Early Dietary Amino acid Restrictions and Flaxseed Oil Supplementation on the Leanness of Pigs and Quality of Pork: Growth Performance, Serum Metabolites, and Carcass Characteristics

by

Chhabi Kiran Adhikari

A thesis submitted to the Graduate Faculty of
Auburn University
in partial fulfillment of the
requirements for the Degree of Master of Science

Auburn, Alabama
May 3, 2014

Keywords: amino acid restrictions, compensatory growth, dietary lipids, growth performance, serum metabolites, carcass traits

Approved by

Lee I. Chiba, Chair, Professor of Nutrition
Werner G. Bergen, Professor of Biochemistry and Nutrition
Christy L. Bratcher, Associate Professor of Meat Science
Daryl L. Kuhlers, Professor of Swine Breeding and Genetics

Abstract

By taking advantage of compensatory growth, carcass fat can be reduced to satisfy consumer demands and intramuscular fat (IMF) can be increased to enhance organoleptic characteristics pork simultaneously. The beneficial effects of IMF can be enhanced further if its increase can be achieved by omega-3 fatty acids (ω-3 FA) supplementation, which can also reduce lipogenesis. In addition, compensatory growth can improve the overall efficiency of nutrient utilization and economic efficiency, and minimize adverse impacts of pig production on the environment. Therefore, using the concept of compensatory growth and dietary supplementation of flaxseed oil, which is high in the ω-3 FA, to address the pork quality issue can contribute greatly to successful and sustainable pig production.

A total of 64 pigs (2 gilts or 2 barrows/pen) were used to investigate the effect of early dietary amino acid (AA) restrictions [100 or 80% of the 2012 NRC standardized ileal digestible (SID) Lys requirements during the grower and finisher-1 phases] and flaxseed oil supplementation [0 or 3% (+ 2% poultry fat)] in a 2 x 2 factorial arrangement of treatments on grower-finisher pigs. At 24.7 ± 0.5 kg, pigs were assigned to 4 grower diets with 4 gilt pens and 4 barrow pens/treatment, and switched to finisher-1 diets when they reached 51.2 ± 0.3 kg. Pigs were switched to common finisher-2 diets at 80.0 ± 0.4 kg, and those received 0 or 5% lipids during the grower and finisher-1 phases were continued to receive 0 or 5% lipids. Ultrasound backfat measurements and blood samples were collected at the end of the grower, finisher-1, and finisher-2 phases, and pigs were harvested at 110.5 ± 0.5 kg. The results of growth performance, serum metabolite profile, and carcass traits are reported in this monograph.

Pigs fed the AA restricted diets consumed less SID Lys and digestible energy (DE; $P < 0.015$), and had slightly depressed average daily gain (ADG) compared with non-restricted pigs during the grower phase, but they grew faster ($P = 0.042$) and utilized feed numerically and SID Lys ($P < 0.001$) more efficiently during the finisher-1 phase. Dietary AA restrictions had no effect on any of the response criteria during the finisher-2 phase, overall ADG, or carcass traits. The efficiency of overall feed, SID Lys, and DE utilization for body weight (BW) gain ($P < 0.004$) and SID Lys utilization for fat-free lean gain ($P < 0.001$) was improved by the AA restrictions. Dietary AA restrictions reduced serum urea N ($P < 0.025$) at the end of the grower and finisher-1 phases and increased glucose ($P = 0.027$) at the end of the grower phase, but had no clear effect on other metabolites. Dietary lipids reduced feed intake during the grower ($P = 0.007$) and finisher-2 ($P = 0.064$) phases, improved gain:feed (G:F) during all phases and overall ($P < 0.047$), and improved ADG during the grower ($P = 0.003$) and finisher-1 ($P = 0.066$) phases. Belly firmness was reduced ($P < 0.001$), but there was no other effect of dietary lipids on carcass traits. Dietary lipids increased serum triglycerides at the end of the grower ($P = 0.075$) and finisher-1 ($P = 0.001$) phases, but reduced ($P = 0.037$) urea-N at the end of the finisher-2 phase. Dietary lipids increased serum cholesterol in pigs fed the unrestricted diets but had no effect on pigs fed the AA restricted diets at the end of the finisher-1 phase (AA restrictions x lipids, $P = 0.029$). The dietary treatment had no effect on ultrasound backfat thickness. In conclusion, as expected, dietary lipids improved G:F but reduced belly firmness. Dietary AA restrictions during the grower and finisher-1 phases had no effect on overall BW gain or carcass traits but improved overall efficiency of AA and DE utilization for BW gain and fat-free lean gain.

Acknowledgment

I would like to express my sincere gratitude and appreciation to my major professor, Dr. Lee I. Chiba, for his teaching, supervision, and guidance throughout the graduate program. I would like to express my gratitude to Dr. Werner G. Bergen, Dr. Christy L. Bratcher, and Dr. Daryl L. Kuhlers for their willingness to serve on the advisory committee and their support, encouragement, and constructive advice. I would like to thank all the faculty and staff of the Department of Animal Sciences, Swine Research and Education Center, and Lambert-Powell Meats Laboratory for their support and inputs throughout the program. I would also like to expresses deep appreciation to the fellow graduate students who helped me along the way through both my research and graduate program.

Table of Contents

List of Tables

I. Introduction

Satisfying the consumer demand by improving the quality and organoleptic characteristics of pork is an integral part of successful and sustainable pig production. Unfortunately, the effort to satisfy consumer demands by supplying lean pork in recent years has resulted in the reduction of intramuscular fat (**IMF**), which has adverse effects on organoleptic characteristics of pork (Cisneros et al., 1996). Increasing the IMF content of pork, while maintaining the leanness of pigs, would benefit consumers greatly because IMF may not only improve eating quality, but may have beneficial effects on human health. And, this potential can be enhanced even further by increasing IMF through dietary supplementation of omega-3 fatty acids (ω-3 FA; Simopoulous, 2001; Corino et al., 2002) because of the direct deposition of dietary fatty acids into body tissues. In addition, de novo lipogenesis can be reduced by dietary fatty acids.

By taking advantage of compensatory growth, carcass fat can be reduced (Chiba, 1994) to satisfy consumer demands and IMF can be increased to enhance eating quality of pork (Fortin et al., 2005) simultaneously. In addition, pigs subjected to early dietary restrictions can utilize nutrients more efficiently, have better carcass traits, and reduce N excretion (Chiba 1995; Chiba et al, 1999; Fabian et al., 2004), which can have a positive impact on the environment. In today's animal production, it is important to alleviate public concerns on the environmental issues. Thus, by using the concept of compensatory growth and supplementing diets with ω-3 FA, it is possible to increase, not only the overall efficiency of pig production, but also the leanness of pigs and IMF and ω-3 FA contents of pork. Furthermore, adverse impacts of pig production on the environment can be minimized by taking advantage of compensatory growth by reducing the excretion of unused nutrients. In addition, elucidating fundamental cellular mechanisms associated with lipid metabolism further by using contemporary molecular technology is crucial in achieving our ultimate research goal to make contributions to the development of environmentally friendly, optimum feeding strategies for successful and sustainable pig production.

As an initial study for this long-term, interdisciplinary project, grower-finisher pigs will be used to investigate the effect of early dietary amino acid (AA) restrictions during the grower and finisher-1 phases and supplementation of flaxseed oil on growth performance, serum metabolites, carcass characteristics, fatty acid content and composition of pork, physical and sensory characteristics of pork, and expression of selected genes associated with lipid metabolism. The hypothesis is that early dietary AA restrictions and flaxseed oil supplementation will result in complete compensatory growth, reduce carcass fat content of pigs, increase the IMF content of pork, increase the ω-3 FA content of pork, and enhance organoleptic characteristics of pork. Alterations in the efficiency of nutrient utilization, lipogenesis, and(or) carcass traits should be reflected in blood metabolite profile and expression of genes associated with lipid metabolism. Therefore, it is also hypothesized that early dietary AA restrictions and flaxseed oil supplementation will induce clear metabolic alterations, which will be reflected in blood metabolites and expression patterns of selected genes associated with lipid metabolism.

II. Literature Review

Compensatory Growth

Introduction

Compensatory growth and catch-up growth are used interchangeably, though the latter seems to be more precise as compensatory growth might be misleading in terms of compensation for the lost part or function (Yu and Robinson, 1992). Hornick et al. (2000) defines compensatory growth (or catch-up growth) as a physiological process by which an organism accelerates its growth after a period of restricted development to reach the weight of contemporary animals, in which growth was never reduced. However, compensatory growth might be affected by age of the animal, severity and duration of restriction, genotype, sex, and quality and duration of realimentation (Wilson and Osbourne, 1960). The concept of compensatory growth has been discussed for a long time. According to Wilson and Osbourne (1960), compensatory growth was documented as far back as in 1908 when nutritionally restricted cattle offered a nutritious diet were able to reach mature height and weight. Osbourne and Mendel (1916) reported that restricted rats could attain greater growth after removal of restriction. Later, the term “compensatory growth” was coined by Bohman (1955). Since then, many studies have been conducted and many data supported the concept of compensatory growth in most farm animals with increased production efficiency, increased carcass lean, reduced excretion of unused nutrients, which could have positive impact on the environment.

Compensatory Growth in Pigs

Compensatory growth has been reported in cattle (Horton and Holmes, 1978; Rompala et al., 1985; Hayden et al., 1993), sheep (Ryan, 1990; Kamalzadeh et al., 1997), poultry (Wilson and Osbourne, 1960 Moran, 1979; Plavnik and Hurwitz, 1991), and also in pigs (Robinson, 1964; Zimmerman and Khajarern, 1973; Mersmann et al., 1987). Several studies have been successful in demonstrating that compensatory growth occurs in pigs (Chiba, 1994; Chiba et al., 1999; Chiba et al., 2001; Fabian et al., 2002; Fabian et al., 2004; Heyer and Lebret, 2007; Kamalakar et al., 2009). The pigs exhibiting compensatory growth utilized the nutrients efficiently (Chiba, 1995; Chiba et al., 2001; Heyer and Lebret, 2007; Kamalakar et al., 2009), thus, reduced the excretion of unused N (Fabian et al., 2004), and perhaps other nutrients.

Early dietary amino acid (AA) restrictions and realimentation have been shown to improve the leanness of pigs (Chiba, 1995; Chiba et al., 1999; Fabian et al., 2002; Fabian et al., 2004; Kamalakar et al., 2009), implying that compensatory growth may have a negative impact on organoleptic characteristics of pork. It has been shown, however, that feeding protein-deficient diets can actually increase intramuscular fat (IMF; Castel et al., 1994; Kerr et al., 1995; 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. Although the exact relationship between early dietary AA restrictions and IMF has not been elucidated, metabolism of ketogenic branched-chain AA (Cisneros et al., 1996; Hyun et al., 2002) and(or) the rate of lean tissue growth (Warkup and Kempster, 1991; Blanchard et al., 1999) may be responsible for the increase in the IMF content of pork in pigs subjected to early dietary restrictions.

Possible Mechanisms of Compensatory Growth

Clear mechanism behind compensatory growth is still to be elucidated but there have been many hypotheses that try to explain the mechanism of compensatory growth in animals. Some of those hypotheses include the increased efficiency of nutrient utilization, increased feed intake, reduced maintenance requirements, increased efficiency of nutrient utilization, and altered hormonal status and gene expression.

Increased Efficiency of Nutrient Utilization. Ryan et al. (1993) studied compensatory growth in cattle and sheep and reported that efficiency of feed utilization was a key to compensatory growth. They measured the compensatory growth of cattle and sheep after their nutrition had been restricted sufficiently to induce losses in body weight. The growth, feed intake, and feed conversion efficiency measured during re-alimentation was compared to control animals fed ad libitum throughout the study. Ryan et al. (1993) concluded that the accelerated growth in compensating cattle and sheep compared to the control animals was possible because of the increased feed conversion efficiency without any difference in feed intake. In the experiment that the pigs were fed the low-AA diet from 20 to 50 kg grew rapidly during 50 to 100 kg, Chiba (1994) showed the dietary restricted pigs utilized feed more efficiently than the unrestricted pigs. Similarly, Fabian et al. (2004) reported that the pigs fed low-AA diets utilized N more efficiently than the pigs fed high-AA diets. In that study, pigs that were fed low-AA grower diet had a greater N utilization in finisher-1 and finisher-2 phases compared to the pigs that were previously fed the high-AA grower diet, thus excreting less urinary N during the finisher-1 and finisher-2 phases. Better utilization of AA or AA deficient diets might be due to reduced A A oxidation or sparing effect of AA (Chiba et al.,1991).

Increased Feed Intake and Digesta Load. Graham and Searle (1975) studied the effect of compensatory growth in weaned sheep by restricting feed for a long period of time. They reported the greater feed intake of restricted sheep compared to the non-restricted sheep as a key factor responsible for the compensatory growth during the realimentation period. Similar results were also reported by Ryan (1990) in cattle and sheep. Some authors suggested that the greater feed intake might result in greater nutrient intake, which might be responsible for the compensatory growth. Critser et al., (1995) reported that the pigs exhibiting compensatory growth during re-alimentation phase had greater feed intake, resulting in greater protein intake in restricted pigs compared to the pigs fed ad libitum, which might be responsible for the greater weight gain. However, some researchers indicated that the digesta load, rather than feed intake, would be more specific contributing factor for the compensatory growth (Carstens et al., 1991; Hornick et al., 1998b). The increased feed intake or the digesta load during re-alimentation, thus contribute to the compensatory growth by increasing the size of the digestive system, modifying endocrine system (Hornick et al., 2000), and increasing the protein deposition.

Reduced Maintenance Requirements. Yambayamba et al. (1996) observed reduced heat production in steers, which gradually increased after re-alimentation, indicating that such decreased maintenance requirements can contribute to the increased gain observed in compensatory growth. Koong et al., (1983) measured fasting heat production in the pigs at the end of the 70-day period of the experiment after fasting all pigs for 30 hours. The authors reported that the pigs fed highly nutritious diets had greater fasting heat production along with heavier metabolically active internal organs compared with pigs fed lower plane of nutrition. The fasting heat production indicates heat loss associated with maintenance (Campbell et al., 1983). Ferrel (1988) reported that 20 to 25% of total energy expenditures of the body can be attributed to energy expenditures of the liver and gastrointestinal tract. Thus, the reduction in maintenance energy during the restriction phase may allow for more energy for growth after realimentation, which can contribute to the compensatory growth.

