. Wittington, A. M. Perry, S. P. Johnson, and M. Enser. 1996. Effects of breed, feed level, and conditioning time on the tenderness of pork. Meat Sci. 44:105-112.

Wood, J. D., G. R. Nute, R. I. Richardson, A. V. Fisher., M. M. Campo, and P. R. Kasapidou. 2003. Effects of fatty acids on meat quality: A review. Meat Sci. 66:21-32.

Wood, J. D., G. R. Nute, R. I. Richardson, F. M. Whittington, O. Southwood, and G. Plastow, R. Mansbridge, N. da Costa, and K. C. Chang. 2004. Effects of breed, diet and muscle on fat deposition and eating quality in pigs. Meat Sci. 67:651-667.

Wykes, L. J., M. Fiorotto, D. G. Burrin, M. del Rosario, M. E. Frazer, W. G. Pond, and F. Jahoor. 1996. Chronic low protein intake reduces tissue protein synthesis in a pig model of protein malnutrition. J. Nutr. 126:1481-1488.

Wyllie, D., V. C. Speer, R. C. Ewan, and V. W. Hays. 1969. Effects of starter protein level on performance and body composition of pigs. J. Anim. Sci. 29:433-438.

Yambayamba, E. S. K., M. A. Prince, and V. W. Hays. 1969. Effects of starter protein level on performance and body composition of pigs. J. Anim. Sci. 29:433-438.

Yu, M. E., and F. E. Robinson. 1992. The application of short-term feed restriction to broiler chicken production: a review. J. Appl. Poult. Res. 1:147.

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

Zubair, A. K., and S. Leeson. 1994. Effect of varying period of early nutrient restriction
on growth compensation and carcass characteristics of male broilers. Poult. Sci.
73:129.

APPENDICES

**Appendix A**: Principle of the Total protein Analysis (Roche Diagnostics, Indianapolis, IN)

Under alkaline conditions, divalent copper in the biuret reagent reacts with protein peptide bonds to form the characteristic purple-colored biuret complex:

Alkaline solution

Protein + Cu^{2+} $\longrightarrow$ Cu-protein complex
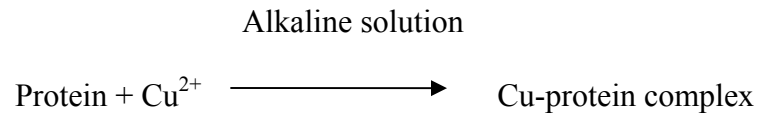
The color intensity is directly proportional to the protein concentration, which can be measured photometrically.

Appendix B: Principle of the Urea nitrogen Analysis (Roche Diagnostics, Indianpolis, IN)

Urea is hydrolyzed by urease to form CO_2 and ammonia:

$$\text{Urea} + H_2O \xrightarrow{\text{Urease}} 2\ NH_4^+ + CO_2$$
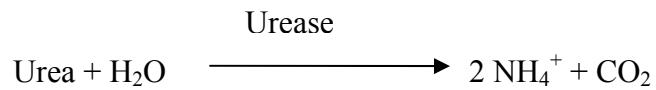
The ammonia formed then reacts with α-ketoglutarate and NADH in the presence of GLDH to yield glutamate and NAD^+:

$$\alpha\text{-ketoglutarate} + NH_4^+ + NADH \xrightarrow{\text{GLDH}} \text{L-glutamate} + NAD^+ + H_2O$$
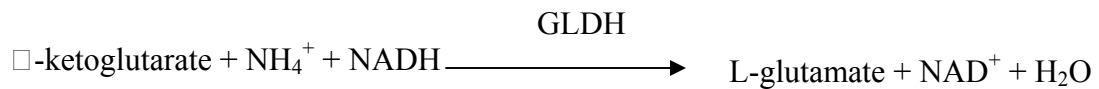
The decrease in absorbance due to consumption of NADH is measured kinetically.

