WHAT PRODUCERS CAN DO TO IMPROVE MEAT QUALITY: THE GENETIC APPROACH

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ABSTRACT

Traditional methods of genetic improvement have yielded long-term, significant improvement in traits relating to production efficiency and overall carcass quality; traits like growth rate, feed conversion, leanness and loin muscle area. These methods require widespread data collection and analysis for continued success. Traits associated with end product or consumer product quality have not received as much emphasis up to this point. These traits are costly to measure and require sampling from or cutting into parts of the carcass. New technology for selecting on molecular genetic markers (marker assisted selection, MAS) will unlock the potential for selecting for these new traits. By taking the costly measurements on smaller groups of pigs and associating differences in the traits with specific markers, the markers can become the selection tool eliminating the need for collecting costly trait data on a large number of pigs. Specialized terminal sire lines can be developed to target a variety of market characteristics and grading grids.

INTRODUCTION

The Ontario swine industry has been very successful in breeding and exploiting superior genetics to improve meat quality. So much so that the time has probably come to take stock of where the industry is and where it should be going. The industry is changing, most dramatically in the marketing and processing of commercial hogs. As the number of hogs sold on the basis of carcass specifications increases, the challenge of successfully marrying genetics and nutrition to produce the hog best suited to a specific grid is becoming more widespread. While it is theoretically possible to follow a genetic selection program to design the optimal hog for each grid, in practice this would be a waste of time and resources. Realistically, the grid specs can change much faster than a genetic program so the game would always be played in catch up mode to the frustration of all involved. Instead, the direction to take with genetic improvement is not going to be a single path. As an industry, we need to design a program that combines both maternal and paternal characteristics that creates a flexible, adaptable and profitable means of producing hogs for different market needs. Breeders will be working on a variety of lines with specific characteristics and documented performance results. Commercial producers will be working with seedstock suppliers to design the best combination of boars and gilts for market opportunities that are available. The fine tuning of these combined genotypes to hit the target grid(s) can then be done through feeding and management.

GENETIC IMPROVEMENT SUCCESS

Valuable lessons can be learned from what has gone before. The industry's success at improving meat quality has focused on traits related to production efficiency and overall product quality. Reducing the amount of fat in the carcass overall increases feed efficiency while at the same time addressing the consumer's growing interest in lean products. Reducing the amount of fat in the carcass has also enabled our industry to increase carcass weights and still achieve acceptable levels of fat on the heavier carcasses. However, this success has been quite uniform in nature. By measuring backfat depth and selecting for reduced backfat, breeders have been removing fat from the entire carcass. The Canadian Centre for Swine Improvement statistics indicate a genetic improvement of the lean yield of the Yorkshire carcass by 0.32%, the loin eye area by 0.4 sq. cm., reduced the age to 100 kg (increased growth rate) by 6.8 days, improved feed conversion by 0.09 kg of gain per kg of feed and reduced backfat by 0.57 mm between 2000 and 2005 (CCSI, 2006). Similar statistics for the Duroc reveal genetic improvement of the lean yield of the Duroc carcass by 1.03%, the loin eye area by 2.31 sq. cm., reduced the age to 100 kg (increased growth rate) by 7.6 days, improved feed conversion by 0.12 kg of gain per kg of feed and reduced backfat by 2.05 mm between 2000 and 2005 (CCSI, 2006). This translates into a change in market hogs of lean yield of the carcass by 0.07%, the loin eye area by 1.5 sq. cm., reduced the age to 100 kg (increased growth rate) by 6.9 days, improved feed conversion by 0.102 kg of gain per kg of feed and reduced backfat by 1.38 mm between 2000 and 2005 CCSI, 2006. The estimated value of this improvement in market hogs at $1.85 per hog in facility overhead savings from faster growth, $2.17 in reduced feed consumption and $0.82 more per hog for lean yield for a total increase in value of $4.84 per hog for the difference between 2000 and 2005 genetics.