Action of Hormones. The effects of growth hormone (**GH**), insulin, and insulin-like growth factor-1 (**IGF-1**) have been studied extensively in the animals during restriction and re-alimentation. Hornick et al. (1998b) reported that a greater nutrient supply to Belgian bulls during compensatory growth increased the concentration of anabolic hormones such as plasma thyroxine and IGF-1, allowing rapid muscle deposition. Hornick et al. (2000) suggested that high concentrations of insulin stimulates the uptake of metabolites by the hypothalamus, leading to a decrease of the production and secretion of GH, indicating a sharp decrease of the ratio GH to insulin as one of the characteristics of compensatory growth. Yambayamba et al. (1996) reported that the IGF-I concentration was low due to insensitivity of hepatic and extra hepatic tissues, inspite of the elevated plasma GH concentration during the feed restriction. They further concluded that uncoupling of the GH-IGF-1 axis is important in compensatory growth, as it is involved in protein synthesis and growth of the animals. In another study, Therkildsen et al. (2003) observed that feed restricted pigs had a lower serum level of IGF-I at the end of the grower period compared to ad libitum-fed pigs**.** And, they further reported that the transition from restricted feeding to ad libitum feeding, GH was reduced, and insulin and IGF-I increased gradually. On the other hand, other reports indicated that GH concentration is actually increased during the early stage of the realimentation phase, rather than decrease in GH concentration. For instance, Więcek et al. (2011) reported increase of the GH concentration in early days of re-alimentation of pigs as an indication of compensatory growth.

Gene Expression. McNeel and Mersmann (2000) observed the reduced concentration of transcript factors in the adipose tissue of pigs fasted for 72 hours along with reduced concentration of several proteins and genes involved in adipocyte energy metabolism. Similarly, da Costa et al. (2004) applied phenotypically divergent skeletal muscles of pigs (psoas and longissimus dorsi) to porcine skeletal muscle cDNA microaary to profile the molecular changes with the dietary restriction. They reported that the restricted diet increased the expression of genes involved in breakdown of glycogen, fatty acids, and proteins. Lametsch et al. (2006) studied the changes in the muscle proteome after compensatory growth in pigs and reported that intensity of markers of protein synthesis and glycolytic potential (HSC70, HSP27, enolase 3, glycerol-3-phosphate dehydrogenase, aldehyde dehydrogenase E2, aldehyde dehydrogenaseE3, and biphosphoglydrate mutase) differed between compensated pigs and control pigs.

Dietary Lipids

Dietary Lipids and Lipogenesis

Triglyceride synthesis can be accomplished with fatty acids resulting from de novo lipogenesis or directly from the diet. Over the years, several investigators have reported the reduction of de novo lipogenesis in pigs by dietary fatty acids (e.g., Allee et al., 1971a,c; Chillard. 1993; Smith et al., 1996; Azain, 2001). Allee et al. (1971b) and Smith et al. (1996) demonstrated that de novo lipogenesis was reduced by dietary lipids regardless of the type. In those studies, the activity of lipogenic enzymes, such as fatty acid synthase, stearoyl-CoA-desaturase, citrate cleavage enzyme, malic enzyme, glucose-6-phosphate dehydrogenase, and 6-phosphogluconate dehydrogenase, was also reduced (Allee et al., 1971a,b,c; Wolfe et al., 1977; Kouba et al., 2003). It is likely that the increased plasma free FA concentration can lead to a negative feedback of acetyl-CoA on accetyl-CoA carboxylase, which is the most limiting enzyme in the de novo FA synthesis, thus resulting in the reduced de novo lipogenesis (Mayes, 2000).

Depending on the dietary energy status of the animal (Jakobsen and Thorbek, 1993; Bee et al., 2002), dietary lipids can reduce de novo lipogenesis from carbohydrates or induce direct deposition of dietary fat. When a sufficient amount of "non-lipid" energy is available, dietary fat would not be used as a source of energy by the pig. Obviously, body fat would be increased by excess dietary energy or fatty acids. If the animal is not consuming adequate energy or is on a high-fatty acid diet, de novo lipogenesis would be reduced. With an appropriate combination of dietary energy and fat, therefore, it is possible to reduce de novo lipogenesis to increase leanness of pigs. Typical corn-soybean meal diets contain a sufficient amount of energy for optimum protein accretion in growing pigs. According to the review of many studies (Moser, 1977), it seems that body fat can be reduced by including up to 5% fat in the pig diet, but more than 5% dietary fat is likely to reduce the leanness of grower-finisher pigs.

Dietary lipids and Omega-3 Fatty Acid Supplementation

It is apparent that de novo lipogenesis can be reduced by dietary lipids, and it is possible that the ω-3 FA content of pork can be increased by dietary supplementation of ω-3 FA. Again depending on the energy status of animals, dietary fatty acids can be deposited directly into body tissues without much transformation. Such a concept is supported by some studies showing that the pattern of dietary fatty acids was reflected in carcass fat (e.g., Brooks, 1971; Morgan et al., 1992; Wiseman and Agunbial, 1998; Averette Gatlin et al., 2002).

Supplementation of the pig diet with ω-3 FA can lead to the increased IMF rich in ω-3 FA, again, because of the direct deposition of dietary fatty acids into body tissues. It has been well-demonstrated that ω-3 FA, especially, eicosapentaenoic acid (**EPA**) and docosahexaenoic acid (**DHA**) that are high in fish oil, have beneficial effects on human health such as the development of brain (Bourre, 2005), prevention of cardiovascular diseases (Vandobgen et al., 1993; Psota et al., 2006; Paschos et al., 2007; Ueshima et al., 2007), cancers

(Rose and Connolly, 1999), and psychiatric disorders (Bourre, 2005), and protection of bones (Sun et al., 2003; Watkins et al., 2003; Griel et al., 2007).

During the human evolution, hunter-gatherer diets may have provided a balanced intake of ω-6 and ω-3 FA, perhaps, in a ratio of 1:1 (Speake and Surai, 2004), but in the Western world, this ratio may be as high as 20:1 (Simopoulos, 1999). The ratio can be reduced by increasing the consumption of fish or taking fish oil supplement. However, the intake of fatty fish is rather low in Western societies and considering the potential of contaminated fish because of water pollution in recent years and a fishy taste associated with the supplement, increasing the intake of ω-3 FA through terrestrial animal products, such as meat and eggs, would be very important (Howe et al., 2006; Haak et al., 2008; Missotten et al., 2009). It is necessary to appreciate, however, that de novo fatty acid synthesis in pigs occurs only in adipose tissues, while much of the understanding is based on both hepatic and adipose tissue metabolism (Bergen and Mersmann, 2005).

Flaxseed Oil

Flaxseed (or linseed) oil contains high proportion of "linolenic acid (53 to 58% of total fatty acids; Romans et al., 1995a; Dugan et al., 2004), and it is converted to long-chain ω-3 FA such as EPA, docosapentaenoic acid (DPA), and even DHA (Romans et al., 1995a; Fontanillas et al., 1998; Kouba et al., 2003; Wiecek and Skomial, 2004; Harper et al., 2006). Although polyunsaturated fatty acids may be considered to be "healthy," they may reduce shelf-life and sensory traits of meat because of oxidation (Bryhni et al., 2002; Haak et al., 2008). Lipid oxidation has been identified as a major problem in the effort to enhance the ω-3 FA content of pork by dietary manipulation (e.g., Romans et al., 1995b; Bryhni et al., 2002; Wood et al., 2003). The results of some studies indicated that up to 4.1%, or even up to 6.15%, flaxseed oil

(Maddock et al., 2005) may not have any adverse effects on growth performance or carcass traits (Romans et al., 1995a; Patience et al., 2005). However, the optimal amount in pig diets seems to be 3% flaxseed oil according to the results of some studies (Hoz et et al., 2003; Pieszka et al., 2005; Lu et al., 2008; Boudry et al., 2009).

Pork Quality

The important aspect of pork quality is sensory quality, which is usually assesses by evaluating tenderness, juiciness, flavor, and overall acceptability. The other aspect of pork quality is technical or physical quality that includes marbling, color, pH, shear force, firmness of fat, and composition of fat (Heyer and Lebret, 2007). Feeding strategy has proven to be important for controlling overall meat quality in pork (Anderson et al., 2005). The other factors contributing to eating quality of pork may be breed (van Laack et al., 2001), IMF content (Goransson et al., 1992), rate of pH decline (Gardner et al., 2005), and muscle fiber type as determined by the proportion of different muscle fibers (Karlssen et al., 1999).

Sensory Quality

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). Blanchard et al. (1999) suggested that the best eating quality of pork, in terms of tenderness, juiciness, and overall acceptability, can be attained through feeding protein deficient diets. 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 can influence 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). Kristensen et al. (2004) later found that pork from re-alimented gilts had improved tenderness compared with the control, whereas pork from re-alimented castrated males was not affected. Many authors suggested that the link between the rate of protein degradation in living muscles and tenderness development postmortem may be through proteolytic system of calpains (e.g., Shackelford et al., 1994).

Effect of Intramuscular Fat on Sensory Attributes

A positive eating experience of pork depends on several attributes such as tenderness, flavor, and juiciness. Bejerholm and Barton-Grade (1986) proposed a minimum of 2% IMF to ensure satisfactory eating experience. Similarly, 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. Recently, Fortin et al. (2005) proposed that the threshold level of IMF that will ensure a pleasing eating experience is 1.5%. The effect of IMF content on the sensory quality of pork is, however, not consistent, even when other known sources of sensory quality variation are under control (Goransson et al., 1992). Lonergan and Prusa (2002) demonstrated negative relationships between the IMF content and objective measures of textural integrity. Blanchard et al. (2000) found no effect of IMF content on juiciness, tenderness, or overall acceptability. Nevertheless, Fernandez et al. (1999a) demonstrated that increasing the IMF content above approximately 2.5% enhanced flavor and juiciness. Juiciness, which depends on the moisture content of meat and saliva released during mastication, is enhanced by IMF because it stimulates production of saliva (Asghar and Pearson, 1980). The flavor arises from water and lipid soluble components and their degradation products such as aldehydes, alcohols, and ketones (Asghar and Pearson, 1980).

Consumer Acceptability of Pork

The pork industry 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). Hence, an appropriate amount of IMF in pork can enhance the eating quality and consumer acceptability of pork.

Technological Quality of Pork

Many studies indicated that the quality traits of pork such as pH, drip loss, and color and pigment were not affected by feed restriction and realimentation. Heyer and Lebret (2007) did not find any differences in drip loss and shear force between pork from pigs fed restrictively and ad libitum. Similar results were reported by several authors (Oksberg et al., 2002; Fortin et al., 2005; Chaosap et al., 2011). However, Wood et al. (1996) found a greater drip loss (22%) when the pigs were fed ad libitum compared with those fed restrictively. Similarly, Fischer (2007) reported the drip loss was increased by 18% when the pigs were fed ad libitum during the finishing period.

Summary

For the pig industry to be successful, it is essential to satisfy the consumers. The consumer satisfaction can be achieved at the point of purchase, as well as at the point of consumption. The consumer's demand for leaner pork has forced the pig industry to make effort to reduce the carcass fat of pigs. Unfortunately, the effort to produce lean carcass resulted in the reduced IMF content of pork. Carcass fat can be reduced to satisfy the consumer demands and IMF can be increased to enhance eating quality of pork simultaneously by taking advantage of compensatory growth. Besides improving eating quality of pork, IMF may have beneficial effects on human health, and this potential can be enhanced even further if its increase can be achieved by supplementation of the pig diet with ω-3 FA because of the direct deposition of dietary lipids into body tissues. Furthermore, dietary lipids can reduce de novo lipogenesis, and compensatory growth can improve the overall efficiency of nutrient utilization and economic efficiency and minimize adverse impacts of pig production on the environment. Therefore, using the concept of compensatory growth and dietary supplementation and flaxseed oil, which is high in the ω-3 FA content, to address the pork quality issue can contribute greatly to successful and sustainable pig production.

References

Allee, G. L. D. H. Baker, and G. A. Leveille. 1971a. Fat utilization and lipogenesis in the young pig. J. Nutr. 101:1415-1422.

Allee, G. L. D. H. Baker, and G. A. Leveille. 1971b. Influence of level of dietary fat on adipose tissue lipogenesis and enzymatic activity in the pig. J. Anim. Sci. 33:1248-1254.

Allee, G. L. E. K. O'Hea, G. A. Leveille, and D. H. Baker. 1971c. Influence of dietary protein and fat on lipogenesis and enzymatic activity in pig adipose tissue. J. Nutr. 101:869-878.

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

Averette Gatlin, L., M. T. See, J. A. Hansen, D. Sutton, and J. Odle. 2002. The effects of dietary fat sources, levels, and feeding intervals on pork fatty acid composition. J. Anim. Sci. 80:1606-1615.

Azain, M. J. 2001. Fat in swine nutrition. In: A. J. Lewis, and L. L. Southern, editor, Swine nutrition. 2nd ed. CRC Press, Boca Raton, FL. p. 95-105

Bee, G., S. Gebert, and R. Meissikommer. 2002. Effect of dietary energy supple and fat source on the fatty acid pattern of adipose and lean tissues and lipogenesis in the pig. J. Anim. Sci. 80:1564-1574.

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.

Bejerjolm, C., and P. Barton-Gade. 1986. Effect of intramuscular fat level on eating quality of pig meat. Manuscript no. 720 E. Danish Meat Research Institute, Roskilde, Denmark.

Bergen, W. G. and H. J. Mersmann. 2005. Comparative aspects of lipid metabolism: impact on contemporary research and use of animal models. J. Nutr. 135:2499-2502.

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

Boudry, Gaelle, V. Douard, J. Mourot, J.-P. Lalles, and I. Le Huerou-Luron. 2009. Linseed oil in the maternal diets during gestation and lactation modifies fatty acid composition, mucosal architecture, and mast cell regulation of the ileal barrier in piglets. J. Nutr. 139:1110-1117.

Bourre, J. M. 2005. Where to find omega-3 fatty acids and how feeding animals with diets enriched in omega-3 fatty acids to increase nutritional value of derived products for human:what is actually useful? J. Nutr. Health Aging 9:232-242.

Brooks, C. C. 1971. Fatty acid composition of pork lipids as affected by basal diet, fat source and fat level. J. Anim. Sci. 33:1224-1231.