Appendix C: Principle of the Albumin Analysis (Roche Diagnostics, Indianapolis, IN)

It is a colorimetric assay with endpoint method. At a pH of 4.1, albumin displays a

sufficiently cationic character to be able to bind with bromocresol green (BCG), an anionic

dyestuff to form a blue-green complex:

$$\text{Albumin + BCG} \xrightarrow{\text{pH 4.1}} \text{albumin BCG complex}$$
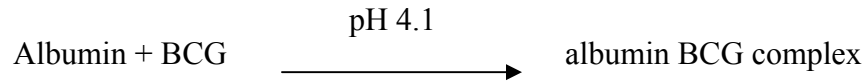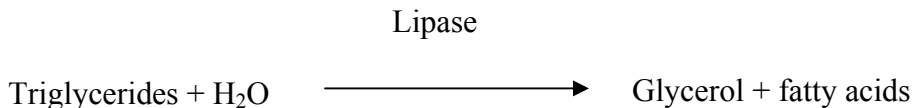
The color intensity of the blue-green color is directly proportional to the albumin

concentration and can be measured photometrically.

Appendix D: Principle of the Triglyceride Analysis (Diagnostic chemicals Ltd., Oxford. CT)

Serum triglycerides are hydrolyzed to glycerol and free fatty acids by lipase:

$$\text{Triglycerides} + H_2O \xrightarrow{\text{Lipase}} \text{Glycerol} + \text{fatty acids}$$

In the presence of ATP and glycerol kinase (GK), the glycerol is phosphorylated to glycerol-1-phosphate:

$$\text{Glycerol} + \text{ATP} \xrightarrow{\text{GK, Mg}^{++}} \text{Glycerol-1-phosphate} + \text{ADP}$$
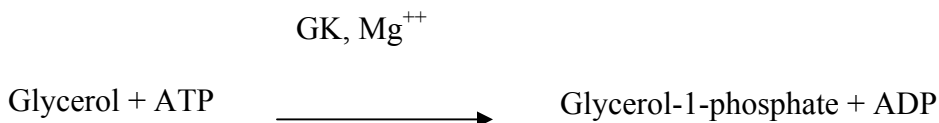
Glycerol-1-phosphate is then oxidized by glycerol phosphate oxidase (GPO) to yield hydrogen peroxide (H_2O_2):

$$\text{Glycerol-1-phosphate} + O_2 \xrightarrow{\text{GPO}} H_2O_2 + \text{dihydroxyacetone phosphate}$$
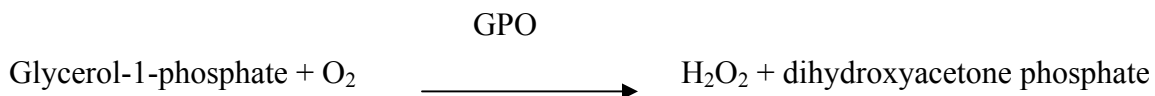
The hydrogen peroxide causes oxidative coupling of p-chlorophenol and 4-aminoantipyrine, producing a red colored quinoneimine dye complex:

$$H_2O_2 + \text{p-cholorophenol} + \text{4- aminoantipyrine} \xrightarrow{\text{Peroxidase}} \text{quinoneimine dye} + H_2O_2$$

The increase in absorbance at 520 nm due to the formation of the quinoneimine dye is directly proportional to the concentration of triglycerides in the sample.

Appendix E: Principle of Cholesterol Analysis (Roche Diagnostics, Indianpolis, IN)

Cholesterol is determined enzymatically using cholesterol esterase and cholesterol oxidase as follows. Cholesterol esters are cleaved by the action of cholesterol esterase to yield free cholesterol and fatty acids:

$$\text{Cholesterol esters} + H_2O_2 \xrightarrow{\text{Cholesterol esterase}} \text{Cholesterol} + \text{RCOOH}$$
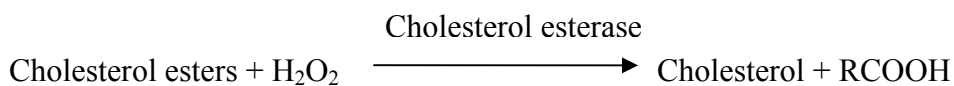
Cholesterol is converted by oxygen with the aid of cholesterol oxidase to cholest-4-en-3-one and hydrogen peroxide:

$$\text{Cholesterol} + O_2 \xrightarrow{\text{Cholesterol oxidase}} \text{Cholest-4-en-3-one} + H_2O_2$$

