

MAPPING OF QUANTITATIVE TRAIT LOCI FOR WEIGHT, CARCASS AND MEAT QUALITY TRAITS ON PIG CHROMOSOMES SIX AND THIRTEEN

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Introduction

The pig has several advantages for QTL mapping including three-generation pedigrees that can be generated in a reasonable amount of time, breeds and lines with variation in traits of economic importance and a well-developed genetic map (Rohrer et al., 1996). The first QTL mapping studies in pigs exploited large differences between the lines such as crosses between commercial lines and Wild Boar (e.g. Andersson et al., 1998) or Chinese Meshian (e.g. Rohrer and Keele, 1998) animals. It is both of scientific and commercial interest to know whether similar effects can be found in breeds commonly used in commercial populations. In 2001, Iowa State published the results of efforts to map QTL using a cross between Berkshire grand sires and Yorkshire grand dams (Malek et al. 2001a,b). In 1999, the Illinois Meat Quality Pedigree (IMQP) was started at the University of Illinois (Moorman Swine Farm) by crossing Berkshire grand sires and Duroc grand dams. The Berkshire breed is known for its desirable meat quality traits but is typically slower growing and fatter. In contrast, the Duroc breed can be characterized as having moderate to good meat quality with high lean growth rate. The purpose of this report is to summarize the results from the University of Illinois study on QTL influencing live weight, carcass and meat quality traits on *Sus Scrofa* (SSC) chromosomes 6 and 13.

Materials

The IMQP population consisted of three Berkshire grand sires, eight Duroc grand dams, six F₁ males and 56 F₁ females. From July 2000 to August 2001, 142 F₂ litters were farrowed, producing 1,068 progeny. Each F₁ sow farrowed one to four times and most multiple mated sows were mated to the same sire, although some were mated to two different sires. Cross fostering was allowed to stabilize litter size and all F₂ animals were weaned at 21 d of age. All protocols used were approved by the Institutional Animal Care and Use Committee. Average, minimum and maximum values for all phenotypes recorded in the F₂ population are provided in Table 1.

Table 1. Number of observations (N), mean, minimum and maximum values for all traits recorded in the F₂ population.

<i>Trait</i> ¹	<i>N</i>	<i>Mean</i>	<i>Minimum</i>	<i>Maximum</i>
Dressing	809	76.93	43.20	83.11
Hot_Car. (kg)	809	191.20	127.00	232.00
45m_pH	809	6.14	5.46	7.14
24h_pH	809	5.65	5.18	6.61
Length (cm)	808	81.20	74.93	87.63
Last_Lum (cm)	809	2.40	1.27	4.83
Last_Rib (cm)	809	2.56	1.27	5.08
Fir_Rib (cm)	808	4.10	1.52	6.35
Ten_Rib (cm)	809	2.34	1.02	4.32
AvgBfat (cm)	808	2.85	1.63	4.83
LEA (cm ²)	809	6.04	3.70	9.30
Color	809	3.13	1.00	5.00
Marbling	809	3.04	1.00	9.00
Firmness	809	2.93	1.00	5.00
h_L	809	53.46	37.69	67.02
h_a	809	8.69	4.68	13.29
h_b	809	15.99	11.65	20.45
Drip Loss	786	3.69	0.30	10.30
Moisture	809	73.73	67.04	76.36
Fat	809	3.47	1.27	13.28
GP	560	124.06	54.00	302.00
Cook_Loss	809	26.08	9.70	40.20
Shear	809	2.46	1.10	5.10
Juicy	809	7.43	2.40	11.00
Tenderness	809	7.27	2.80	12.30
Off_Flavor	809	14.93	13.60	15.00
B_Wt (kg)	806	1.67	0.66	2.76
21d_wt (kg)	804	5.76	1.98	9.98
42d_wt (kg)	808	12.29	5.40	20.65
63d_wt (kg)	770	22.70	10.70	36.75
84d_wt (kg)	589	36.19	22.95	51.60
105d_wt (kg)	751	39.96	13.50	64.70
126d_wt (kg)	661	54.23	22.75	84.25
147d_wt (kg)	662	70.39	32.35	105.05
168d_wt (kg)	620	86.01	48.30	121.25
189d_wt (kg)	494	99.16	62.50	132.20
210d_wt (kg)	224	104.45	74.75	127.40
240d_wt (kg)	18	108.52	94.20	118.25