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

Bryhni, E. A., N. P. Kjos, R. Pfstad, and M. Hunt. 2002. Polyunsaturated fat and fish oil in diets for growing-finishing pigs: effects on fatty acid composition and meat, fat, and sausage quality. Meat Sci. 62:1-8.

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.

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.

Chaosap C., T. Parr, and J. Wiseman 2011. Effect of compensatory growth on performance, carcass composition and plasma IGF-1 in grower finisher pigs. Animal 5:749–756.

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

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

Chiba, L. I. 2000. Feeding systems for pigs. In: M. Theodorou and J. France, editors, Feeding systems and feed evaluation Models. CABI Publishing, Wallingford, UK. p. 189-209.

Chiba, L. I. 2001. Protein supplements. In: A. J. Lewis, and L. L. Southern, editors, Swine nutrition. 2nd ed. CRC Press, Boca Raton, FL. p. 803-837.

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 acids and energy interrelationships in pigs weighing 20 to 50 kilograms. I. Rate and efficiency of weight gain. J. Anim. Sci. 69:694-707.

Chillard, Y. 1993. Dietary fat and adipose tissue metabolism in ruminants, pigs, and rodents: A review. J. Dairy Sci. 76:3897-3931.

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..

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.

DeVol, D. L., F.K.McKeith, P. J. Bechtel, J. Novakofski, R. D. Shanks, and T. R. Carr. 1988. Variation 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

Dugan, M. E. R., J. L. Aalhus, W. M. Robertson, L. L. Gibson, D. C. Rolland, and I. L. Larsen. 2004. Feeding flax seed to pigs: effects on pork fatty acid composition and palatability. Adv. Pork Prod. 15. Abstr. #14.

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.

Fabian, J., L. I. Chiba, D. L. Kuhlers, L. T. Frobish, K. Nadarajah, and W. H. McElhenny. 2003. Growth performance, dry matter and nitrogen digestibilities, serum profile, and carcass and meat quality of pigs with distinct genotypes. J. Anim. Sci. 81:1142-1149.

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.

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

Fischer, K. 2007. Drip loss in pork influencing factors and relation to further meat quality traits. J. Anim. Breed. & Genetics 124:12-18.

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

Fontanillas, R., A. Barroeta, M. D. Baucells, and F. Guardiola. 1998. Backfat fatty acid evolution in swine fed diets high in either cis-monounsaturated, trans, or (n-3) fats. J. Anim. Sci. 76:1045-1055.

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.

Gardner, G. E., D. W. Pethick, P. L. Greenwood, and R. S. Hegarty. 2005. The effect of genotype and plane of nutrition on the rate of pH decline in lamb carcasses and the expression of metabolic enzymatic markers. Crop and Pasture Sci. 57:661-670.

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.

Graham, NMcC, and T. W. Searle. 1975. Studies of weaner sheep during and after a period of weight stasis: Energy and nitrogen utilization. Crop Pasture Sci. 26: 343-353.

Griel, A. E., P. M. Kris-Etherton, K. F. Hilpert, G. Zhao, S. G. West, and R. L. Corwin. 2007. An increase in dietary n-3 fatty acids decreases a marker of bone resorption in humans. Nutr. J. 6:2-10.

Haak, L. S. De Smet, D. Fremaut, K. Van Walleghem, and K. Raes. 2008. Fatty acid profile and oxidative stability of pork as influenced by duration and time of dietary linseed oil or fish oil supplementation. J. Anim. Sci. 86:1418-1425.

Harper, C. R., M. J. Edwards, A. P. DeFilippis, and T. A. Jacobson. 2006. Flaxseed oil increases the plasma concentrations of cardioprotective (n-3) fatty acids in humans. J. Nutr. 136:83-87

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.

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.

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.

Hornick, J.L., C. Van Eenaemea, O. Gérarda, I. Dufrasneb, and L. Istassea. 2000. Mechanisms of reduced and compensatory growth. Domestic Anim. Endocrinol. 19:121-132.

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.

Hoz, L., C. L. Lopez-Bote, M. I. Cambero, M. D'Arrigo, C. Pin, C. Santos, and J. A. Ordonez.

2003. Effect of dietary linseed oil and α-tocopherol on pork tenderloin (*Psos major*) muscle. Meat Sci. 65:1039-1044.

Howe, P., B. Meyer, S. Record, and K. Baghurst. 2006. Dietary intake of long-chain omega-3 polyunsaturated fatty acids: Contribution of meat sources. Nutr. 22:47-53.

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 1 November 2002.)

Jakobsen, K., and G. Thorbek. 1993. The respiratory quotient in relation to fat deposition in fattening-growing pigs. Br. J. Nutr. 69:333-343.

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.

Kamalakar, R. B., L. I. Chiba, K. C. Divakala, S. P. Rodning, E. G. Welles, W. G. Bergen, C. R. Kerth, D. L. Kuhlers, and N. Nadarajah. 2009. Effect of the degree and duration of early dietary amino acid restrictions on subsequent and overall pig performance and physical and sensory characteristics of pork. J. Anim. Sci. 87:3596-3606.

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

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.

Karlsson, A. H., R. E. Klont, and X. Fernandez. 1999. Skeletal muscle fibres as factors for pork quality. Livest. Prod. Sci. 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.

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.

Kouba, M. M. Enser, F. M. Whittington, G. R. Nute, and J. D. Wood. 2003. Efect of a high- linolenic acid diet on lipogenic enzyme activities, fatty acid composition, and meat quality in the growing pig. J. Anim. Sci. 81:1967-1979.

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.

Lu, P., L. Y. Zhang, J. D. Yin, A. K. R. Everts, and D. F. Li. 2008. Effects of soybean oil and linseed oil on fatty acid compositions of muscle lipids and cooked pork flavour. Meat Sci. 80:910-918

Maddock, T. D., V. L. Anderson, and G. P. Lardy. 2005. Using flax in livestock diets. AS-1283. NDSU Ext. Service and North Dakoda Agric. Exp. Sta., North Dakota State Univ., Fargo, ND.

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

McNeel, R. L., S.-T. Ding, E. O'Brian Smith, and H. J. Mersmann. 2000. Effect of feed restriction on adipose tissue transcript concentrations in genetically lean and obese pigs. J. Anim. Sci. 78:934-942.

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.

Missotten, J., S. De Smet, K. Raes, and O. Doran. 2009. Effect of supplementation of the maternal diet with fish oil or linseed oil on fatty-acid composition and expression of Δ5- and Δ6-desaturase in tissues of female piglets. Animal 3:1196-204.

Morgan, C. A., R. C. Noble, M. Cocchi, and R. McCartney. 1992. Manipulation of the fatty acid composition of pig meat lipids by dietary means. J. Sci. Food Agric. 58:357-368.

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

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.

Paschos, G. K., F. Magkos, D. B. Panagiotakos, V. Votteas, and A. Zampelas. 2007. Dietary supplementation with flaxseed oil lowers blood pressure in dyslipidaemic patients. Eur. J. Clin. Nutr. 61:1201-1206.

Patience, J. F., A. van Kessel, M. Drew, R. T. Zijlstra, P. Leterme, and A. D. Beaulieu. 2005. Response of growing pigs to graded levels of flaxseed. In: 2005 Annu. Res. Rep., Prairie Research Center, Saskatoon, SK, Canada. p. 24-26.

Pieszka, M., T. Barowicz, T. Migda, and B. Zivkowic. 2005. Effect of mono- and polyunsaturated fatty acids on muscle cholesterol level in fattening pigs. Biotechnol. Anim. Husbandry 21:49-54.

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

Psota, T. L., S. K. Gebauer, P. Kris-Etherton. 2006. Dietary omega-3 fatty acid intake and cardiovascular risk. Am. J. Cardiol. 98:3i-18i.

Resurreccion, A. V. A. 2004. Sensory aspects of consumer choices for meat and meat products. Meat Sci. 66:11-20.

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

Romans, J. R., D. M. Wulf, R. C. Johnson, G. W. Libal, and W. J. Cosello. 1995b. Effects of ground flaxseed in swine diets on pig performance and on physical and sensory characteristics and omega-3 fatty acid content of pork: II. Duration of 15% dietary flaxseed. J. Anim. Sci. 73:1987-1999.

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.

Rose, D. P., and J. M. Connolly. 1999. Omega-3 fatty acids as cancer chemopreventive agents. Pharm. Therapeutics 83:217-244.

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

Ryan, W. J., I. H. Williams, and R. J. Moir. 2003. Compensatory growth in sheep and cattle: Growth pattern and feed intake. Crop and Pasture Sci. 44:1609-1621.

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

Simopoulos, A. P. 1999. New products from agri-food industry: The return of n-3 FA into the food supply. Lipids 34(Suppl.):S297-S301.

Simopoulos, A. P. 2001. N–3 fatty acids and human health: Defining strategies for public policy. Lipids 36:S83–S89.

Smith, D. R., D. A. Knabe, and S. B. Smith. 1996. J. Anim. Sci. Depression of lipogenesis in swine adipose tissue by specific dietary fatty acids. J. Anim. Sci. 74:975-983.

Speake, B. K., and P. F. Surai. 2004. Omega-3 and -6 fatty acids. In: W. G. Pond and A. W. Bell, editors, Encyclopedia of animal science. Marcel Dekker, Inc., New York. p. 681-683.

Sun, D., A. Krishnan, K. Zaman, R. Lawrence, A. Bhattacharya, and G. Fernandez. 2003. Dietary n-3 fatty acids decrease osteoclastogenesis and loss of bone mass in ovariectomized mice. J. Bone Mineral Res. 18:1206-1216.

Ueshima, H., J. Stamler, P. Elliot, Q. Chan, I. J. Brown, M. R. Carnethon, M. L. Daviglus, K. He, A. Moag-Stahlberg, B. L. Rodriguez, L. M. Steffen, L. van Horn, J. Yarnell, and B. Zhou. 2007. Food omega-3 fatty acid intake of individuals (total, linolenic acid, long-chain) and their blood pressure: INTERMAP study. Hypertension 50:313-319.

Vandongen, R. T. A. Mori., V. Burke, L. J. Beilin, J. Morris, and J. Ritchie. 1993. Effects of blood pressure of omega 3 fats in subjects at increased risk of cardiovascular disease. Hypertension 22:371-379.

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.

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.)

Watkins, B. A., Y. Li, H. E. Lippman, and S. Feng. 2003. Modulatory effect of omega-3 polyunsaturated fatty acids on osteoblastic function and bone metablism. Prostgalindins Leukot Essential Fatty Acids 68:387-398.

Wiecek, J., A. Rekiel, and J. Skomial 2011.Effect of restricted feeding and realimentation periods on compensatory growth performance and physiological characteristics of pigs. Archives of Anim.l Nutri. 65, 34-45.

Wiecek, J., and J. Skomial. 2004. Restricted feeding and linseed oil as modifiers on the fatty acid profile in pork. J. Anim. Feed Sci. 13(Suppl. 2):43-46.

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

Wiseman, J. and J. A. Agunbiade. 1998. The influence of changes in dietary fat and oils on fatty acid profiles of carcass fat in finishing pigs. Livest. Prod. Sci. 54:217-227.

Wolfe, R. C., C. V. Maxwell, E. C. Nelson, and R. J. Johnson. 1977. Effect of dietary fat level on gorwth and lipogenesis in the colostrum deprived neonatal pig. J. Nutr. 2100-2108.

Wood, J. D., R. I. Richardson, G. R. Nute, A. V. Fisher, M. M. Campo, E. K. Kasapidou, P. R.

Sheard, and M. Enser. 2003. Effects of fatty acids on meat quality: a review. Meat Sci. 66:21-32.

Wood, J. D., S. N. Brown, G. R. Nute, F. M. Whittington, 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.

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. 1:147-153.

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. 73:129-136.

III. Early Dietary Amino acid Restrictions and Flaxseed Oil Supplementation on the Leanness of Pigs and Quality of Pork: Growth Performance, Serum metabolites, and Carcass Characteristics

Early dietary amino acid restrictions and flaxseed oil supplementation on the leanness of pigs and quality of pork: Growth performance, serum metabolites, and carcass characteristics[1]

C. K. Adhikari,* L. I. Chiba,*[2] S. D. Brotzge,* M. D. Vieira,* S. P. Rodning,* W. G. Bergen,* C. L. Bratcher,* and E. G. Welles†

*Department of Animal Sciences, College of Agriculture, and †Department of Pathobiology, College of Veterinary Medicine, Auburn University, AL 36849

---

[1]This research project was funded in part by Alabama Agricultural Experiment Station Hatch Funding Program. Technical assistance of B. Anderson, R. Britton, C. M. Lin, J. Pate and the staff at the Auburn University Poultry Research Farm, and B. Wilborn and his staff at the Auburn University Meat Laboratory is gratefully acknowledged.

[2]Corresponding author: chibale@auburn.edu

ABSTRACT: A total of 64 pigs (2 gilts or 2 barrows/pen) were used to investigate the effect of early dietary AA restrictions [100 or 80% of the 2012 NRC standardized ileal digestible (SID) Lys requirements during the grower (G) and finisher (F)-1 phases] and flaxseed oil supplementation [0 or 3% (+ 2% poultry fat)] in a 2 x 2 factorial arrangement of treatments on G-F pigs. At 24.7 ± 0.5 kg, pigs were assigned to 4 G diets with 4 gilt pens and 4 barrow pens/treatment, and switched to F-1 diets when they reached 51.2 ± 0.3 kg. Pigs were switched to common finisher-2 diets at 80.0 ± 0.4 kg, and those received 0 or 5% lipids during the G and F-1 phases were continued to receive 0 or 5% lipids. Ultrasound backfat measurements and blood samples were collected at the end of the G, F-1, and F-2 phases, and pigs were harvested at 110.5 ± 0.5 kg. The results of growth performance, serum metabolite profile, and carcass traits are reported in this monograph. Pigs fed the AA restricted diets consumed less SID Lys and DE ($P <$ 0.015), and had slightly depressed ADG compared with non-restricted pigs during the G phase, but they grew faster ($P = 0.042$) and utilized feed numerically and SID Lys ($P < 0.001$) more efficiently during the F-1 phase. Dietary AA restrictions had no effect on any of the response criteria during the F-2 phase, overall ADG, or carcass traits. The efficiency of overall feed, SID Lys, and DE utilization for BW gain ($P < 0.004$) and SID Lys utilization for fat-free lean gain ($P < 0.001$) was improved by the AA restrictions. Dietary AA restrictions reduced serum urea N ($P < 0.025$) at the end of the G and F-1 phases and increased glucose ($P = 0.027$) at the end of the G-phase, but had no clear effect on other metabolites. Dietary lipids reduced feed intake during the G ($P = 0.007$) and F-2 ($P = 0.064$) phases, improved G:F during all phases and overall ($P <$ 0.047), and improved ADG during the G ($P = 0.003$) and F-1 ($P = 0.066$) phases. Belly firmness was reduced ($P < 0.001$), but there was no other effect of dietary lipids on carcass traits. Dietary lipids increased serum triglycerides at the end of the G ($P = 0.075$) and F-1 ($P = 0.001$) phases,

but reduced (*P* = 0.037) urea-N at the end of the F-2 phase. Dietary lipids increased serum cholesterol in pigs fed the unrestricted diets but had no effect on pigs fed the AA restricted diets at the end of the F-1 phase (AA restrictions x lipids, *P* = 0.029). The dietary treatment had no effect on ultrasound backfat thickness. In conclusion, as expected, dietary lipids improved G:F but reduced belly firmness. Dietary AA restrictions during the grower and finisher-1 phases had no effect on overall BW gain or carcass traits but improved overall efficiency of AA and DE utilization for BW gain and fat-free lean gain.

