



Nutrigenomics Approach-A Strategy for Identification of Nutrition Responsive Genes Influencing Meat Edible Quality Traits in Swine^{*}, ^{**}

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ABSTRACT : In the last 20 years, meat quality, especially meat edible quality has become a more intriguing topic in the field of swine production. In this paper, we briefly review the progress of meat quality research from the aspects of genetic selection and nutritional modulation, and propose a possible approach -nutrigenomics- to explore the nutrition-responsive major genes that affect meat quality formation during the growing and fattening of pigs. (**Key Words :** Pig, Meat Quality, Intramuscular Fat, Major Gene, Nutrigenomics)

INTRODUCTION

Meat quality describes the attractiveness of meat to consumers. It covers many different characteristics, including nutritional quality, processing quality, eating quality and hygiene quality. In general, meat quality refers to the meat eating quality or edible quality, including color, tenderness, juiciness, smell, flavor, and the consistency of the meat in its raw and cooked states, which are influenced by animal heredity, feeding system, nutritional status, pre-slaughter and slaughter condition, and meat process. Although customer's preferences for meat edible quality can be various with the different dietetic cultural background and cuisine, meat edible quality is a decisive factor that influences the consumer's desire for purchase. Therefore, meat quality attracts more and more attention from the field of genetics, breeding and nutrition. In this paper, we mainly review the advance of the mechanism of meat quality trait formation during pig growing and fattening.

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MEAT QUALITY AND ITS GENETIC BACKGROUND

In pig breeding, long-term selection for lean rate and high growth speed has led to increased concern about quality problems in pork meat quality. These problems focus primarily on color, firmness, marbling, and water holding capacity in pork muscle. For example, before the early 1990's, pig malignant hyperthermia caused a two billion dollar loss each year in global pig production. Fujii et al. (1991) firstly identified a mutation in porcine ryanodine receptor associated with malignant hyperthermia, which surged the studies of relation between meat quality and genes. However, due to the complicated determinants involving genetics, epigenetics, and nutrition, only two major genes, Halothane (Hal) and Napole yield (RN) genes have been recognized, which significantly influenced the meat quality of pork.

The Halothane Gene PSE meat, that is pale, soft and exudative meat, is a general term used to describe poor pork quality. Malignant hyperthermia in pigs leads to a rapid pH fall (pH 45 minutes postmortem <6.1), which results in PSE meat (Pommier et al., 1998). A locus for malignant hyperthermia susceptibility (MHS) was localized on chromosome 19q12-13.2 (McCarthy et al., 1990). Almost at the same time, the gene encoding the skeletal muscle ryanodine receptor (RYR1) also was mapped to this region and was shown to be tightly linked to MHS (MacLennan et al., 1990). In 1991, it was demonstrated that malignant

hyperthermia in pigs was caused by a mutation at position 1, 843 of the gene that encode for the ryanodine receptor (locus *ryr-1*) (Fujii et al., 1991).

In pigs the Hal gene locates on chromosome 6 and contains 2 alleles: a normal allele (HalN) and a recessive mutant allele (Haln). The three possible genotypes (NN, Nn, and nn) can now be specifically identified using a molecular marker to test pig tissues such as blood, skin, or hair (Houde et al., 1993). Haln allele has been gradually removed from most of pig populations nowadays. In spite of heterozygote pigs with the Hal gene generally have a lower quality of meat, but they have improved feed conversion, reduced backfat depth, increased loin muscle size, and leaner carcass than pigs with Hal NN gene. Therefore, it is worth considering how to use the Haln gene in the pig industry.

The RN Gene A dominant mutation (denoted RN⁻) in Hampshire pigs plays a vital role in meat quality formation. Meat from RN⁻ pigs has a low ultimate pH (measured at 24 h after slaughter), reduced water-holding capacity, and lowered yield of cure cooked ham (Gariépy et al., 1999). These effects are caused by a ~70% augment in the content of muscle glycogen in RN⁻ carriers. The RN gene is a dominant gene discovered by Naveau et al. (1985) using segregation analysis of phenotypic data, which can be identified by a Napole yield evaluation, an indicator of the technological yield of ham production, or by an evaluation of the glycolytic potential of muscle. This gene appears in the form of 2 alleles: the *m*⁺ allele (normal allele) and the RN allele (the allele with a negative effect on Napole yield). Currently, the presence of this gene has been found in the Hampshire breed and Hampshire-based composite lines. The unfavorable allele (RN⁻) dramatically increases glycogen levels by approximately 70% in the sarcoplasm of white fibres and reduces the protein content of muscle, which seriously results in the worse technological quality of meat. Unlike the Hal gene, the RN gene has an effect on the extent, but not the rate, of pH fall (pH 24 h <5.5), which leads to the acidic type of meat. The RN⁻ allele causes a large drip loss in fresh meat and also increases cooking loss, which produces major financial losses in carrier pig.