All of these improvements, even when looking at just the last five years, represent a dramatic improvement in carcass value. Looking back over longer time frames shows that the trend started slowly in the 1960's with the introduction of performance recording. The trend grew stronger in the 1970's as technology like ultrasound was used to measure leanness of the live animal and, grew stronger again in the 1980's when genetic improvement statistics like estimated breeding values (EBVs) became widely available through the Federal-Provincial Record of Performance program (Kennedy et al., 1986). In the 1990's and new millennium, the trend dramatically accelerated as the number of traits increased and the integration of the data collection and data analysis systems added more value to the information being provided.

Today, the tools are available within the regional-national improvement system to custom tailor genetic improvement programs for a full spectrum of general or specific selection goals (De Vries, 1989; CCSI, 2006). Information is also available to support decision making for choosing replacement stock for commercial production systems with specific targets. So, at this point there are resources in place to assist us to achieve a variety of genetic improvement and seedstock selection goals.

GENETIC IMPROVEMENT DIRECTIONS

Noticeably absent from this discussion is any mention of consumer product quality. One can argue that reduced fat is a component of consumer product quality. A counter argument is that our motivation as an industry for reducing carcass fat was a combination of reducing fat in the product and improving production efficiency because lean hogs convert feed better; fat is expensive to produce. So addressing fat as a consumer product characteristic was only part of the goal when reducing carcass fat. As an industry, there has not been significant investment of genetic improvement resources to address consumer product quality traits such as marbling, meat colour, flavour, tenderness, water holding capacity, pH and other measures of meat characteristics that affect consumer product quality. At the same time, there is a challenge to define quality from the consumer perspective when production systems potentially have both domestic and international markets (Ngapo, 2005). Product quality data is expensive and difficult to collect and with varying definitions of quality, the benefit to building a selection and production program around consumer product quality is difficult to identify. All of the traits that have been the focus of an improvement program so far have been traits that can be measured easily and relatively cheaply on the live animal either directly or indirectly using non-invasive technology like ultrasound.

So, here we are with an efficient system of genetic improvement and aggressive uptake of new genetics by commercial producers. This system works well with our traditional traits but it is time to look to the future and determine how best to work on traits that are much more closely related to product quality.

While accurate predictions of the future are limited to expensive phone calls advertised on late night television, extrapolating from existing trends and observing trends in other countries and commodities may give some idea of what the future holds for pork. One very clear trend is the segmentation of the marketplace, this is being experienced by many commodities. Each year a greater percentage of pork is being processed on the basis of a specification for a particular carcass. Some of these specifications include traits that we do not routinely consider in our genetic programs like colour and marbling (Webb, 2005). As these characteristics find widespread inclusion in carcass specifications, the economic incentive for genetic improvement that has been missing up to this point is now in place. A missing component so far has been economic return for investment in genetic improvement of meat quality traits. It is clear that the carcass specification trend will continue and it is very likely that there will be more meat quality characteristics that become part of the specifications. Now that the economic picture is becoming clearer, how can genetic improvement chase a moving target?

Adapting will take some new approaches on the genetic improvement side and will mean some new information for commercial producers to use to select their replacement stock. Breeding programs have long been specialized into maternal and terminal sire lines (Moav and Hill, 1966). Production systems are generally based on crossbred females bred to terminal sires to produce market hogs. Female lines are selected for fertility as well as (but with less emphasis overall) current production and carcass traits. These female lines are crossed to produce females with hybrid vigour for reproductive traits to maximize piglet production. These crossbred females are then bred to a terminal sire boar to create the commercial hogs

for market. Although variations exist on this theme, it is a generally accepted production system, even within vertically integrated operations.