¹ Dressing=dressing percentage; Hot_Car=hot carcass weight; 45m_pH=pH at 45 m post mortem; 24h_pH=pH at 24 h post mortem; Length=carcass length; Last_Lum=last lumbar fat; Last_Rib= last rib fat; Fir_Rib=first rib fat; Ten_Rib=tenth rib fat;

AvgBfat=average backfat; LEA=loin eye area; Color=taste panel color; Marbling=marbling; Firmness=firmness; h_L=CIE Hunter's L* score; h_a=CIE Hunter's a* score; h_b=CIE Hunter's b* score; Drip Loss=drip loss; Moisture=moisture; Fat=fat percentage; GP=glycolitic potential; Cook_Loss=cooking loss; Shear=shear force; Juicy=juiciness; Tenderness=tenderness; Off_Flavor=off-flavor; B_Wt= birth weight; 21d_wt= live weight at 21 d; 42d_wt= live weight at 42 d; 63d_wt= live weight at 63 d; 84d_wt= live weight at 84 d; 105d_wt= live weight at 105 d; 126d_wt= live weight at 126 d; 147d_wt= live weight at 147 d; 168d_wt= live weight at 168 d; 189d_wt= live weight at 189 d; 210d_wt= live weight at 210 d; 240d_wt= live weight at 240 d.

Measurements

Live weight measurements were obtained from birth to 240 d of age, approximately every 21 d. Pigs were weaned at 21 d, reared in nursery units, and move to grower units and then finisher units. Pigs had ad libitum access to water and a corn-soybean meal-based finisher diet. Pens of pigs were taken off test and sent to harvest when their average weight was within 3 kg of the target weight of 113 kg.

All animals were harvested at the University of Illinois Meat Sciences Laboratory. Pigs were slaughtered using standard commercial procedures and the carcasses were stored in a 4°C chiller. Hamilton et al. (2003) provide a more detailed description of the slaughter procedures and measurement protocols.

Hot carcass weight was measured and carcass measurements were recorded from the left side of each carcass at 24 h postmortem. Carcass length (measured from the cranial tip of the aitch bone to the cranial edge of the first rib adjacent to the thoracic vertebra), midline subcutaneous fat measurements (opposite the first rib, last rib, and last lumbar vertebra), loin area (measured at three-quarters of the distance across the longissimus muscle at the 10th rib) were recorded. Longissimus color, firmness, and marbling were assessed using a five (color and firmness) or ten point (marbling) subjective scale. The longissimus muscle from the right side of each carcass was removed for further analysis.

Glycolitic potential and pH measurements were obtained at the University of Illinois Meat Science Laboratory. Ultimate pH was determined on the carcass. Drip loss percentage was calculated using a 2.5-cm-thick chop from the longissimus that was weighed, placed in a Whirl-pak bag (NASCO, Modesto, CA), suspended in a 4°C cooler for 48 h, and then reweighed. A similar chop was used to estimate glycolitic potential (GP) using Monin and Sellier (1985) formula: $GP(\mu\text{mol/g wet tissue}) = 2(\text{glycogen} + \text{glucose-6-phosphate} + \text{glucose}) + \text{lactate}$. Glycogen, glucose-6-phosphate, lactate and glucose measurements are described by Hamilton et al. (2003).

A 10-cm section of the longissimus muscle was frozen for at least 7 d prior to shear force and taste panel evaluations. For Instron shear force measurements, the chops were cooked on open-hearth grills and to compute the cooking loss percentage, chops were weighed before and after cooking. For sensory evaluation, the panelists assessed tenderness, juiciness, and off-flavor using a twelve point subjective scale. Objective indicators of color (CIE L*, a*, and b*) were measured on the cut surface of the longissimus muscle using a Hunter LabScan Spectrocolorimeter (model XE, Hunter Associates Laboratory,