The hydrogen peroxide created forms a red dyestuff by reacting with 4-aminophenazone and phenol under the catalytic action of peroxidase:

$$2H_2O_2 + \text{4-aminophenazone} + \text{phenol} \xrightarrow{\text{Peroxidase}} \text{4-(p-benzoquinonemonoimino)-phenazone} + 4H_2O$$
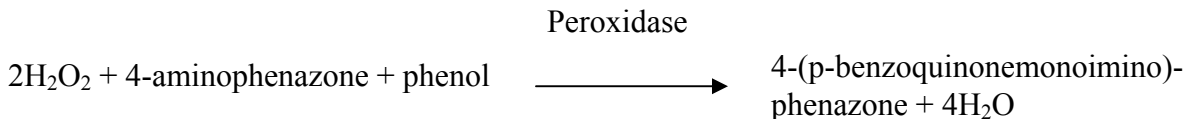
The color intensity is directly proportional to the concentration of cholesterol and can be determined photometrically.

Appendix F: Principle of Glucose Analysis (Diagnostic Chemicals Ltd)

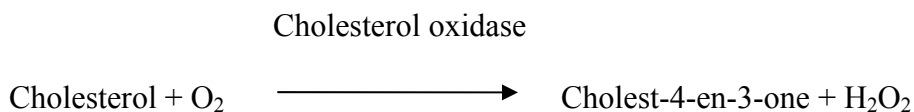Glucose is phosphorylated to hexokinase in the presence of adenosine triphosphate (ATP) and magnesium to form glucose-6-phosphate (G-6-P)

$$\text{Glucose + ATP} \xrightarrow{\text{Hexokinase, Mg2}^+} \text{Glucose-6-phosphate + ADP}$$
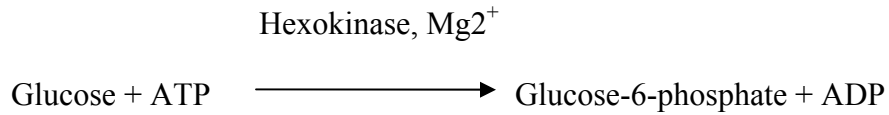
G-6-P is then oxidized by glucose-6-phosphate dehydrogenase (G-6-PDH) in the presence of nicotinamide adenine dinucleotide (NAD^+) producing 6-phosphogluconate and NADH:

$$\text{Glucose-6-phosphate + NAD}^+ \xrightarrow{\text{G-6-PDH}} \text{6-phosphogluconate + NADH + H}^+$$
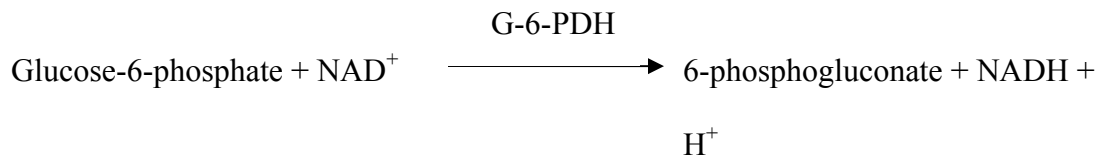
The formation of NADH causes an increase in absorbance at 340 nm which is directly proportional to the concentration of glucose in the sample.

Appendix G. Minimum and Maximum daily temperatures (°C) during the animal study[1]
Table 1. Daily minimum and maximum temperatures inside the building during the animal study