Within this general production system, the female resources represent a significant investment at all levels. Therefore rapid genetic change in female lines to respond to differences in carcass characteristics is probably next to impossible and definitely economically unsound (Smith, 1985). Longer term trends can and should be built into the female selection program but short term adjustments would be far too slow and expensive. That leaves us with the male side of the equation. Most breeding programs are already geared towards using the characteristics of the terminal sire lines to define the market hog characteristics. To incorporate meat quality traits in the breeding program, for the foreseeable future the place to do that is in the terminal sire lines.

WHAT TRAITS WILL BE IMPORTANT

One of the advantages of the initial approach of looking at traits of economic importance to the production system is the clear definition of what traits are important. By defining a production scope, the importance and relevance of traits are very clear. When defining the importance of traits closer to the consumer and further removed from the production economics, the challenge increases.

Traits with emerging importance will be more closely related to consumer product quality. Consumer preference surveys suggest appearance has a lot to do with a perception of quality that leads to a purchase decision. Preferred appearance factors differ regionally and globally. Once the product is purchased, the eating experience should live up to the perception to complete the picture (Ngapo, 2005). Appearance factors for meat include colour, marbling, lack of fat cover and lack of seepage in the package. Lack of fat cover we have already addressed with conventional selection but colour and marbling (or intramuscular fat – IMF) are more challenging. Colour and IMF can be scored visually on the loin of a hanging carcass as part of the grading process so routine measurement of these traits can be done with additional labour in the processing plant. There is, however, an additional cost because these measurements require ribbing the carcass like a beef carcass which splits the loin in two sections, something not usually done for pork. Lack of seepage in packaging is related to pH and water holding capacity both of which require analysis of a sample of muscle post-mortem which escalates the cost of measurement rapidly. Water holding capacity also has a large impact on the potential for successful further processing. Other traits may emerge in the future but the focus of new traits will be centred around the consumer and will be difficult and costly to measure on large numbers of animals.

New genetic improvement technology makes the challenge somewhat easier. In addition to traditional approaches with EBVs (See, 2005), we also have the capability to use molecular genetic markers in the selection process. Swine breeders in Ontario were world-leading adopters of marker assisted selection (MAS) technology with the malignant hypothermia or PSS gene which is now known to be the ryanodine receptor gene (*RYR1*) (O'Brien et al., 1993). The deleterious allele was very quickly eliminated from many breeders' herds through

the use of the HAL-1843™ molecular genetic test. Similar technology is being developed and will be developed for important genes influencing meat and carcass quality traits.

MAS requires a marker or difference in the DNA sequence that is identified in the lab and associated with a difference in an important trait or traits. The process of finding the association requires collecting data on a limited number of animals and matching the difference in the DNA with the difference in the trait(s). The difference in the DNA is usually not the actual sequence change that creates the difference in the trait. Instead, the difference in the DNA that we use as a marker is just a convenient handle with which to track the nearby section of DNA that contains the causative difference. An analogy is an eartag in a pig; each individual pig is very difficult to recognize just by sight but with a unique eartag, it becomes very easy to locate and track a pig we are interested in. With MAS, the opportunities open up dramatically for traits that can be the focus of genetic improvement programs. The work to develop the association between the molecular genetic markers and the meat quality traits can be done on relatively small groups of pigs and, once validated in other lines, can be used widely to make selection decisions with the need for collecting data on the carcasses. Table 1 shows a list of molecular genetic markers detected by studying specific genes with a suspected role in biochemical aspects of meat and carcass quality; what is referred to as a candidate gene approach. Table 2 shows a list of regions of the genome by chromosome that have been associated with differences in meat and carcass quality traits by scanning the genome for regions associated with various phenotypes.

Table 1.   Candidate genes associated with quantitative traits in swine.