Keywords: amino acid restrictions, compensatory growth, flaxseed oil, growth performance, carcass characteristics, 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 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 IMF and subcutaneous fat thickness (Jones et al., 1992), however, the IMF content can be increased while maintaining the leanness of pigs. Also, it is possible that IMF has some additional attributes on human health such as beneficial effects on low density lipoprotein-cholesterol and coronary heart disease (Baghurst, 2002), and such effects can be enhanced further if its increase can be achieved by omega-3 fatty acids (**ω-3 FA**; Davenel et al., 1999; Simopoulos, 2001; Corino et al., 2002).The results of previous studies indicated that pigs subjected to early dietary AA 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 and environment by reducing the excretion of unused nutrient. Moreover, carcass fat can be reduced to satisfy the consumer demand for leaner pork and the IMF content can be increased to enhance eating quality of pork simultaneously by taking advantage of compensatory growth.

Over the years, several investigators have reported that de novo lipogenesis in pigs can be reduced by dietary lipids (Allee et al., 1971a,b; Chillard. 1993; Smith et al., 1996; Lin et al., 2013). It seems that body fat can be reduced by including up to 5% lipids in the pig diet, but more than 5% dietary lipids is likely to reduce the leanness of grower-finisher pigs (Moser, 1977). It is possible that dietary supplementation of flaxseed oil, which is high in ω-3 FA, can enhance leanness of pigs, and it can also increase ω-3 FA content of pork. A study was conducted to investigate the effect of early dietary AA restrictions during the grower and finisher-1 phases and supplementation of flaxseed oil, which is high in ω-3 FA, on: a) compensatory growth, b) serum metabolite profile, c) carcass characteristics, d) IMF content, e) fatty acid composition, f) physical and sensory traits of pork, and g) expression of selected genes associated with lipid metabolism. In this article, the results of growth performance, serum metabolite profile, and carcass characteristics are reported, and other response criteria are reported elsewhere.

MATERIALS AND METHODS

The protocol for animal care was approved by the institutional Animal Care and Use Committee of Auburn University.

Animals and Facilities

A total of 64 pigs were selected and moved into an open-sided grower finisher unit. Pigs were assigned to 32 pens (> 1.35 m^2/pig) based on their weight, sex, and ancestry with 2 gilts or 2 castrated males per pen. The pens were assigned randomly to 4 dietary treatments in a 2 x 2 factorial arrangement of treatments with 4 gilt pens and 4 castrated male pens per treatment. Because the availability of pigs at one time was limited, the study was conducted in 2 trials. Each trial used 16 gilts and 16 castrated males, and 2 trials were approximately 4 wk apart. The average minimum and maximum daily temperature during the study were 7.9 and 19.3°C, respectively.

When the average pen weight reached 24.7 ± 0.5 kg, pigs were offered the grower diets. Pigs were switched to finisher-1 and finisher-2 diets when they reached 51.2 ± 0.3 and 80 ± 0.4 kg, respectively. Pigs fed 0 or 5% lipids during the grower and finisher-1 phases were continued to receive 0 or 5% dietary lipids during the finisher-2 phase. The pigs were slaughtered after overnight fasting when they reached the target weight of 110.5 ± 0.5 kg. Pigs were allowed ad libitum access to feed and water throughout the study. Pig weights and feed consumption data were collected weekly.

Dietary Treatments

A fundamental assumption of the dietary treatment was that Lys is the first-limiting AA in all diets. Diets were supplemented with 5% supplemental lipids (3% flaxseed oil + 2% poultry fat) to take advantage of inhibitory effect of dietary lipids on lipogenesis (Moser, 1977) and avoid potential adverse effects of excess flaxseed oil supplementation on pork characteristics (e.g., Romans et al., 1995; Bryhni et al., 2002; Wood et al., 2003). The chemical composition of corn and soybean meal and fatty acid composition of flaxseed oil and poultry fat are presented in Tables 1 and 2, respectively.

For the grower and finisher-1 phases, 2 corn-soybean meal diets were formulated to contain 100 or 80% of the standardized ileal digestible (**SID**) Lys recommendation (NRC, 2012), and each diet was supplemented with 0 or 5% lipids (3% flaxseed oil + 2% poultry fat; Table 3). For the finisher-2 phase, a common, corn-soybean meal diet was formulated to satisfy the SID Lys recommendation (NRC, 2012), and it was supplemented with 0% lipids or 3% flaxseed oil + 2% poultry fat (Table 4). The effort was not made to maintain a constant AA balance, but a proportion of each indispensable AA relative to Lys was above the balanced protein (NRC, 2012). Dietary Lys (and other AA), Ca, and P contents were adjusted according to changes in the DE content. Flaxseed oil and poultry fat samples were analyzed for the fatty acid composition (Cameron et al., 2000). Feed samples were collected from every batch of diets prepared and pooled, and subsamples were 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 grower, finisher-1, and finisher-2 phases using an ultrasound instrument (Lean-Meater; Renco, Minneapolis, MN). To assess metabolite profile, 10 mL of blood was collected from each pig via vena cava puncture using a sterile needle and syringe at the end of the grower, finisher-1, and finisher-2 phases. All blood samples were collected between 0800 and 1000 h after overnight fast. Blood samples were allowed to clot and centrifuged at 1,500 x *g* for 15 min at room temperature to obtain cleaner serum samples, and an aliquot was stored 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 Auburn University Clinical Pathology Laboratory (Chiba et al., 2002; Mule et al., 2006).

Harvest Procedures, Carcass Characteristics, and Sample Collection

At an average pen weight of 110 ± 3 kg, pigs were harvested at Auburn University Meat Laboratory using conventional procedures after 24-h fast. The eviscerated carcass was split longitudinally through the vertebrae midline, and HCW was recorded. After chilling for 24 h at 2°C, each carcass was weighed and LM of the right side was exposed by a perpendicular cut between the 10th and 11th ribs. Longissimus muscle was traced and backfat thickness at the 10th rib (about ¾ distance along the LM toward the belly) was measured. The exposed LM area was used to determine subjective meat quality scores (NPPC, 1991). The proportion of carcass lean and the rate of carcass lean accretion were estimated by equations reported by NPPC (2000).

After exsanguination, adipose and muscle tissue samples were taken immediately and frozen in liquid N, and stored at -80°C to determine the expression of selected genes associated with lipid metabolism. Also, a section of LM from the 10^{th} to 12^{th} rib was removed from each pig for the determination of the fat content, fatty acid composition, and physical and sensory characteristics of pork. Detailed procedures to achieve other objectives are presented accordingly elsewhere.

Statistical Analysis

The data were analyzed using the GLM procedure of SAS (SAS Inst. Inc., Cary, NC) and the pen was the experimental unit. Initially, treatment, sex, trial, and appropriate interactions, along with appropriate BW as a covariate or covariates, were included in the statistical model. The initial and final BW for growth performance data, appropriate BW for serum metabolite data, and final BW for the carcass data were initially considered as a covariate(s). The results indicated that trial and trial x treatment interactions were not an important source of variation, thus, those terms were removed from the final model. In addition, interactions and covariates that did not reach statistically significant trend ($P > 0.10$) were removed from the final model. The results are considered a statistically significant if $P \leq 0.05$ and a trend if $P \leq 0.10$.

RESULTS

Growth Performance

Grower Phase. There was no restriction x lipid supplementation on any of the response criteria. Feed intake of pigs was greater ($P = 0.015$) in non-restricted pigs compared to restricted pigs (Table 5). Similarly, feed intake of pigs fed the diets with lipids was less ($P = 0.007$ compared with those fed the diets without lipids. As expected, there was a reduction of Lys (SID Lys; $P < 0.001$) and DE intake ($P = 0.013$) in restricted pigs, but there was no effect of supplemental lipids on Lys or DE intake. The ADG in pigs was slightly depressed numerically by dietary AA restrictions, but the diets had no effect on ultrasound backfat thickness. Pigs fed the diets containing 5% lipids had greater ($P = 0.03$) ADG. Similarly, as expected, G:F was improved by dietary lipid supplementation. Because of their reduced Lys intake, restricted pigs utilized SID Lys more efficiently for BW gain compared to non-restricted pigs ($P < 0.001$).

Finisher-1 Phase. There was no restriction x lipid supplementation on any of the response criteria (Table 5). Although feed intake of pigs was not affected by dietary AA restrictions, SID Lys intake was reduced in pigs fed the restricted diets. Pigs subjected to dietary AA restrictions during the grower phase grew faster ($P = 0.042$), tended to have greater G: F numerically, and greater gain:Lys intake ($P < 0.001$) compared with non-restricted pigs.

Dietary AA restrictions, however, had no effect on ultrasound backfat thickness. Dietary lipid supplementation had no effect on ADFI, Lys intake, or DE intake, but ADG tended to be greater (P = 0.066) and G:F was greater (P < 0.047) in pigs fed the diets containing 5% lipids.

Finisher-2 Phase. No dietary AA restrictions x supplemental lipid interaction were observed in any of the response criteria (Table 5). There was no effect of dietary AA restrictions on ADFI, Lys intake, or DE intake. Similarly, there was no effect of dietary AA restrictions on the ADG or efficiency of feed, Lys, or DE utilization for BW gain. Dietary lipid supplementation tended to reduce (P = 0.064) ADFI and improved (P = 0.015) G:F, but it had no effect on Lys or DE intake or the efficiency of their utilization for BW gain. Similarly, there were no differences in ultrasound backfat thickness at the end of finisher-2 phase subjected to various treatments.

Grower-finisher Phase. As in the grower and finisher phases, there was no dietary restriction x supplementary lipid interaction in any of the response criteria during the grower-finisher phases. The ADG was not affected by dietary AA restrictions or supplemental lipids. The Lys intake was reduced (P < 0.001) and its utilization for BW gain was greater (P < 0.001) in restricted pigs compared with non-restricted pigs. Similarly, DE utilization for BW gain was better (P = 0.004) in restricted pigs compared with non-restricted pigs. The G:F was greater (P = 0.005) in pigs fed the AA restricted diets compared with those fed the non-restricted diets. As expected, pigs fed diets supplemented with lipid improved (P < 0.001) overall G:F compared with those fed the diets without lipids.

Serum Metabolites

Grower Phase. There was a trend for dietary AA restrictions x supplemental lipids (P = 0.078) in serum cholesterol at the end of the grower phase (Table 6). Serum cholesterol in pigs fed the non-restricted diets increased with 5% lipids, but it decreased in pigs fed the restricted diet with 5% lipids. As expected, serum urea N concentration during the grower phase was reduced (P = 0.007) by dietary AA restrictions, whereas serum glucose concentration was increased (P = 0.027) in restricted pigs. Serum triglycerides concentration tended to be greater (P = 0.075) in the pigs fed the diets with supplemental lipids compared with pigs fed the diets without lipids. Pigs fed the diets with 5% lipids tended to have serum triglycerides. The concentration of serum total protein and albumin was not affected by dietary AA restrictions or dietary lipids.

Finisher-1 Phase. There was an interaction (P = 0.029) in serum cholesterol. Serum cholesterol increased in pigs fed the non-restricted diet with 5% lipids, but it was not changed in pigs fed the restricted diet with dietary lipids. There was also a trend for an interaction (P = 0.001) in serum triglycerides. The increase in serum triglycerides by supplementation with 5% dietary lipids was much greater in pigs fed the non-restricted diet. Urea N concentration was significantly reduced ($P < 0.05$) in pigs fed the restricted diets compared with those fed the non-restricted diets. Serum total protein, albumin, and glucose concentrations were not affected by dietary treatments.

Finisher-2 Phase. There was no interaction, and dietary AA restrictions had no effect on any of the response criteria in serum metabolites at the end of the finisher-2 phase. Serum urea N (P = 0.037) and triglycerides (P = 0.018) concentrations were reduced in pigs fed the diets with lipids compared with pigs fed the diets without lipids. The treatments had no effect on serum total protein, albumin, glucose, and cholesterol concentrations**.**

Carcass Characteristics and Subjective Meat Quality Scores

There were no dietary AA restrictions x lipid supplementation on carcass characteristics, and the dietary treatment had no effects on 10th rib backfat thickness, LM area, fat-free lean percentage, and fat-free lean gain (Table 7). Dietary AA restrictions had no effect on fat-free lean gain:feed intake, but it increased (P < 0.001) the efficiency of Lys utilization for fat-free lean gain and tended to increase (P = 0.095) fat-free lean gain:DE intake. Dietary lipid supplementation had no effect on any of the response criteria.

There was a trend for dietary AA x lipid supplementation (P = 0.081) on muscling score. Muscling score in pigs fed the non-restricted diets seemed to increase with dietary lipids, but it seemed to decrease with dietary lipids in those fed the restricted diets. Belly firmness tended to be lower (P = 0.078) in pigs fed the non-restricted diets, and it was reduced (P < 0.001) by dietary lipids. There was no effect of dietary treatments on subjective meat color, firmness, or marbling score.