The mechanism of RN in modulating glycogen content remained unclear until recently. Milan et al. (2000) firstly proved a mutation in AMP-activated protein kinase γ 3 (PRKAG3) associated with excess glycogen content in pig skeletal muscle. AMP-activated protein kinase (AMPK) is a heterotrimeric enzyme maintaining cellular and whole body energy homeostasis. Studies in experimental animals demonstrated that activation of AMPK in skeletal muscle could protect against insulin resistance. The regulatory γ 3 subunit of AMPK (PRKAG3) is expressed exclusively in skeletal muscle, and gamma subunit mutations interfere specifically with AMP activation. Subsequent studies

disclosed that a number of mutation in PRKAG3 encoding region. A mutation of R200Q mainly exists in Hampshire pigs and mutations of T32N, G52S and I199V exist in other breeds of pigs, which are the causes for mutation of *m*/*RN* in pigs.

The RN gene has been localized on chromosome 15, and a mutation in PRKAG3 gene associated with excess glycogen content could be identified with a new molecular test for better control of the RN gene (Milan et al., 2000).

A significant interaction between the Hal gene and the RN gene was demonstrated on porcine carcass and meat quality characteristics including subjective color, firmness, marbling scores, and for shear force (Hamilton et al., 2000). In their study, Halothane and RN carrier (Nn/RN⁻ *m*⁺) Hampshire boars were mated to dams that were homozygous for the normal allele of both genes (NN/*m*⁺ *m*⁺) to produce progeny of four genotypes: 1, NN/*m*⁺ *m*⁺; 2, Nn/*m*⁺ *m*⁺; 3, NN/RN⁻ *m*⁺; and 4, Nn/RN⁻ *m*⁺. Pigs with normal genes (NN/*m*⁺ *m*⁺) had the highest subjective scores for color, firmness, and marbling for genotypes 1, 2, 3, and 4, respectively. This study illustrates the negative effects of the Halothane and RN genes on fresh pork quality and suggests that in combination the detrimental effects of the two genes are additive for ultimate pH, objective color, and water-holding capacity.

Other candidate major genes Since Fujii et al. (1991) demonstrated that a mutation of ryanodine receptor (locus *ryr-1*) causes malignant hyperthermia in pigs, which leads to PSE meat, numerous studies have been launched into the field of genetic background and major gene identification for meat quality. Andersson et al. (1994) mapped the Quantitative Trait Loci (QTL) for growth and fatness in pigs using 105 genetic markers, and detected that a single region on chromosome 4 accounted for a large part of the breed difference in growth rate, fatness, and length of the small intestine. Over the past 15 years, the advances in the porcine genetic linkage map and discovery of useful candidate genes have led to valuable genes and trait information being discovered. QTL scans and candidate gene analyses have led to 110 publications which have identified 1, 675 QTL (Rothschild et al., 2007). More than 1,285 QTL associated with pork carcass characteristics and meat quality were identified until now. However, only few major genes were recognized as mentioned above.

By Bayesian statistical analyses, Janss et al. (1997) segregated two major genes that affecting a number of meat quality traits. It was postulated that cooking loss, two pH measurements, and possible backfat thickness are influenced by one gene, while the intramuscular fat and possibly shearforce and drip loss are influenced by the another gene.

Recently, Fernández et al. (2008) investigated associations between mitochondrial DNA polymorphisms

and meat quality traits (intramuscular fat and protein content of the longissimus) in an Iberian porcine line. The detected candidate non-sense substitutions are located in essential mitochondrial genes. Although the substitutions do not change the amino acid composition, a potential change in the secondary structure of their corresponding messengers can not be neglected.

Do et al. (2008) provided the SNP marker information to fine map QTL regions on pig chromosome 2 and clarified the relevance of SNP and quantitative traits in commercial pig populations.