Date	Min. T	Max. T	Date	Min. T	Max. T	Date	Min. T	Max. T
8-Nov	-2.2	20.0	15- Dec	4.4	13.3	13- Jan	-2.2	22.2
9-Nov	-2.2	14.4	16- Dec	-4.4	12.2	14- Jan	-2.2	22.2
10-Nov	0	24.4	17- Dec	-3.3	17.7	15- Jan	-0.5	13.8
11-Nov	5.0	25.6	18- Dec	2.2	13.3	16- Jan	-1.1	3.8
12-Nov	5.6	20.0	19- Dec	10.0	18.8	17- Jan	1.1	6.1
13-Nov	5.6	25.6	20- Dec	7.7	16.6	18- Jan	0	8.8
14-Nov	5.6	27.8	21- Dec	6.6	12.7	19- Jan	-7.7	1.1
15-Nov	6.7	20.0	22- Dec	6.6	8.8	20- Jan	-7.2	8.8
16-Nov	-	-	23- Dec	-2.7	16.6	21- Jan	-0.5	12.7
17-Nov	-	-	24- Dec	2.2	11.7	22- Jan	5.0	10.0
18-Nov	-	-	25- Dec	3.3	10.0	23- Jan	5.5	14.4
19-Nov	7.2	25.6	26- Dec	5.0	14.4	24- Jan	-7.7	11.1
20-Nov	6.7	28.9	27- Dec	8.3	13.8	25- Jan	0	4.4
21-Nov	8.9	23.3	28- Dec	11.6`	20.0	26- Jan	-1.6	7.7
22-Nov	1.1	16.7	29- Dec	11.6	16.6	27- Jan	-3.3	20.5
23-Nov	1.1	17.8	30- Dec	1.1	11.1	28- Jan	1.1	18.8
24-Nov	0.6	11.1	31- Dec	2.2	18.8	29- Jan	-2.2	18.8
25-Nov	7.2	11.1	1- Jan	-5.5	15.5	30- Jan	-2.2	17.7
26-Nov	4.4	17.8	2- Jan	-	-	31- Jan	3.3	11.1
27-Nov	-2.2	20.0	3- Jan	-	-	1-Feb	-3.3	16.6
28-Nov	7.8	22.2	4- Jan	-1.6	13.3	2- Feb	1.1	20.5
29-Nov	4.4	27.2	5- Jan	3.8	15.5	3- Feb	5.0	21.6
30-Nov	5.6	23.3	6- Jan	7.2	24.4	4- Feb	11.1	23.8
1-Dec	8.9	21.1	7- Jan	11.1	24.4	5- Feb	13.8	22.7
2- Dec	8.9	21.1	8- Jan	13.8	20.5	6- Feb	-1.1	20.5
11- Dec	20.0	22.2	9- Jan	14.4	20.0	7- Feb	-1.1	18.8
12- Dec	20.0	23.3	10- Jan	10.0	18.8	8- Feb	1.6	22.2
13- Dec	20.0	23.3	11- Jan	0.5	22.2	9- Feb	-0.5	26.6
14- Dec	10.0	25.5	12- Jan	1.1	22.2	10-Feb	1.1	26.6

Date	Min. T	Max. T	Date	Min. T	Max. T	Date	Min. T	Max. T
11- Feb	6.6	22.7	28- Feb	-2.7	15.0	16- Mar	7.7	28.3
12- Feb	3.8	21.1	29- Feb	6.1	16.1	17- Mar	10.0	22.2
13- Feb	-7.2	5.5	1- Mar	3.3	27.7	18- Mar	10.5	23.3
14- Feb	-1.1	18.8	2- Mar	7.7	24.4	19- Mar	3.3	16.6
15- Feb	4.4	18.8	3- Mar	8.8	22.2	20- Mar	2.2	23.8
16- Feb	10.0	19.4	4- Mar	1.1	22.7	21- Mar	3.8	22.7
17- Feb	6.1	20.0	5- Mar	-0.5	22.2	22- Mar	2.7	28.8
18- Feb	-2.2	20.5	6- Mar	8.8	23.3	23- Mar	-2.2	22.7
19- Feb	-1.1	21.1	7- Mar	-	-	24- Mar	-4.4	17.2
20- Feb	6.6	24.4	8- Mar	-	-	25- Mar	-1.6	17.2
21- Feb	5.5	8.8	9- Mar	-	-			
22- Feb	10.0	13.3	10- Mar	-	-			
23- Feb	-1.1	21.1	11- Mar	-	-			
24- Feb	2.2	25.5	12- Mar	-	-			
25- Feb	12.7	16.6	13- Mar	7.7	22.7			
26- Feb	1.1	13.3	14- Mar	7.7	24.4			
27- Feb	-7.7	10.0	15- Mar	5.5	28.3			

[1]Missing data were not included. Min. T = minimum temperature. Max. T = maximum temperature.

Table 2. Mean minimum and maximum temperatures

Month	Minimum temperature	Maximum temperature
November	4.0	21.1
December	6.8	16.3
January	1.1	12.8
February	2.8	19.1
March	4.4	23.4
Mean	3.4	17.8