DISCUSSION

In the current study, the effect of early dietary AA restrictions during the grower and finisher-1 phases and lipid supplementation on compensatory growth, carcass characteristics, fatty acid content and composition of pork, physical and sensory characteristics of pork, and expression of genes associated with the lipid metabolism was investigated. Improving carcass quality and organoleptic characteristics of pork is an integral part of successful and sustainable pig production. The de novo lipogenesis can be reduced by dietary lipids (Smith et al., 1996; Lin et al., 2013) and carcass fat can be reduced by taking advantage of compensatory growth (Chiba, 1995; Chiba et al., 1999). In addition, the IMF and ω-3 FA contents of pork can be increased by supplementing diets with lipids high in ω-3 FA, such as flaxseed oil, and the IMF content of pork can be increased by compensatory growth. Thus, by using the concept of compensatory growth and supplementing diets with flaxseed oil, it is possible to increase, not only the overall efficiency of pig production, but also the leanness of pigs and IMF and ω-3 FA contents of pork. In this article, again, only the results on growth performance, serum metabolites, and carcass characteristics are reported.

During the grower phase, dietary AA restrictions during the grower phase depressed ADG only numerically, perhaps, because the dietary formulation was based on the SID Lys recommendation (NRC, 2012), and 80% of the SID Lys recommendation was, probably, not severe enough to clearly depress the growth performance. The feed intake of grower pigs fed the restricted diets was lower than those fed the non-restricted diets, which is different from other reports (Chiba, 1994; Kamalakar et al., 2009). This was, perhaps, due to lower feed intake of pigs fed the restricted diet with 5% lipids, even though there was no dietary AA restriction x supplemental lipid interaction. It had, however, no substantial effect on depressing ADG of pigs fed the AA restricted diets. In addition, there was no effect of dietary AA restrictions on ultrasound backfat thickness at the end of the grower phase, which is contrary to earlier reports (e.g., Chiba et al., 1999, 2002; Kamalakar et al., 2009),

As expected, the restricted pigs consumed less Lys and had improved efficiency of SID Lys utilization for BW gain, which is in agreement with previous reports (Chiba, 1994, 1995; Chiba et al., 1999, 2002; Fabian et al., 2002; Kamalakar et al., 2009). The efficient utilization of Lys for weight in Lys restricted pigs can be attributed the sparing effect of AA related to pigs fed AA restricted diets as mentioned by Chiba et al. (1991). The ADG of pigs fed the diets with lipids was greater compared to those fed the diets without lipids.

During the finisher-1 phase, there was an indication of compensatory growth in pigs subjected to dietary AA restrictions during the grower phase. Pigs fed the AA restricted grower diets had greater ADG and G:F compared with those fed the non-restricted diets, even though the growth performance was only numerically or slightly depressed by the dietary restrictions during the grower phase. Similar effects of early dietary AA restrictions on growth performance has been reported by Fabian et al. (2002) and Kamalakar et al. (2009). It should be pointed out, however, that the pigs subjected to AA restrictions during the grower phase continued to receive the restricted diets during the finisher-1 phase. Yet, those pigs had greater growth performance than those fed the non-restricted diets. It is possible that, similar to the grower phase, the dietary AA restrictions imposed during the finisher-1 phase may not have been severe enough.

As in the grower phase, Lys intake of restricted pigs was lower, and they utilized Lys more efficiently for BW gain compared with non-restricted pigs, which was consistent with aforementioned reports (e.g., Kamalakar et al., 2009). Also, as in the grower phase, ultrasound backfat thicknesses at the end of the finisher-1 did not differ because of the dietary treatment. The ADG tended to be greater with dietary lipid supplementation, and, as expected, the efficiency of feed utilization was greater in pigs fed the diets with supplemental lipids compared with those fed the diets without lipids, which is consistent with many report over the years (e.g., Moser, 1977; Chiba et al., 1985, 1987; Lin et al., 2013).

There was no effect of dietary AA restrictions on any of the response criteria during the finisher-2 phase, which was expected. Pigs subjected to the dietary AA restrictions during the grower phase apparently exhibited compensatory growth during the finisher-1 phase, and there was the lack of growth depression by feeding the restricted diets during the finisher-1 phase. Thus, growth performance of pigs may not have been affected by the dietary treatment because pigs were fed common diets during the finisher-2 phase. Pigs fed the supplemental lipids consumed less feed and utilized feed more efficiently for BW gain that those fed the diets without supplemental lipids.

Because of the possible compensatory BW gain during the finisher-1 phase, pigs subjected to dietary AA restrictions during the grower and finisher-1 phases had similar overall BW gain to those fed the non-restricted diets. And, perhaps, because of the slight numerical increase in ADG, pigs subjected to early dietary AA restrictions had improved efficiency of feed, SID Lys, and DE utilization for BW gain compared with those fed the non-restricted grower and finisher-1 diets. Thus, feeding the diets containing 80% of SID Lys and other AA during the grower and finisher-1 phases had some beneficial effects on overall growth performance of grower-finisher pigs, and it certainly had no adverse effects. There have been some reports that the differences in BW gain associated with early dietary AA restrictions had completely disappeared by the time pigs reached the market weight (Chiba, 1994, 1995; Fabian et al., 2002; Kamalakar et al., 2009). In the present study, although no adverse effect of early dietary AA restrictions on growth performance was observed, there was no clear depression of growth during the grower or finisher-1 phase. As expected, pigs fed the diets supplemented with lipids had greater G:F during the grower-finisher phase.

Serum metabolite profile may be a reflection of changes in physiological and metabolic activities in response to dietary manipulations (Kamalakar et al., 2009), and it is likely that dietary manipulations affect the metabolites possibly through the modulation of enzymes associated with N and lipid metabolism (Clarke and Abraham, 1992; McNeel and Mersmann, 2000). At the end of the grower phase, serum urea N was lower in the restricted pigs, clearly a reflection of the reduced Lys and other AA intakes by those pigs and their efficient utilization of Lys (Chiba et al., 1991). Similar results were observed by Fabian et al. (2002). Serum glucose concentration was greater in pigs fed the AA restricted diets, which can be observed with the moderate restriction as described by Hornick et al. (2000). Serum total protein or albumin, which can be a reflection of protein adequacy or positive protein metabolism (Lowrey et al., 1962; Mule et al., 2006), was not affected by the dietary treatment at the end of grower phase. Serum triglyceride concentration was greater in the pigs fed the diets supplemented with lipids, which was expected.

As in the grower phase, serum urea N was lower in pigs subjected to dietary AA restrictions compared with those fed the non-restricted diets at the end of finisher-1 phase. Serum cholesterol and triglyceride concentrations seem to be greater with the supplementary lipids, but the response was not clear because of the interaction in those criteria. At the end of the finisher-2 phase, none of the serum metabolites were affected by dietary AA restrictions. However, serum urea N and triglycerides concentrations were reduced by the supplementation of diets with 3% flaxseed oil + 2% poultry fat, perhaps, reflecting better utilization of AA and energy for growth.

As with overall BW gain, there was no difference in fat-free lean gain of pigs fed the restricted and non-restricted grower and finisher-1 diets, which is consistent with the finding of previous research (Fabian et al., 2002; Kamalakar et al., 2009). Also, similar to overall BW gain to Lys or DE intake, the efficiency of SID Lys or DE utilization for fat-free lean gain was greater in pigs fed the AA restricted diets compared with those fed the diets without AA restrictions. The increased efficiency of Lys utilization for fat-free lean gain has been reported previously (Fabianet al., 2002; Kamalakar et al., 2009). Backfat thickness at 10th rib did not differ among the diets, however, it increased numerically in pigs fed the restricted diets, which is contrary to Chiba (1995) and Chiba et al. (1999) who reported the improved carcass characteristics in pigs subjected to early dietary AA restrictions. Dietary treatments had no effect of LM area, proportion of fat-free lean, or efficiency of feed utilization for fat-free lean.

There were no differences in subjective color, firmness, marbling, and muscling scores among the pigs subjected to different dietary treatments, even though there was a dietary AA restriction x supplemental interaction in the muscling score. Kamalakar et al. (2009) reported similar results for color and firmness score in pigs subjected to the early dietary AA restrictions. However, marbling was shown to be greater in pigs fed the AA restricted diets in their study. Some other studies (Castell et al., 1994; Cisneros et al., 1996; Blanchard et al., 1999) also reported the increased marbling score in the pigs fed protein deficient diets, and such increased marbling score may be associated with the metabolism of branched chain AA (Hyun et al., 2002). Belly firmness score was reduced in pigs fed the diets with supplemental lipids compared with those fed the diets without lipids. The result indicated that supplementation with flaxseed oil, which is high in PUFA such as ω-3 FA, may have some beneficial effects on human health (Baghurst, 2002; Calder and Yaqoob, 2009), but it can result in soft pork (Averette Gatlin et al., 2002; Lin et al., 2013) or other adverse effects on pork characteristics, including the reduction of oxidative stability (Romans et al., 1995; Bryhni et al., 2002; Wood et al., 2003).

In conclusion, as expected, dietary lipids improved G:F but reduced belly firmness. The results also indicated that pigs subjected to dietary AA restrictions during the grower phase exhibited compensatory growth, even though their growth performance was only numerically depressed during the grower phase. Dietary treatments had no effect on overall BW gain, and pigs subjected to early dietary AA restrictions seemed to have improved overall efficiency of AA and energy utilization for BW gain and fat-free lean gain. Feeding the diets containing 80% of SID Lys and other AA during the grower and finisher-1 phases, therefore, had no adverse effects on overall growth performance or carcass characteristics of grower-finisher pigs, and it may even had some beneficial effects on the performance of grower-finisher pigs.

LITERATURE CITED

Allee, G. L. D. H. Baker, and G. A. Leveille. 1971a. Fat utilization and lipogenesis in the young pig. J. Nutr. 101:1415-1422.

Allee, G. L. E. K. O'Hea, G. A. Leveille, and D. H. Baker. 1971b. Influence of dietary protein and fat on lipogenesis and enzymatic activity in pig adipose tissue. J. Nutr. 101:869-878.

AOAC. 1995. Official methods of analysis. 16th ed. Assoc. Off. Anal. Chem., Washington, DC.

Averette Gatlin, L., M. T. See, D. K. Larick, X. Lin, and J. Odle. 2002. Conjugated linoleic acid in combination with supplemental dietary fat alters pork fat quality. J. Nutr. 132:3105-3112.

Baghurst, K. 2004. Dietary fats, marbling and human health. Aust. J. Exp. Agric. 44:635-644. Bryhni, E. A., N. P. Kjos, R. Pfstad, and M. Hunt. 2002. Polyunsaturated fat and fish oil in diets for growing-finishing pigs: Effects on fatty acid composition and meat, fat, and sausage quality. Meat Sci. 62:1-8.

Calder, P. C., and P. Yaqoob. 2009. Omega-3 polyunsaturated fatty acids and human health outcomes. Biofactors 35:266-272.

Cameron, N. D., M. Enser, G. R. Nute, F. M. Whittington, J. C. Penman, A. C. Fisken, A. M. Perry, and J. D. Wood. 2000. Genotype with nutrition interaction on fatty acid composition of intramuscular fat and the relationship with flavour of pig meat. Meat Sci. 55:187-195.

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 kg and 50 and 100 kg live weight on the subsequent and overall performance of pigs. Livest. Prod. Sci. 39:213-221.

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

Chiba, L. I. 2000. Feeding systems for pigs. In: M. Theodorou and J. France, editors, Feeding systems and feed evaluation models. CABI Publishing, Wallingford, UK. p. 189-209.

Chiba, L. I. 2001. Protein supplements. In: A. J. Lewis and L. L. Southern, editors, Swine nutrition. 2nd ed. CRC Press, Boca Raton, FL. p. 803-837.

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 acids and energy interrelationships in pigs weighing 20 to 50 kilograms. I. Rate and efficiency of weight gain. J. Anim. Sci. 69:694-707.

Chiba, L. I., A. J. Lewis, and E. R. Peo, Jr. 1991. Amino acids and energy interrelationships in pigs weighing 20 to 50 kilograms. II. Rate and efficiency of protein and fat deposition. J. Anim. Sci. 69:708-718.

Chillard, Y. 1993. Dietary fat and adipose tissue metabolism in ruminants, pigs, and rodents: A review. J. Dairy Sci. 76:3897-3931.

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. 63:517-52.

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

Corino, C., S. Magni, E. Pagliarini, R. Rossi, G. Pastorelli, and L. M. Chiesa. 2002. Effects of dietary fats on meat quality and sensory characteristics of heavy pig loins. Meat Sci. 60:1–8.

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.

Fabian, J., L. I. Chiba, D. L. Kuhlers, L. T. Frobish, K. Nadarajah, and W. H. McElhenny. 2003. Growth performance, dry matter and nitrogen digestibilities, serum profile, and carcass and meat quality of pigs with distinct genotypes. J. Anim. Sci. 81:1142-1149.

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.

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 1 November 2002.)

Hornick, J. L., C. van Eenaeme, O. Gérard, I. Dufrasne, and L. Istasse. 2000. Mechanisms of reduced and compensatory growth. Domest. Anim.Endocrinol.19:121-312.

Kamalakar, R. B., L. I. Chiba, K. C. Divakala, S. P. Rodning, E. G. Welles, W. G. Bergen, C. R. Kerth, D. L. Kuhlers, and N. Nadarajah. 2009. Effect of the degree and duration of early dietary amino acid restrictions on subsequent and overall pig performance and physical and sensory characteristics of pork. J. Anim. Sci. 87:3596-3606.

Lin, X., M. Azain, and J. Odle. 2013. Lipids and lipid utilization in swine. In: L. I. Chiba, editor, Sustainable swine nutrition. Wiley-Blackwell, A John Wiley & Sons, Inc., Hoboken, NJ. p. 59-79.

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.

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

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. 1991. Procedures to evaluate market hog performance. 3rd ed. Natl. Pork Prod. Council, Des Moines, IA.

NPPC. 2000. Pork composition and quality assessment procedures. Natl. Pork Prod. Council, Des Moines, IA

NRC. 2012. Nutrient requirements of swine. 10th rev. ed. Natl. Acad. Press, Washington, DC.

Romans, J. R., D. M. Wulf, R. C. Johnson, G. W. Libal, and W. J. Cosello. 1995. Effects of ground flaxseed in swine diets on pig performance and on physical and sensory characteristics and omega-3 fatty acid content of pork: II. Duration of 15% dietary flaxseed. J. Anim. Sci. 73:1987-1999.

Simopoulos, A. P. 1999. New products from agri-food industry: The return of n-3 FA into the food supply. Lipids 34(Suppl.):S297-S301.

Simopoulos, A. P. 2001. N−3 fatty acids and human health: Defining strategies for public policy. Lipids 36:S83–S89.