Heart fatty acid binding protein gene (H-FABP) and adipocyte fatty acid binding protein gene (A-FABP) were supposed to influence intramuscular fat (IMF) deposition and backfat thickness. The polymorphism of H-FABP had been shown to be associated with IMF, and the pigs with aa/dd/HH genotype had the highest content of IMF (Gerbens et al., 1999). Furthermore, it was also reported there was a significant difference (about 1%) among genotypes of A-FABP in Duroc pigs.

NUTRITIONAL REGULATION OF MEAT QUALITY CHARACTERISTIC FORMATION

Since most characteristics of meat quality are quantitative traits determined by minor genes during pig growing and fattening. Formation of these characteristics virtually depends on the breeding circumstance of pigs. The nutritional ingredients may be more decisive than other factors. Therefore, nutritional modulation is then considered to be an approach to improve pork meat quality.

It has been well summarized that ractopamine, conjugated linoleic acid (CLA), and Vitamin E are three of the most promising feed additives to enhance pork composition and quality. Ractopamine hydrochloride (Paylean) has been registered for use in finishing pigs in the United States, but not yet in other countries. Ractopamine is a β -1 agonist, and exerts its action through the pathway of cyclic adenosine monophosphate (cAMP) by binding to receptors on membranes of muscle fiber cells and adipocytes (Mersmann 1998). Dietary supplementation with ractopamine during the finishing phase of pigs can improve average daily gain and feed conversion efficiency, but decrease carcass fatness (Anderson, 2000) and increase carcass leanness (Dunshea et al., 1993; Xiao et al., 1999). In order to maximize the effects of ractopamine, Dikeman (2000) indicated to increase the nutrient density in diets because of increased lean deposition without a corresponding increase in feed consumption.

Ractopamine can increase in shear force (decrease in tenderness) in some studies (Aalhus et al., 1992; Uttaro et al., 1993). However, Merkel (1988) and Dikeman (2000)

reported that ractopamine only contributed minor effects on most meat quality characteristics.

Beside as an energy source, CLA also has physiological activities (Chin et al., 1994). It could protect against atherosclerosis (Lee et al., 1994; Nicolosi et al., 1997), many types of cancer (Belury 1995; Ip, 1997) in laboratory animals, and improve the pork meat quality in pigs (Sun et al., 2004; Lauridsen et al., 2005). Interestingly, CLA displays the function of reducing subcutaneous fat, but consistently increasing intramuscular fat of loin muscle in pigs, which contributes positively to meat palatability (Dugan et al., 1997). Zhou et al. (2007) documented that CLA could differently regulate adipogenesis in stromal vascular cells from porcine subcutaneous adipose and skeletal muscle tissues, respectively. Martin et al. (2008) showed that dietary CLA increased the intramuscular fat content and modified the fatty acid profile in pigs, regardless of the multi unsaturated fatty acid (MUFA) level of the diets. Feeding CLA can increase fat hardness and reverse the softening effect of feeding canola oil on subcutaneous fat.

Vitamin E is a potent and lipid-soluble antioxidant, and its primary functions is to maintain and protect biological membranes against lipid peroxidation. Membrane phospholipids oxidation is a major cause of deterioration in meat quality and can affect many quality characteristics such as flavor, color, texture, nutritive value, and safety of the food (Buckley et al., 1995). Thus, inclusion of Vitamin E above dietary requirements can effectively reduced quality defects associated with lipid peroxidation. In pigs, Vitamin E is generally supplemented at the 200 mg/kg of feed level to improve meat color stability and reduce drip loss during refrigerated storage without any negative effects on growth performance and carcass quality (Monahan et al., 1990; Asghar et al., 1991; Dikeman 2000). Beneficial effects on sensory qualities involving freshness, tenderness and juiciness, and on the oxidative stability of pork have also been reported (Dirinck et al., 1996). Kerth et al. (2001) proved that feeding 600 IU/kg of vitamin E to the pigs at 36 to 70 d before slaughter increased the pH value of longissimus muscle, improved color and juiciness of lumbar muscle, and significantly decreased the happening of PSE muscle.

Major aspects of meat quality including flavor can be affected by nutrition, principally through its effects on the amount and type of fat in meat (Lu et al., 2008). Nutritional treatment can be used to manipulate the fatty acid content of muscle to improve nutritional balance, i.e. increasing the ratio of polyunsaturated fatty acids (PUFA): saturated fatty acid and reducing the ratio of n-6: n-3 PUFA. Increasing PUFA levels may also change flavor because of their greater susceptibility to oxidative breakdown and the

generation of abnormal volatile compounds during cooking (Lu et al., 2007). Obviously, supra-nutritional supplementation of Vitamin E in the diet can effectively prevent the deleterious effects of oxidative lipids on odour or flavor, especially for modification of fatty acid composition by adding PUFA in pig diets.