Candidate gene	Normal function	Main traits the gene is associated with	Main references
RYR1	The major Ca2+ release channel	PSE pork, lean content	Estany et al., 1998; Hamilton et al., 2000
RN	Adenosine monophos-phate-activated protein kinase	Muscle pH, lean content	Fernandez et al., 1992; Reinsch et al., 1998; Miller et al., 2000
Pit1	Pituitary-specific positive transcription factor	Backfat, growth	Yu et al., 1995; Brunsch et al., 2002
Obese	Leptin protein	Fat deposition, body weight	Jiang and Gibson, 1999; Kennes et al., 2001
IGF-1	Insulin-like growth factor	Daily gain	Casas-Carrillo et al., 1997
GH	Growth hormone	Fat deposition, lean percentage	Knorr et al., 1997
SLA	Major histocompatability complex (swine lymphocyte antigen system)	Body weight, litter size	Rothschild et al., 1986; Milan et al., 1998
H-FABP	Fatty acid transport	Fat deposition, IMF	Gerbens et al., 2001
A-FABP	Fatty acid transport	Fat deposition, IMF	Gerbens et al., 2001
Myostatin	Transforming growth factor	Muscle mass	Sonstegard et al., 1998

Table 2. **Growth and carcass composition Quantitative Trait Loci (QTL) detected on different swine chromosomes.**

Chromosome	QTL	Main references
1	Backfat, body weight, loin eye area, leanness, daily gain, marbling score, drip loss.	Moser et al., 1998; Rohrer and Keele, 1998a, b; Paszek et al., 1999; Rohrer, 2000; Malek et al., 2001a, b.
2	Backfat, intramuscular fat content, growth rate, drip loss, water-holding capacity.	de Koning et al., 2000; Rohrer, 2000; Malek et al., 2001a, b.
3	Birth weight, number of fibres in muscle, intestinal length.	Knott et al., 1998; Milan et al., 1998; Malek et al., 2001a.
4	Backfat, abdominal fat, growth rate, meat firmness score.	Andersson et al., 1994; Rothschild et al., 1995; Knott et al., 1998; Walling et al., 1998; Knott et al., 2002.
5	Backfat, average daily gain, loin colour, loin pH	Knott et al., 1998. Malek et al., 2001a, b.
6	Backfat, intramuscular fat, daily gain, carcass length.	Moser et al., 1998; de Koning et al., 1999, 2000; Rohrer, 2000; Malek et al., 2001a, b.
7	Backfat, meat color and firmness score, average daily gain.	Rothschild et al., 1995; Rohrer and Keele, 1998a, b; Wang et al., 1998; de Koning et al., 1999; Rohrer, 2000.
8	Backfat, average daily gain, carcass weight.	Rohrer, 2000; Malek et al., 2001a, b.
9	Average daily gain, backfat.	Rohrer, 2000; Wada et al., 2000; Malek et al., 2001a, b.
10	Growth rate, tenderness and marbling score.	Knott et al., 1998; Wada et al., 2000; Malek et al., 2001a, b.
11	Carcass length, drip loss.	Malek et al., 2001a, b.
12	Early growth rate, last rib fat depth and loin colour score.	Rohrer, 2000; Malek et al., 2001a, b.
13	Backfat, carcass weight, water-holding capacity, average daily gain.	Andersson et al., 1994; Knott et al., 1998, Malek et al., 2001a, b
14	Loin eye area, backfat, ham pH, colour and percent cooking loss, tenderness score.	Rohrer and Keele, 1998a, b; Malek et al., 2001a, b.
15	Loin colour, ham and loin pH, tenderness scores.	Malek et al., 2001b.
17	Colour score, juiciness score, loin colour.	Malek et al., 2001b.
18	Average backfat, loin colour.	Malek et al., 2001a, b
X	Backfat, loin eye area, carcass length.	Rohrer and Keele, 1998a, b; Rohrer, 2000.