Smith, D. R., D. A. Knabe, and S. B. Smith. 1996. Depression of lipogenesis in swine adipose tissue by specific dietary fatty acids. J. Anim. Sci. 74:975-983.

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

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

Item	Soybean meal	Corn
DM	87.66	86.14
CP	48.06	8.20
Arg	3.27	0.41
His	1.17	0.25
Ile	2.09	0.30
Leu	3.42	1.04
Lys	2.82	0.27
Met	0.62	0.19
Cys	0.65	0.20
Met + Cys	1.27	0.39
Phe	2.33	0.39
Thr	1.80	0.31
Trp	0.62	0.07
Val	2.17	0.05

[1]Samples were analyzed by a commercial lab (Ajinomoto Heartland, Chicago, IL).
[2]Reported the values of 1 batch of sample.

Table 2. Fatty acid composition of flaxseed oil and poultry fat[1,2]

Item	Poultry fat	Flaxseed oil
Saturated fatty acids, %		
C8	0.05	0.04
C10	0.05	0.11
C11	0.24	0.11
C12	0.21	0.08
C13	0.32	0.11
C14	0.30	0.14
C15	0.33	0.08
C16	22.60	0.11
C17	0.18	0.01
C18	0.21	0.06
C19	0.06	0.01
C20	38.80	9.44
C21	0.02	0.00
C22	0.42	0.09
C23	0.12	0.01
C24	0.41	0.33
Monounsaturated fatty acids, %		
C14:1	0.79	0.11
C15:1	0.22	0.11
C16:1	6.82	4.76
C17:1	0.11	0.10
C18:1n9c	0.18	0.03
C18:1n9t	0.16	0.06
C20:1	0.11	0.00
C24:1	1.19	0.33
Polyunsaturated fatty acids, %		
C22:1n9	0.96	0.00
C18:2n6t	0.01	0.79
C18:2n6c	5.62	2.08
C18:3n3	0.02	0.01
C18:3n6	0.36	0.19
C20:2	17.55	15.29
C20:3n3	0.12	58.84
C20:3n6	0.36	0.19
C20:4n6	0.14	0.00
C20:5n3	0.33	0.03
C22:2	0.37	0.07
C22:6n3	0.61	0.24

[1]Analyzed as described by Cameron et al. (2000).

[2]Reported the values of 1 batch of samples analyzed in duplicate.

Table 3. Composition of grower diets (as-fed basis)[1]

	100%		80%	
Item	No lipids	5% lipids	No lipids	5% lipids
Ingredient, g/kg				
Corn	648.3	556.5	726.8	642.2
Soybean meal (47.5% CP)	326.5	366.0	246.6	278.7
Dicalcium phosphate	10.8	13.4	12.8	15.6
Limestone	8.4	8.1	7.8	7.5
Salt	3.5	3.5	3.5	3.5
Vitamin-trace mineral premix[2]	2.5	2.5	2.5	2.5
Calculated composition				
DE, Mcal/kg	3.4	3.7	3.4	3.7
CP, g/kg	209.3	220.5	177.6	186.0
Ca, g/kg	7.0	7.62	7.0	7.62
P, g/kg	6.0	6.53	6.0	6.53
Ca:P	1.17	1.17	1.17	1.17
Lys, g/kg	9.80	10.67	8.53	8.53
Lys:DE, g/Mcal	2.88	2.88	2.31	2.31
Trp, g/kg	2.27	2.57	2.09	2.09
Thr, g/kg	2.56	6.99	5.79	5.79
His, g/kg	5.05	5.33	4.49	4.49
Ile, g/kg	7.71	8.25	6.78	6.78
Analyzed composition				
CP, g/kg	196.0	202.7	166.7	178.0

[1]Four dietary treatments in a 2 x 2 factorial arrangement of treatments [100 or 80% standard ileal digestible Lys recommendation (NRC, 2012) and 0 or 5% (3% flaxseed oil + 2% poultry fat) lipid supplementation] during the grower and finisher-1 phases. Pigs were fed a common diet during the finisher-2 phase.

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

	100% finisher-1		80% finisher-1		Finisher-2	
Item	No lipids	5% lipids	No lipids	5% lipids	No lipids	5% lipids
Ingredient, g/kg						
Corn	700.8	613.9	768.9	688.1	748.9	666.2
Soybean meal (47.5% CP)	273.4	308.0	204.1	232.6	224.5	254.8
Dicalcium phosphate	11.9	14.6	13.6	16.4	13.1	15.9
Limestone	7.9	7.5	7.4	6.9	7.5	7.1
Salt	3.5	3.5	3.5	3.5	3.5	3.5
Vitamin-trace mineral premix[2]	2.5	2.5	2.5	2.5	2.5	2.5
Calculated composition						
DE, Mcal/kg	3.4	3.7	3.4	3.7	3.4	3.7
CP, g/kg	188.6	197.6	160.8	167.7	168.8	176.5
Ca, g/kg	7.0	7.62	7.0	7.62	7.0	7.62
P, g/kg	6.0	6.53	6.0	6.53	6.0	6.63
Ca:P	1.17	1.17	1.17	1.17	1.17	1.17
Lys, g/kg	8.50	9.25	6.80	7.40	7.30	7.94
Lys:DE, g/Mcal	2.50	2.50	2.00	2.00	2.15	2.15
Trp, g/kg	1.98	2.25	1.60	1.83	1.71	1.96
Thr, g/kg	5.83	6.19	4.89	5.16	5.16	5.47
His, g/kg	4.55	4.77	3.88	4.05	4.08	4.26
Ile, g/kg	6.82	7.28	5.65	6.01	6.00	6.38
Analyzed composition						
CP, g/kg	179.3	185.3	155.8	160.1	158.6	164.1

[1]Four dietary treatments in a 2 x 2 factorial arrangement of treatments [100 or 80% standard ileal digestible Lys recommendation (NRC, 2012) and 0 or 5% (3% flaxseed oil + 2% poultry fat) lipid supplementation] during the grower and finisher-1 phases. Pigs were fed a common diet during the finisher-2 phase.

[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 5. Effect of dietary AA restrictions (R) and lipid supplementation (L) 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]

	100%		80%			*P*-value		
Item[3]	No lipids	5% lipids	No lipids	5% lipids	SEM[4]	R	L	R x L
Grower phase								
ADFI, g/d	2,175	2,096	2,108	1,894	51	0.015	0.007	0.194
Avg Lys intake, g/d	21.3	22.4	16.4	16.2	0.5	<0.001	0.431	0.176
DEI, Mcal/d	7.40	7.77	7.18	7.00	0.18	0.013	0.607	0.134
ADG, g/d	864	906	831	894	23	0.346	0.030	0.657
G:F, g/kg	397	434	395	474	14	0.207	0.003	0.158
Gain:Lys intake, g/g	41.6	41.9	50.7	55.3	1.5	<0.001	0.111	0.155
Gain:DE intake, g/kg	117.0	117.8	116.2	127.5	4.0	0.294	0.149	0.200
Ultrasound backfat, mm	10.2	10.3	10.2	10.5	0.4	0.839	0.590	0.778
Finisher-1 phase								
ADFI, g/d	2,507	2,268	2,374	2,342	119	0.803	0.269	0.395
Avg Lys intake, g/d	21.3	21.0	16.2	17.3	1.0	<0.001	0.688	0.476
DEI, Mcal/d	8.51	8.40	8.09	8.70	0.41	0.890	0.557	0.407
ADG, g/d	899	968	975	1,039	34	0.042	0.066	0.953
G:F, g/kg	366	431	412	450	24	0.176	0.045	0.565
Gain:Lys intake, g/g	43.1	46.6	61.0	60.8	3.1	<0.001	0.730	0.450
Gain:DE intake, g/kg	107.8	116.5	121.7	121.7	6.7	0.166	0.522	0.524
Ultrasound backfat, mm	13.9	14.2	14.3	14.3	1.0	0.586	0.813	0.745
Finisher-2 phase								
ADFI, g/d	2,815	2,574	2,708	2,542	99	0.483	0.064	0.709
Avg Lys intake, g/d	20.5	20.6	19.8	20.3	0.8	0.504	0.731	0.737
DEI, Mcal/d	9.57	9.52	9.21	9.38	0.36	0.484	0.880	0.749
ADG, g/d	949	997	989	995	40	0.632	0.526	0.606
G:F, g/kg	338	388	368	393	14	0.199	0.015	0.365
Gain:Lys intake, g/g	46.3	48.5	50.3	49.1	1.8	0.190	0.789	0.345
Gain:DE intake, g/kg	99.3	104.7	108.0	106.1	3.8	0.191	0.672	0.348
Ultrasound backfat, mm	18.3	17.9	19.1	18.3	0.7	0.365	0.358	0.779
Overall								

ADFI, g/d	2,514	2,312	2,587	2,268	79	0.364	0.202	0.986
Avg Lys intake, g/d	21.0	21.2	17.5	18.0	0.4	<0.001	0.382	0.693
DEI, Mcal/d	8.50	8.54	8.13	8.34	0.17	0.114	0.467	0.584
ADG, g/d	905	948	932	971	79	0.334	0.137	0.939
G:F, g/kg	362	410	389	428	7	0.005	<0.001	0.549
Gain:Lys intake, g/g	43.2	44.7	53.3	53.8	0.9	<0.001	0.301	0.545
Gain:DE intake, g/kg	106.5	110.9	114.6	115.7	2.0	0.004	0.180	0.449

[1]Four dietary treatments in a 2 x 2 factorial arrangement of treatments [100 or 80% standard ileal digestible Lys recommendation (NRC, 2012) and 0 or 5% (3% flaxseed oil + 2% poultry fat) lipid supplementation] during the grower (24.7 ± 0.5 to 51.2 ± 0.3 kg) and finisher-1 phases (51.2 ± 0.3 to 80 ± 0.4 kg). Pigs were fed a common diet during the finisher-2 phase (80 ± 0.4 to 110.5 ± 0.5 kg).

[2]Least squares means based on 8 pens containing 2 gilts or 2 castrated males/pen.

[3]Lys intake = based on standardized ileal digestible Lys.

[4]Pooled SEM.

Table 6. Effect of dietary AA restrictions (R) and lipid supplementation (L) on serum metabolites of pigs at the end of the grower, finisher-1, and finisher-2 phases[1,2]

	100%		80%			*P*-value		
Item	No lipids	5% lipids	No lipids	5% lipids	SEM[3]	R	L	R x L
Grower phase								
Total protein, g/dL	5.26	5.57	6.01	5.72	0.30	0.156	0.976	0.323
Albumin, g/dL	3.67	3.82	4.01	3.70	0.16	0.522	0.616	0.170
Urea nitrogen, mg/dL	15.8	15.2	12.7	11.5	0.9	0.007	0.338	0.712
Glucose, mg/dL	89.1	90.1	103.4	95.0	4.1	0.027	0.358	0.248
Cholesterol, mg/dL	80.2	85.3	94.9	86.1	3.8	0.053	0.629	0.078
Triglycerides, mg/dL	36.4	55.7	43.6	55.4	8.5	0.694	0.075	0.660
Finisher-1 phase								
Total protein, g/dL	5.91	6.24	6.07	6.01	0.20	0.860	0.482	0.323
Albumin, g/dL	4.15	4.34	4.22	4.20	0.14	0.774	0.540	0.456
Urea nitrogen, mg/dL	15.1	17.4	13.7	13.1	1.2	0.026	0.514	0.251
Glucose, mg/dL	91.1	90.5	95.2	95.4	5.9	0.453	0.977	0.939
Cholesterol, mg/dL	82.0	96.0	89.1	89.4	3.0	0.940	0.023	0.029
Triglycerides, mg/dL	33.1	55.6	41.2	48.5	3.4	0.466	0.001	0.113
Finisher-2 phase								
Total protein, g/dL	6.14	6.30	5.95	5.98	0.22	0.241	0.677	0.770
Albumin, g/dL	4.37	4.44	4.23	4.17	0.15	0.184	0.965	0.666
Urea nitrogen, mg/dL	18.1	15.5	17.6	15.3	1.1	0.742	0.037	0.856
Glucose, mg/dL	84.6	85.8	87.4	80.4	3.7	0.725	0.456	0.270
Cholesterol, mg/dL	97.4	89.6	94.8	92.0	4.1	0.981	0.225	0.542
Triglycerides, mg/dL	39.9	36.2	50.4	35.0	3.7	0.211	0.018	0.115

[1]Four dietary treatments in a 2 x 2 factorial arrangement of treatments [100 or 80% standard ileal digestible Lys recommendation (NRC, 2012) and 0 or 5% (3% flaxseed oil + 2% poultry fat) lipid supplementation] during the grower (24.7 ± 0.5 to 51.2 ± 0.3 kg) and finisher-1 phases (51.2 ± 0.3 to 80 ± 0.4 kg). Pigs were fed a common diet during the finisher-2 phase (80 ± 0.4 to 110.5 ± 0.5 kg).

[2]Least squares means based on 8 pens containing 2 gilts or 2 castrated males/pen.

[3]Pooled SEM.

Table 7. Effect of dietary AA restrictions (R) and lipid supplementation (L) on carcass traits, and subjective meat quality scores at the end of the finisher-2 phase[1,2]

	100%		80%			*P*-value		
Item[3]	No lipids	5% lipids	No lipids	5% lipids	SEM[4]	R	L	R x L
Carcass traits								
10th rib backfat, mm	17.2	17.3	19.0	18.1	0.87	0.154	0.661	0.569
LM area, cm^2	39.4	40.6	43.0	38.8	1.60	0.588	0.361	0.102
FFL, %	53.2	53.9	53.4	53.1	0.70	0.659	0.333	0.767
FFLgain, g/d	367	384	377	386	13.41	0.779	0.511	0.711
FFL gain:feed intake, g/kg	147	151	147	148	3.84	0.782	0.199	0.705
FFL gain:Lys intake, g/g	17.5	18.3	21.6	21.9	0.59	<0.001	0.380	0.638
FFL lean gain:DE intake, g/kg	43.3	45.5	46.4	47.2	1.4	0.095	0.273	0.596
Subjective meat quality scores								
Color	2.89	3.00	2.73	2.64	0.21	0.231	0.966	0.625
Firmness	1.75	1.73	1.81	1.67	0.09	0.995	0.408	0.496
Belly firmness	5.08	2.05	6.73	3.04	0.72	0.078	<0.001	0.644
Marbling	1.44	1.48	1.57	1.32	0.11	0.896	0.370	0.217
Muscling	2.00	2.14	2.06	2.00	0.06	0.524	0.476	0.081

[1]Four dietary treatments in a 2 x 2 factorial arrangement of treatments [100 or 80% standard ileal digestible Lys recommendation (NRC, 2012) and 0 or 5% (3% flaxseed + 2% poultry fat) lipid supplementation] during the grower (24.7 ± 0.5 to 51.2 ± 0.3 kg) and finisher-1 phases (51.2 ± 0.3 to 80 ± 0.4 kg). Pigs were fed a common diet during the finisher-2 phase (80 ± 0.4 to 110.5 ± 0.5 kg).