Other dietary additives can change the meat quality as well. Wang et al. (2008) reported that supplemental humic substances in diets at 5% or 10% levels significantly decreased backfat thickness ($p < 0.05$), and increased the marbling score significantly at a level of 10%.

It was indicated that a high level of magnesium (1,000 mg/kg) retarded glycogen degradation, alleviated the decrease of the pH value, and prevented the occurrence of PSE meat (Campion et al., 1971). Higher levels of manganese and zinc in diets were also demonstrated to prevent the occurrence of PSE meat (Coelho et al., 1994). However, there is no report on influence of manganese and zinc on hal gene expression. Some other nutrients could be used to improve meat quality, for example selenium, vitamin D, tryptophan, and their combinations (Nuernberg et al., 2002; Swigert et al., 2004).

APPLICATION OF NUTRIGENOMICS IN IMPROVING MEAT QUALITY

Companied with the advance of molecular biology, emergences of “-omics”, including genomics, transcriptomics, proteomics, highlight the solution to analyse the integrity and the relationship among complex factors during a particularly physiological process. Cagnazzo (2006) compared the gene expression profiles in prenatal muscle tissue of two pig breeds (Pietrain and Duroc) that differed in muscle characteristics using the microarray containing more than 500 genes related to myogenesis, energy metabolism, muscle structural genes, and some other genes from a porcine muscle cDNA library. It was shown that the genes involved in energy metabolism were expressed higher in prenatal Pietrain than in Duroc muscle tissue, meanwhile, the fatty acid metabolism genes show an opposite expression profile to the energy metabolism genes.

Lobjois et al. (2008) studied the relationship between gene expression variability and tenderness of cooked meat by using transcriptome analysis. They found the samples with Warner-Bratzler Shear Force (WBSF) values above 30 N could be effectively analysed for genes exhibiting a significant association of their expression level with shear force. The genes responding to the meat tenderness were involved in three functional networks: cell cycle, energy metabolism, and muscle development.

Pork meat quality formation is affected by breeds, nutritional status, and feeding systems in swine growing

and fattening. Skeletal intramuscular fat (IMF) is positively related to the meat quality and it may be one of the most important candidate traits that could be selected to understand the interaction of genes and nutrition supplies during meat quality formation in pigs. It has been shown that IMF along with shear force and drip loss was influenced by one recessive allele (Janss et al., 1997). However, the allele was not positioned yet. In addition, Janss et al. (1997) predicated that recessive allele might originate from a Chinese native breed (Maishan) and be absent in the Western founder lines.

Actually, some quantitative traits of meat quality including intramuscular fat can exhibit a various extent of phenotypes under different nutritional supplies, especially for some breeds of pigs which do not experience the strict selection for lean rate and growth performance. These pigs considerably carry the special genes who contribute to the certain meat quality. Thus, it is important that selecting the special breed of pigs to identify the major genes that influence the certain meat quality trait.

Until now, a number of studies have been implemented to detect quantitative trait loci (QTL) or major genes affecting porcine intramuscular fat. However, porcine intramuscular fat is not influenced by genetic background, but also by the nutritional status of pigs. Regardless of the nutritional influence, it is difficult to identify the major genes who affect these quantitative traits. Nutrigenomics is a study of the relationship between animal nutritional status and gene expressions using genomics, proteomics and metabolomics approaches, which provide advantageous protocols to identify the genes whose expression respond to phenotype formation of meat quality traits under different nutritional status.

In conclusion, the isolated or combined effects of environmental factors containing nutritional and genetic factors impose vital influences on pork meat quality. Some genes have a direct impact on the technological quality of meat and processed products, determining meat quality trait formation. However, most characteristics of meat quality were quantitative traits, which were determined by minor genes and whose expressions were impacted by nutritional levels and feeding systems. Recently, nutrigenomics is undergoing a gigantic progress, and it provides a promising approach to implore the relationship between nutritional and genetic factors during the process of certain economic meat trait formation and to evaluate the contributions of genes and nutrition. It may lift a new page in identifying the nutrition-responsive major genes for meat quality trait formation.

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