Tables 1 and 2 represent a shopping list of resources for MAS. The genes identified in Table 1 were found through their potential involvement in a particular biochemical pathway involved in meat quality. As a result, if the connection to a meat quality trait is significant the

application to MAS tends to be more direct. Some of these genes are already the target of MAS; *RYR1* through the HAL-1843™ test and *RN*. Both of these genes have a variant that has a detrimental effect on meat quality and as such are treated like genetic diseases where the deleterious allele is being selected out of the population. Other genes have variants (alleles) that have a beneficial effect on the trait they are associated with. In these cases the goal is to increase the frequency of the beneficial allele in the population while maintaining ongoing selection using EBVs for the traits that we continue to select for "the old fashioned way". This can be done in a variety of ways but the most common is to combine the marker information and the EBVs in an overall index that weights each by the value the traits contribute to the carcass value (Dekkers, 1999). By adjusting the emphasis on the various components in the index, terminal sire lines can be fine tuned to emphasize specific meat quality traits. That specificity is then information that can be used by commercial producers to select replacement sire line stock to target specific carcass and meat quality traits for specific markets and grading grids.

CONCLUSIONS

The traditional methods of selecting on EBVs have produced a lean, fast growing hog that produces a reasonable quality carcass in an efficient manner. Moving forward to incorporate selection for meat quality traits will involve using new genetic improvement technology like MAS in combination with the traditional EBVs for ongoing improvement of production traits.

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LITERATURE CITED

Andersson, L., C.S. Haley, H. Ellegren, S.A. Knott, M. Johansson, K. Andersson, L. Andersson-Eklund, I. Edfors-Lilja, M. Fredholm, I. Hansson, J. Håkansson and K. Lundström. 1994. Genetic mapping of quantitative trait loci for growth and fatness in pigs. Science 263: 1771-4.

Brunsch, C., I. Sternstein, P. Reinecke and J. Bieniek. 2002. Analysis of associations of PIT1 genotypes with growth, meat quality and carcass composition traits in pigs. J. Appl. Genet. 43: 85-91.

CCSI, 2006. Canadian Centre for Swine Improvement. http://www.ccsi.ca/ 06/02/20.

Casas-Carrillo, E., A. Prill-Adams, S.G. Price, A.C. Clutter and B.W. Kirkpatrick. 1997. Relationship of growth hormone and insulin-like growth factor-1 genotypes with growth and carcass traits in swine. Anim. Genet. 28: 88-93.

Dekkers, J.C.M. 1999. Optimizing Strategies for Marker-Assisted Selection. Proc. Plant and Animal Genome VII, San Diego, California, Jan. 18-22, 1999.

de Koning, D.J., L.L. Janss, A.P. Rattink, P.A. van Oers, B.J. de Vries, M.A. Groenen, J.J. van der Poel, P.N. de Groot, E.W. Brascamp and J.A. van Arendonk. 1999. Detection of quantitative trait loci for backfat thickness and intramuscular fat content in pigs (Sus scrofa). Genetics 152: 1679-90.

de Koning, D.J., A.P. Rattink, B. Harlizius, J.A. van Arendonk, E.W. Brascamp and M.A. Groenen. 2000. Genome-wide scan for body composition in pigs reveals important role of imprinting. Proc. Natl. Acad. Sci. USA: 7947-50.

De Vries, A.G., 1989. A model to estimate economic values of traits in pig breeding. Livest. Prod. Sci. 21, 49-66.

Estany, J., J. Tibau, J. Soler and J.L. Noguera. 1998. Responses in production, carcass and meat quality traits after an hyperprolific cycle of selection in pigs. *In* 6th World Congr. on Genet. Appl. to Livest. Prod., pp. 628-631.

Fernandez, X., E. Tornberg, J. Naveau, A. Talmant and G. Monin. 1992. Bimodal distribution of the muscle glycolytic potential in French and Swedish populations of Hampshire crossbred pigs. J. Sci. Fd. Agric. 59: 307-311.