[2]Least squares means based on 8 pens containing 2 gilts or 2 castrated males/pen.

[3]FFL = fat-free lean; Lys intake = based on standardized ileal digestible Lys.

[4]Pooled SEM.

IV. Summary and Conclusion

The effort to satisfy consumer demands by supplying leaner pork in recent years has resulted in a reduction of intramuscular fat (IMF), which has adverse effects on organoleptic characteristics of pork. Clearly, increasing the IMF content of pork, while maintaining the leanness of pigs, would benefit consumers greatly. By taking advantage of compensatory growth, carcass fat can be reduced to satisfy consumer demands and IMF can be increased to enhance eating quality of pork simultaneously. Besides improving eating quality of pork, IMF may have beneficial effects on human health, and this potential can be enhanced further if its increase can be achieved by supplementation of the pig diet with omega-3 fatty acids (ω-3 FA) because of the direct deposition of dietary fat into body tissues. In addition, de novo lipogenesis can be reduced by dietary lipids. Furthermore, compensatory growth can improve the overall efficiency of nutrient utilization and economic efficiency, and minimize adverse impacts of pig production on the environment. Therefore, using the concept of compensatory growth and dietary supplementation of flaxseed oil, which is high in the ω-3 FA content, to address the pork quality issue can contribute greatly to successful and sustainable pig production.

A total of 64 pigs (2 gilts or 2 barrows/pen) were used to investigate the effect of early dietary amino acid (AA) restrictions [100 or 80% of the 2012 NRC standardized ileal digestible (SID) Lys requirements during the grower and finisher-1 phases] and flaxseed oil supplementation [0 or 3% (+ 2% poultry fat)] in a 2 x 2 factorial arrangement of treatments on grower-finisher pigs. At 24.7 ± 0.5 kg, pigs were assigned to 4 grower diets with 4 gilt pens and

4 barrow pens/treatment, and switched to finisher-1 diets when they reached 51.2 ± 0.3 kg. Pigs were switched to common finisher-2 diets at 80.0 ± 0.4 kg, and those received 0 or 5% lipids during the grower and finisher-1 phases were continued to receive 0 or 5% lipids. Ultrasound backfat measurements and blood samples were collected at the end of the grower, finisher-1, and finisher-2 phases, and pigs were harvested at 110.5 ± 0.5 kg. The results of growth performance, serum metabolite profile, and carcass traits are reported in this monograph.

Pigs fed the AA restricted diets consumed less SID Lys and DE ($P < 0.015$), and had slightly depressed ADG compared with non-restricted pigs during the grower phase, but they grew faster ($P = 0.042$) and utilized feed numerically and SID Lys ($P < 0.001$) more efficiently during the finisher-1 phase. Dietary AA restrictions had no effect on any of the response criteria during the finisher-2 phase, overall ADG, or carcass traits. The efficiency of overall feed, SID Lys, and DE utilization for body weight (BW) gain ($P < 0.004$) and SID Lys utilization for fat-free lean gain ($P < 0.001$) was improved by the AA restrictions. Dietary AA restrictions reduced serum urea N ($P < 0.025$) at the end of the grower and finisher-1 phases and increased glucose ($P = 0.027$) at the end of the grower phase, but had no clear effect on other metabolites.

Dietary lipids reduced feed intake during the grower ($P= 0.007$) and finisher-2 ($P = 0.064$) phases, improved gain:feed (G:F) during all phases and overall ($P < 0.047$), and improved ADG during the grower ($P = 0.003$) and finisher-1 ($P = 0.066$) phases. Belly firmness was reduced ($P < 0.001$), but there was no other effect of dietary lipids on carcass traits. Dietary lipids increased serum triglycerides at the end of the grower ($P = 0.075$) and finisher-1 ($P = 0.001$) phases, but reduced ($P = 0.037$) urea-N at the end of the finisher-2 phase. Dietary lipids increased serum cholesterol in pigs fed the unrestricted diets but had no effect on pigs fed the AA restricted diets at the end of the finisher-1 phase (AA restrictions x lipids, $P = 0.029$). The dietary treatment had no effect on ultrasound backfat thickness.

In conclusion, as expected, dietary lipids improved G:F but reduced belly firmness. The results also indicated that pigs subjected to dietary AA restrictions during the grower phase exhibited compensatory growth, even though their growth performance was only numerically depressed during the grower phase. Dietary treatments had no effect on overall BW gain, and pigs subjected to early dietary AA restrictions seemed to have improved overall efficiency of AA and energy utilization for BW gain and fat-free lean gain. Feeding the diets containing 80% of SID Lys and other AA recommendations during the grower and finisher-1 phases, therefore, had no adverse effects on overall growth performance or carcass characteristics of grower-finisher pigs, and it may even had some beneficial effects on growth performance of grower-finisher pigs.

V. Cumulative Biography

Allee, G. L. D. H. Baker, and G. A. Leveille. 1971a. Fat utilization and lipogenesis in the young pig. J. Nutr. 101:1415-1422.

Allee, G. L. D. H. Baker, and G. A. Leveille. 1971b. Influence of level of dietary fat on adipose tissue lipogenesis and enzymatic activity in the pig. J. Anim. Sci. 33:1248-1254.

Allee, G. L. E. K. O'Hea, G. A. Leveille, and D. H. Baker. 1971c. Influence of dietary protein and fat on lipogenesis and enzymatic activity in pig adipose tissue. J. Nutr. 101:869-878.

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

AOAC. 1995. Official methods of analysis. 16th ed. Assoc. Off. Anal. Chem., Washington, DC.

Averette Gatlin, L., M. T. See, J. A. Hansen, D. Sutton, and J. Odle. 2002. The effects of dietary fat sources, levels, and feeding intervals on pork fatty acid composition. J. Anim. Sci. 80:1606-1615.

Azain, M. J. 2001. Fat in swine nutrition. In: A. J. Lewis, and L. L. Southern, editors, Swine nutrition. 2nd ed. CRC Press, Boca Raton, FL. p. 95-105.

Baghurst, K. 2004. Dietary fats, marbling and human health. Aust. J. Exp. Agric. 44:635-644. Bee, G., S. Gebert, and R. Meissikommer. 2002. Effect of dietary energy supple and fat source on the fatty acid pattern of adipose and lean tissues and lipogenesis in the pig. J. Anim. Sci. 80:1564-1574.

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.

Bejerjolm, C., and P. Barton-Gade. 1986. Effect of intramuscular fat level on eating quality of pig meat. Manuscript no. 720 E. Danish Meat Research Institute, Roskilde, Denmark.

Bergen, W. G. and H. J. Mersmann. 2005. Comparative aspects of lipid metabolism: impact on contemporary research and use of animal models. J. Nutr. 135:2499-2502.

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

Boudry, Gaelle, V. Douard, J. Mourot, J.-P. Lalles, and I. Le Huerou-Luron. 2009. Linseed oil in the maternal diets during gestation and lactation modifies fatty acid composition, mucosal architecture, and mast cell regulation of the ileal barrier in piglets. J. Nutr. 139:1110-1117.

Bourre, J. M. 2005. Where to find omega-3 fatty acids and how feeding animals with diets enriched in omega-3 fatty acids to increase nutritional value of derived products for human:what is actually useful? J. Nutr. Health Aging 9:232-242.

Brooks, C. C. 1971. Fatty acid composition of pork lipids as affected by basal diet, fat source and fat level. J. Anim. Sci. 33:1224-1231.

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

Bryhni, E. A., N. P. Kjos, R. Pfstad, and M. Hunt. 2002. Polyunsaturated fat and fish oil in diets for growing-finishing pigs: effects on fatty acid composition and meat, fat, and sausage quality. Meat Sci. 62:1-8.

Calder, P. C., and P. Yaqoob. 2009. Omega-3 polyunsaturated fatty acids and human health outcomes. Biofactors 35:266-272.

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

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.

Chaosap C., T. Parr, and J. Wiseman 2011. Effect of compensatory growth on performance, carcass composition and plasma IGF-1 in grower finisher pigs. Animal 5:749–756.

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

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

Chiba, L. I. 2000. Feeding systems for pigs. In: M. Theodorou, and J. France, editors. Feeding systems and feed evaluation models. CABI Publishing, Wallingford, UK. p. 189-209.

Chiba, L. I. 2001. Protein supplements. In: A. J. Lewis and L. L. Southern, editors. Swine nutrition. 2nd ed. CRC Press, Boca Raton, FL. p. 803-837.

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. 1991a. Amino acids and energy interrelationships in pigs weighing 20 to 50 kilograms. I. Rate and efficiency of weight gain. J. Anim. Sci. 69:694-707.

Chiba, L. I., A. J. Lewis, and E. R. Peo, Jr. 1991b. Amino acids and energy interrelationships in pigs weighing 20 to 50 kilograms. II. Rate and efficiency of protein and fat deposition. J. Anim. Sci. 69:708-718.

Chillard, Y. 1993. Dietary fat and adipose tissue metabolism in ruminants, pigs, and rodents: A review. J. Dairy Sci. 76:3897-3931.

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.

Cochran, W. G., and G. M. Cox. 1957. Experimental design. John Wiley and Sons, Inc., New York.

Corino, C., S. Magni, E. Pagliarini, R. Rossi, G. Pastorelli, and L. M. Chiesa. 2002. Effects of dietary fats on meat quality and sensory characteristics of heavy pig loins. Meat Sci. 60:1–8.

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.

DeVol, D. L., F.K.McKeith, P. J. Bechtel, J. Novakofski, R. D. Shanks, and T. R. Carr. 1988. Variation 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

Dugan, M. E. R., J. L. Aalhus, W. M. Robertson, L. L. Gibson, D. C. Rolland, and I. L. Larsen. 2004. Feeding flax seed to pigs: effects on pork fatty acid composition and palatability. Adv. Pork Prod. 15. Abstr. #14

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.

Fabian, J., L. I. Chiba, D. L. Kuhlers, L. T. Frobish, K. Nadarajah, and W. H. McElhenny. 2003. Growth performance, dry matter and nitrogen digestibilities, serum profile, and carcass and meat quality of pigs with distinct genotypes. J. Anim. Sci. 81:1142-1149.

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.

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

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

Fischer, K. 2007. Drip loss in pork influencing factors and relation to further meat quality traits. J. Anim. Breed. & Genetics 124:12-18.

Fontanillas, R., A. Barroeta, M. D. Baucells, and F. Guardiola. 1998. Backfat fatty acid evolution in swine fed diets high in either cis-monounsaturated, trans, or (n-3) fats. J. Anim. Sci. 76:1045-1055.

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.

Gardner, G. E., D. W. Pethick, P. L. Greenwood, and R. S. Hegarty. 2005. The effect of genotype and plane of nutrition on the rate of pH decline in lamb carcasses and the expression of metabolic enzymatic markers. Crop and Pasture Sci. 57:661-670.

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. In: Proc. 38th Int. Congr. Meat Sci. Technol., Clermont-Ferrand, France. p. 245-248.

Graham, NMcC, and T. W. Searle. 1975. Studies of weaner sheep during and after a period of weight stasis: Energy and nitrogen utilization. Crop Pasture Sci. 26:343-353.

Griel, A. E., P. M. Kris-Etherton, K. F. Hilpert, G. Zhao, S. G. West, and R. L. Corwin. 2007. An increase in dietary n-3 fatty acids decreases a marker of bone resorption in humans. Nutr. J. 6:2.

Haak, L. S. De Smet, D. Fremaut, K. Van Walleghem, and K. Raes. 2008. Fatty acid profile and oxidative stability of pork as influence dby duration and time of dietary linseed oil or fish oil supplementation. J. Anim. Sci. 86:1418-1425.

Halsey, C. H. C., P. S. Weber, S. S. Reiter, B. N. Stronach, J. L. Bartosh, and W. G. Bergen. 2011. The effect of ractopamine hydrochloride on gene expression in adipose tissues of finishing pigs. J. Anim Sci. 89:1011-1019.

Harper, C. R., M. J. Edwards, A. P. DeFilippis, and T. A. Jacobson. 2006. Flaxseed oil increases the plasma concentrations of cardioprotective (n-3) fatty acids in humans. J. Nutr. 136:83-87.

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.

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.

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.

Hornick, J.L., C. Van Eenaemea, O. Gérarda, I. Dufrasneb, and L. Istassea. 2000. Mechanisms of reduced and compensatory growth. Domestic Anim. Endocrinol. 19:121-132.

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.

Hoz, L., C. L. Lopez-Bote, M. I. Cambero, M. D'Arrigo, C. Pin, C. Santos, and J. A. Ordonez. 2003. Effect of dietary linseed oil and α-tocopherol on pork tenderloin (*Psos major*) muscle. Meat Sci. 65:1039-1044.

Howe, P., B. Meyer, S. Record, and K. Baghurst. 2006. Dietary intake of long-chain omega-3 polyunsaturated fatty acids: Contribution of meat sources. Nutr. 22:47-53.

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 1 November 2002.)

Jakobsen, K., and G. Thorbek. 1993. The respiratory quotient in relation to fat deposition in fattening-growing pigs. Br. J. Nutr. 69:333-343.

Kamalakar, R. B., L. I. Chiba, K. C. Divakala, S. P. Rodning, E. G. Welles, W. G. Bergen, C. R. Kerth, D. L. Kuhlers, and N. Nadarajah. 2009. Effect of the degree and duration of early dietary amino acid restrictions on subsequent and overall pig performance and physical and sensory characteristics of pork. J. Anim. Sci. 87:3596-3606.

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

Kouba, M. M. Enser, F. M. Whittington, G. R. Nute, and J. D. Wood. 2003. Efect of a high- linolenic acid diet on lipogenic enzyme activities, fatty acid composition, and meat quality in the growing pig. J. Anim. Sci. 81:1967-1979.

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

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.

Karlsson, A. H., R. E. Klont, and X. Fernandez. 1999. Skeletal muscle fibres as factors for pork quality. Livest. Prod. Sci. 60:255-269.

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.

Lin, X., M. Azain, and J. Odle. 2013. Lipids and lipid utilization in swine. In: L. I. Chiba, editor, Sustainable swine nutrition. Wiley-Blackwell, A John Wiley & Sons, Inc., Hoboken, NJ.

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.

Lu, P., L. Y. Zhang, J. D. Yin, A. K. R. Everts, and D. F. Li. 2008. Effects of soybean oil and linseed oil on fatty acid compositions of muscle lipids and cooked pork flavour. Meat Sci. 80:910-918.

Maddock, T. D., V. L. Anderson, and G. P. Lardy. 2005. Using flax in livestock diets. AS-1283. NDSU Ext. Service and North Dakoda Agric. Exp. Sta., North Dakota State Univ., Fargo, ND.

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.

McNeel, R. L., S.-T. Ding, E. O'Brian Smith, and H. J. Mersmann. 2000. Effect of feed restriction on adipose tissue transcript concentrations in genetically lean and obese pigs. J. Anim. Sci. 78:934-942.

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.

Missotten, J., S. De Smet, K. Raes, and O. Doran. 2009. Effect of supplementation of the maternal diet with fish oil or linseed oil on fatty-acid composition and expression of Δ5- and Δ6-desaturase in tissues of female piglets. Animal 3:1196-204.

Morgan, C. A., R. C. Noble, M. Cocchi, and R. McCartney. 1992. Manipulation of the fatty acid composition of pig meat lipids by dietary means. J. Sci. Food Agric. 58:357-368.

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

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

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

NRC. 2012. 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. Anim. Sci. 52:85-90.

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

Paschos, G. K., F. Magkos, D. B. Panagiotakos, V. Votteas, and A. Zampelas. 2007. Dietary supplementation with flaxseed oil lowers blood pressure in dyslipidaemic patients. Eur. J. Clin. Nutr. 61:1201-1206.

Patience, J. F., A. van Kessel, M. Drew, R. T. Zijlstra, P. Leterme, and A. D. Beaulieu. 2005. Response of growing pigs to graded levels of flaxseed. In: 2005 Annu. Res. Rep., Prairie Research Center, Saskatoon, SK, Canada. p. 24-26.

Pieszka, M., T. Barowicz, T. Migda, and B. Zivkowic. 2005. Effect of mono- and polyunsaturated fatty acids on muscle cholesterol level in fattening pigs. Biotechnol. Anim. Husbandry 21:49-54.

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

Psota, T. L., S. K. Gebauer, P. Kris-Etherton. 2006. Dietary omega-3 fatty acid intake and cardiovascular risk. Am. J. Cardiol. 98(4A):3i-18i.

Resurreccion, A. V. A. 2004. Sensory aspects of consumer choices for meat and meat products. Meat Sci. 66:11-20.

Romans, J. R., R. C. Johnson, D. M. Wulf, G. W. Libal, and W. J. Cosello. 1995a. Effects of ground flaxseed in swine diets on pig performance and on physical and sensory characteristics and omega-3 fatty acid conetnt of pork: I. Dietary level of flaxseed. J. Anim. Sci. 73:1982-1986.

Romans, J. R., D. M. Wulf, R. C. Johnson, G. W. Libal, and W. J. Cosello. 1995b. Effects of ground flaxseed in swine diets on pig performance and on physical and sensory characteristics and omega-3 fatty acid conetnt of pork: II. Duration of 15% dietary flaxseed. J. Anim. Sci. 73:1987-1999.

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.

Rose, D. P., and J. M. Connolly. 1999. Omega-3 fatty acids as cancerchemopreventive agents. Pharm. Therapeutics 83:217-244.

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

Ryan, W. J., I. H. Williams, and R. J. Moir. 2003. Compensatory growth in sheep and cattle: Growth pattern and feed intake. Crop Pasture Sci. 44: 1609-1621.

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

Simopoulos, A. P. 1999. New products from agri-food industry: The return of n-3 FA into the food supply. Lipids 34(Suppl.):S297-S301.

Simopoulos, A. P. 2001. N−3 fatty acids and human health: Defining strategies for public policy. Lipids 36:S83–S89.

Smith, D. R., D. A. Knabe, and S. B. Smith. 1996. J. Anim. Sci. Depression of lipogenesis in swine adipose tissue by specific dietary fatty acids. J. Anim. Sci. 74:975-983.

Speake, B. K., and P. F. Surai. 2004. Omega-3 and -6 fatty acids. In: W. G. Pond and A. W. Bell, editors. Encyclopedia of animal science. Marcel Dekker, Inc., New York. p. 681-683.

Sun, D., A. Krishnan, K. Zaman, R. Lawrence, A. Bhattacharya, and G. Fernandez. 2003. Dietary n-3 fatty acids decrease osteoclastogenesis and loss of bone mass in ovariectomized mice. J. Bone Mineral Res. 18:1206-1216.

Ueshima, H., J. Stamler, P. Elliot, Q. Chan, I. J. Brown, M. R. Carnethon, M. L. Daviglus, K. He, A. Moag-Stahlberg, B. L. Rodriguez, L. M. Steffen, L. van Horn, J. Yarnell, and B. Zhou. 2007. Food omega-3 fatty acid intake of individuals (total, linolenic acid, long-chain) and their blood pressure: INTERMAP study. Hypertension 50:313-319.

Vandongen, R. T. A. Mori., V. Burke, L. J. Beilin, J. Morris, and J. Ritchie. 1993. Effects of blood pressure of omega 3 fats in subjects at increased risk of cardiovascular disease. Hypertension 22:371-379.

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.

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.)

Watkins, B. A., Y. Li, H. E. Lippman, and S. Feng. 2003. Modulatory effect of omega-3 polyunsaturated fatty acids on osteoblastic function and bone metablism. Prostgalindins Leukot Essential Fatty Acids 68:387-398.

Wiecek, J., A. Rekiel, and J. Skomial 2011.Effect of restricted feeding and realimentation periods on compensatory growth performance and physiological characteristics of pigs. Archives of Anim.l Nutri. 65, 34-45.

Wiecek, J., and J. Skomial. 2004. Restricted feeding and linseed oil as modifiers on the fatty acid profile in pork. J. Anim. Feed Sci. 13(Suppl. 2):43-46.

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

Wiseman, J. and J. A. Agunbiade. 1998. The influence of changes in dietary fat and oils on fatty acid profiles of carcass fat in finishing pigs. Livest. Prod. Sci. 54:217-227.

Wolfe, R. C., C. V. Maxwell, E. C. Nelson, and R. J. Johnson. 1977. Effect of dietary fat level on gorwth and lipogenesis in the colostrum deprived neonatal pig. J. Nutr. 2100-2108.

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

Wood, J. D., S. N. Brown, G. R. Nute, F. M. Whittington, 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.

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. 1:147-153.

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. 73:129-136.

VI. 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:

$$\text{Protein} + Cu^{2+} \xrightarrow{\text{Alkaline solution}} \text{Cu-protein complex}$$

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^+:

$$\alpha\text{-ketoglutarate} + NH_4^+ + \text{NADH} \xrightarrow{\text{GLDH}} \text{L-glutamate} + NAD^+ + H_2O$$

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:

$$\text{Triglycerides} + \text{H2O} \xrightarrow{\text{Lipase}} \text{Glycerol} + \text{fatty acids}$$

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 (H2O2):

$$\text{Glycerol-1-phosphate} + O_2 \xrightarrow{\text{GPO}} H_2O_2 + \text{dihydroxyacetone phosphate}$$

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:

$$\text{Cholesterol esters} + H_2O_2 \xrightarrow{\text{Cholesterolesterase}} \text{Cholesterol} + RCOOH$$

Cholesterol is converted by oxygen with the aid of cholesterol oxidase to cholest-4-en-3-one and hydrogen peroxide:

$$\text{Cholesterol} + O2 \xrightarrow{\text{Cholesterol oxidase}} \text{Cholest-4-en-3-one} + H2O2$$

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

$$2H_2O_2 + \text{4-aminophenazone} + \text{phenol} \xrightarrow{\text{Peroxidase}} \text{4-(p-benzoquinone-monoimino)-phenazone} + 4H_2O$$

The color intensity is directly proportional to the concentration of cholesterol and can be determined photometrically.

Appendix F: Maximum (Max) and minimum (min) temperatures of the grower-finisher unit during the study period (°C)

Date	Max	Min	Date	Max	Min	Date	Max	Min
30-Nov-12	16.1	7.2	21-Jan-13	17.2	2.8	14-Mar-13	15.0	0.0
1-Dec-12	18.9	8.9	22-Jan-13	11.1	-1.1	15-Mar-13	23.3	0.6
2-Dec-12	21.1	10.0	23-Jan-13	12.8	1.1	16-Mar-13	26.1	2.2
3-Dec-12	22.8	10.0	24-Jan-13	17.8	7.8	17-Mar-13	28.3	4.4
4-Dec-12	22.8	10.0	25-Jan-13	17.8	7.2	18-Mar-13	26.1	4.4
5-Dec-12	22.2	13.9	26-Jan-13	15.0	7.2	19-Mar-13	25.6	15.6
6-Dec-12	22.8	12.8	27-Jan-13	17.8	7.2	20-Mar-13	20.0	12.8
7-Dec-12	20.0	12.8	28-Jan-13	21.1	10.0	21-Mar-13	12.8	2.2
8-Dec-12	20.0	12.8	29-Jan-13	23.9	12.8	22-Mar-13	18.9	0.6
9-Dec-12	-	-	30-Jan-13	22.8	6.1	23-Mar-13	23.9	0.6
10-Dec-12	22.2	17.8	31-Jan-13	11.1	1.1	24-Mar-13	25.0	3.9
11-Dec-12	17.2	7.8	1-Feb-13	8.9	0.0	25-Mar-13	18.3	5.0
12-Dec-12	10.0	3.9	2-Feb-13	16.1	-2.2	26-Mar-13	30.0	7.8
13-Dec-12	12.2	2.8	3-Feb-13	16.1	2.2	27-Mar-13	31.7	3.3
14-Dec-12	16.1	3.9	4-Feb-13	12.2	2.2	28-Mar-13	-	-
15-Dec-12	17.2	10.0	5-Feb-13	18.9	7.2	29-Mar-13	26.7	5.0
16-Dec-12	17.2	12.8	6-Feb-13	22.2	6.1	30-Mar-13	28.9	11.1
17-Dec-12	17.8	12.8	7-Feb-13	12.8	8.9	31-Mar-13	31.7	15.6
18-Dec-12	17.8	10.0	8-Feb-13	12.8	3.9	1-Apr-13	33.9	18.9
19-Dec-12	17.2	7.8	9-Feb-13	17.2	1.1	2-Apr-13	32.8	22.2
20-Dec-12	16.7	5.6	10-Feb-13	17.8	7.8	3-Apr-13	33.3	22.2
21-Dec-12	8.9	1.1	11-Feb-13	17.2	12.2	4-Apr-13	32.8	20.0
22-Dec-12	12.8	-2.2	12-Feb-13	12.2	7.2	5-Apr-13	26.7	12.2
23-Dec-12	6.7	2.8	13-Feb-13	11.1	2.8	6-Apr-13	27.2	7.8
24-Dec-12	-	-	14-Feb-13	12.8	2.2	7-Apr-13	25.6	11.7
25-Dec-12	-	-	15-Feb-13	17.2	2.2	8-Apr-13	26.1	11.7
26-Dec-12	2.8	2.2	16-Feb-13	7.8	-1.1	9-Apr-13	30.6	20.0
27-Dec-12	6.1	1.1	17-Feb-13	8.9	-3.9	10-Apr-13	-	-
28-Dec-12	12.8	0.0	18-Feb-13	15.0	0.0	11-Apr-13	-	-
29-Dec-12	7.2	0.0	19-Feb-13	17.2	5.0	12-Apr-13	21.1	7.2
30-Dec-12	10.0	-2.8	20-Feb-13	12.8	-1.1	13-Apr-13	26.7	11.1
31-Dec-12	12.2	1.1	21-Feb-13	18.9	2.2	14-Apr-13	28.9	13.3
1-Jan-13	17.8	10.0	22-Feb-13	18.3	4.4	15-Apr-13	25.0	13.9
2-Jan-13	12.2	6.1	23-Feb-13	25.6	2.2	16-Apr-13	27.8	17.2
3-Jan-13	7.8	2.2	24-Feb-13	20.0	9.4	17-Apr-13	-	-
4-Jan-13	12.8	0.0	25-Feb-13	19.4	12.8	18-Apr-13	-	-
5-Jan-13	11.1	1.1	26-Feb-13	15.6	11.1	19-Apr-13	25.0	17.8
6-Jan-13	12.2	5.0	27-Feb-13	14.4	3.3	20-Apr-13	25.6	20.0
7-Jan-13	12.8	2.2	28-Feb-13	19.4	4.4	21-Apr-13	22.2	20.0
8-Jan-13	16.1	5.0	1-Mar-13	18.3	4.4	22-Apr-13	-	-
9-Jan-13	17.2	12.2	2-Mar-13	25.6	2.2	23-Apr-13	26.7	12.2
10-Jan-13	18.9	17.2	3-Mar-13	20.0	9.4	24-Apr-13	31.1	25.6
11-Jan-13	23.9	17.2	4-Mar-13	19.4	12.8	25-Apr-13	28.9	25.0
12-Jan-13	23.9	17.2	5-Mar-13	15.6	11.1	26-Apr-13	26.1	8.9
13-Jan-13	22.2	17.2	6-Mar-13	14.4	3.3	27-Apr-13	27.2	13.9
14-Jan-13	22.2	12.8	7-Mar-13	19.4	4.4	28-Apr-13	23.9	17.2
15-Jan-13	23.9	12.8	8-Mar-13	18.9	1.1	29-Apr-13	26.1	16.1
16-Jan-13	18.9	13.9	9-Mar-13	20.0	6.1	30-Apr-13	27.2	12.8
17-Jan-13	13.9	2.2	10-Mar-13	22.8	11.1	1-May-13	23.9	17.2
18-Jan-13	13.9	-1.1	11-Mar-13	8.9	2.2	2-May-13	23.3	17.2
19-Jan-13	16.1	1.1	12-Mar-13	16.1	2.2	3-May-13	25.0	16.1
20-Jan-13	17.8	2.8	13-Mar-13	15.0	2.8	4-May-13	-	-