Gerbens, F., F.J. Verburg, H.T. Van Moerkerk, B. Engel, W. Buist, J.H. Veerkamp and M.F. te Pas. 2001. Associations of heart and adipocyte fatty acid-binding protein gene expression with intramuscular fat content in pigs. J. Anim. Sci. 79: 347-54.

Hamilton, D.N., M. Ellis, K.D. Miller, F.K. McKeith, and D.F. Parrett. 2000. The effect of the Halothane and Rendement Napole genes on carcass and meat quality characteristics of pigs. J. Anim. Sci. 78: 2862-7.

Jiang, Z.H. and J.P. Gibson. 1999. Genetic polymorphisms in the leptin gene and their association with fatness in four pig breeds. Mamm Genome 10: 191-3.

Kennedy, B.W., G.F.S. Hudson and L.R. Schaeffer. 1986. Evaluation of genetic change in performance tested pigs in Canada. Proc. 3-rd World Congr. on Genet. Appl. to Livest. Prod., Lincoln, Nebraska. X:149-154.

Kennes, Y.M., B.D. Murphy, F. Pothier and M.F. Palin. 2001. Characterization of swine leptin (LEP) polymorphisms and their association with production traits. Anim. Genet. 32: 215-8.

Knorr, C., G. Moser, E. Muller and H. Geldermann. 1997. Associations of GH gene variants with performance traits in F2 generations of European wild boar, Pietrain and Meishan pigs. Anim. Genet. 28: 124-8.

Knott, S.A., L. Marklund, C.S. Haley, K. Andersson, W. Davies, H. Ellegren, M. Fredholm, I. Hansson, B. Hoyheim, K. Lundstrom, M. Moller and L. Andersson. 1998. Multiple marker mapping of quantitative trait loci in a cross between outbred wild boar and large white pigs. Genetics 149: 1069-80.

Knott, S.A., P.E. Nystrom, L. Andersson-Eklund, S. Stern, L. Marklund, L. Andersson and C.S. Haley. 2002. Approaches to interval mapping of QTL in a multigeneration pedigree: the example of porcine chromosome 4. Anim. Genet. 33: 26-32.

Malek, M., J.C. Dekkers, H.K. Lee, T.J. Baas and M.F. Rothschild. 2001a. A molecular genome scan analysis to identify chromosomal regions influencing economic traits in the pig. I. Growth and body composition. Mamm. Genome 12: 630-6.

Malek, M., J.C. Dekkers, H.K. Lee, T.J. Baas, K. Prusa, E. Huff-Lonergan and M.F. Rothschild. 2001b. A molecular genome scan analysis to identify chromosomal regions influencing economic traits in the pig. II. Meat and muscle composition. Mamm. Genome 12: 637-45.

Milan, D., J.P. Bidanel, P. Le Roy, C. Cevalet, N. Woloszyn, J.C. Caritez, J. Gruand, H. Lagant, M. Bonneau, L. Lefaucheur, C. Renard, M. Vaiman, P. Mormède, C. Désautés, Y. Amigues, F. Bourgeois, J. Gellin and L. Ollivier. 1998. Curent status of QTL detection in Large White x Meishan crosses in France. *In* 6th World Congr. on Genet. Appl. to Livest. Prod., pp. 414-417.

Miller, K.D., M. Ellis, F.K. McKeith, B.S. Bidner and D.J. Meisinger. 2000. Frequency of the Rendement Napole RN- allele in a population of American Hampshire pigs. J. Anim. Sci. 78: 1811-5.

Moav, R. and W.G. Hill, 1966. Specialized sire and dam lines. IV. Selection within lines. Anim..Prod. 8, 395-390.

Moser, G., E. Muller, P. Beeckman, G. Yue and H. Geldermann. 1998. Mapping of QTL in F_2 generations of Wild boar, Pietrain and Meishan pigs. *In* 6th World Congr. on Genet. Appl. to Livest. Prod., pp. 478-481.

Ngapo, T. 2005. Findings of International Consumer Studies. Proc. NSIF Conf., December 2005, Ottawa, Ontario.

O'Brien, P.J., H. Shen, C.R. Cory and X. Zhang. 1993. Use of a DNA-based test for the mutation associated with porcine stress syndrome (malignant hyperthermia) in 10,000 breeding swine. J. Am. Vet. Med. Assoc. 203: 842-51.

Paszek, A.A., P.J. Wilkie, G.H. Flickinger, G.A. Rohrer, L.J. Alexander, C.W. Beattie and L.B. Schook. 1999. Interval mapping of growth in divergent swine cross. Mamm. Genome 10: 117-22.

Reinsch, N., C. Looft, I. Rudat and E. Kalm. 1998. Is the porcine RN locus a pleiotropic QTL? A Bayesian marker assisted segregaton analysis. Genet. Sel. Evol. 30: 257-273.

Rohrer, G.A. 2000. Identification of quantitative trait loci affecting birth characters and accumulation of backfat and weight in a Meishan-White Composite resource population. J. Anim. Sci. 78: 2547-53.

Rohrer, G.A. and J.W. Keele. 1998a. Identification of quantitative trait loci affecting carcass composition in swine: I. Fat deposition traits. J. Anim. Sci. 76: 2247-54.

Rohrer, G.A. and J.W. Keele. 1998b. Identification of quantitative trait loci affecting carcass composition in swine: II. Muscling and wholesale product yield traits. J. Anim. Sci. 76: 2255-62.

Rothschild, M.F., H.C. Liu, C.K. Tuggle, T.P. Yu and L. Wang. 1995. Analysis of pig chromosome 7 genetic markers for growth and carcass performance traits. J. Anim. Breed Genet. 112: 341-348.

Rothschild, M.F., C. Renard, G. Bolet, P. Dando and M. Vaiman. 1986. Effect of swine lymphocyte antigen haplotypes on birth and weaning weights in pigs. Anim. Genet. 17: 267-72.

See, T. 2005. Incorporation of new reproduction and meat quality traits into genetic evaluation programs. Proc. NSIF Conf., December 2005, Ottawa, Ontario.

Smith, C., 1985. Scope for selecting many breeding stocks of possible economic value in the future. Anim. Prod. 41, 403-412.

Sonstegard, T.S., G.A. Rohrer and T.P. Smith. 1998. Myostatin maps to porcine chromosome 15 by linkage and physical analyses. Anim. Genet. 29: 19-22.

Walling, G.A., A.L. Archibald, J.A. Cattermole, A.C. Downing, H.A. Finlayson, D. Nicholson, P.M. Visscher, C.A. Walker and C.S. Haley. 1998. Mapping of quantitative trait loci on porcine chromosome 4. Anim. Genet. 29: 415-24.

Wada, Y., T. Akita, T. Awata, T. Furukawa, N. Sugai, Y. Inage, K. Ishii, Y. Ito, E. Kobayashi, H. Kusumoto, T. Matsumoto, S. Mikawa, M. Miyake, A. Murase, S. Shimanuki, T. Sugiyama, Y. Uchida, S. Yanai and H. Yasue. 2000. Quantitative trait loci (QTL) analysis in a Meishan x Gottingen cross population. Anim. Genet. 31: 376-84.

Wang, L., T.P. Yu, C.K. Tuggle, H.C. Liu M.F. and Rothschild. 1998. A directed search for quantitative trait loci on chromosomes 4 and 7 in pigs. J. Anim. Sci. 76: 2560-7.

Webb, J. 2005. Traceability: Implications on Genetic Improvement and Consumers DNA-based tracking opportunities. Proc. NSIF Conf., December 2005, Ottawa, Ontario.

Yu, T.P., C.K. Tuggle, C.B. Schmitz and M.F. Rothschild. 1995. Association of PIT1 polymorphisms with growth and carcass traits in pigs. J. Anim. Sci. 73: 1282-8.