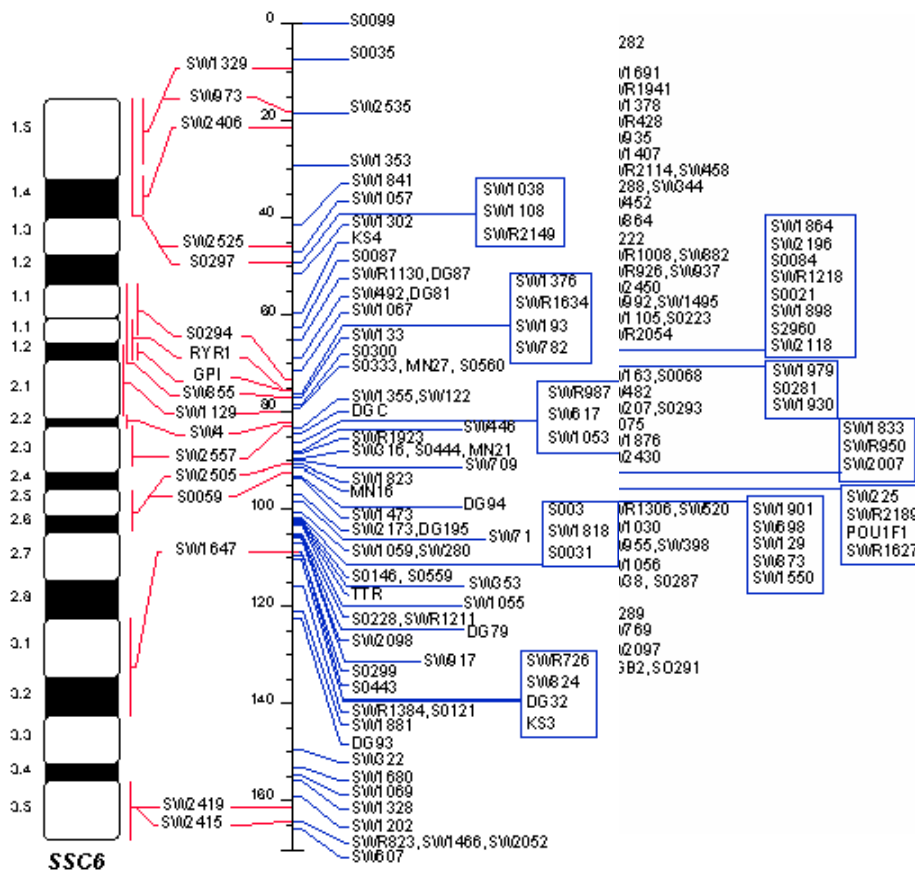
Inc., Reston, VA) set at the D65 and 10° angle of reflection. A homogenized longissimus muscle sample was used to measure fat and moisture contents, expressed as a percentage, as described by Novakofski et al. (1989). Samples were oven dried and fat was extracted as described by Hamilton et al. (2003).

Genotypic data

Ten microsatellite markers were genotyped in all parental, 65 F1 and 811 F2 animals on SSC 6. Marker genotypes were checked against pedigree information for inconsistencies. Genotypic information was considered missing if the genotyping inconsistency could not be resolved. Linkage maps were produced using CRI-MAP (Green et al., 1990). The marker identification and marker spacing based on the ARS USDA MARC map and the IMQP data set (in parenthesis) are: S0035, 34.2 cM (39.6 cM), SW1841, 27.2 cM (27.5 cM), SW492, 6.6 cM (7.8 cM), RYR1, 4.9 cM (2.9 cM), SW1129, 13.7 cM (not available), SW1473, 14.8 cM (33.4 cM from last available marker), SW1647, 7.3 cM (13.2 cM), S0121, 33.8 cM (28.5 cM), SW322, 11.6 cM (8.6 cM), and SW2419. Distances and orders were consistent with published results and so analysis was based on the public map values (Figure 1).

Nine microsatellite markers on SSC 13 were genotyped on 801 F2 animals across 86 families. The estimated sex-averaged map used ten markers spanned 125.7 cM and was compared with the ARS USDA-MARC current public map available. The marker identification and marker spacing based on the ARS USDA MARC map and the IMQP data set (in parenthesis) are: S0282, 14.1 cM (12.0 cM), SWR1941, 5.0 cM (9.7 cM), SW1378, 16.3 cM (25.2 cM), SW344, 22.6 cM (21.7 cM), SW1495, 12.1 cM (15.7 cM), SW225, 4.3 cM (7.4 cM), SW520, 27.8 cM (20.3 cM), SW2440, 9.9 cM (13.5 cM), and S0289. Relative distances and orders were consistent with published results and so analysis was based on the public map values (Figure 1).

Figure 1. ARS USDA-MARC Swine Genome Map for chromosomes 6 and 13. (<http://www.genome.iastate.edu/maps/marcmap.html>).



The information content distribution along SSC 6 and 13 for the additive, dominance and imprinting components are presented in Figure 2a and 2b, respectively. A least square regression interval mapping analysis following the approach of Haley et al. (1994) was implemented in QTL Express (Seaton et al., 2002) using the outbred F₂ population option. Briefly, a diallelic QTL with alternative alleles fixed in each parental breed was assumed and the basic model used to describe the phenotype is:

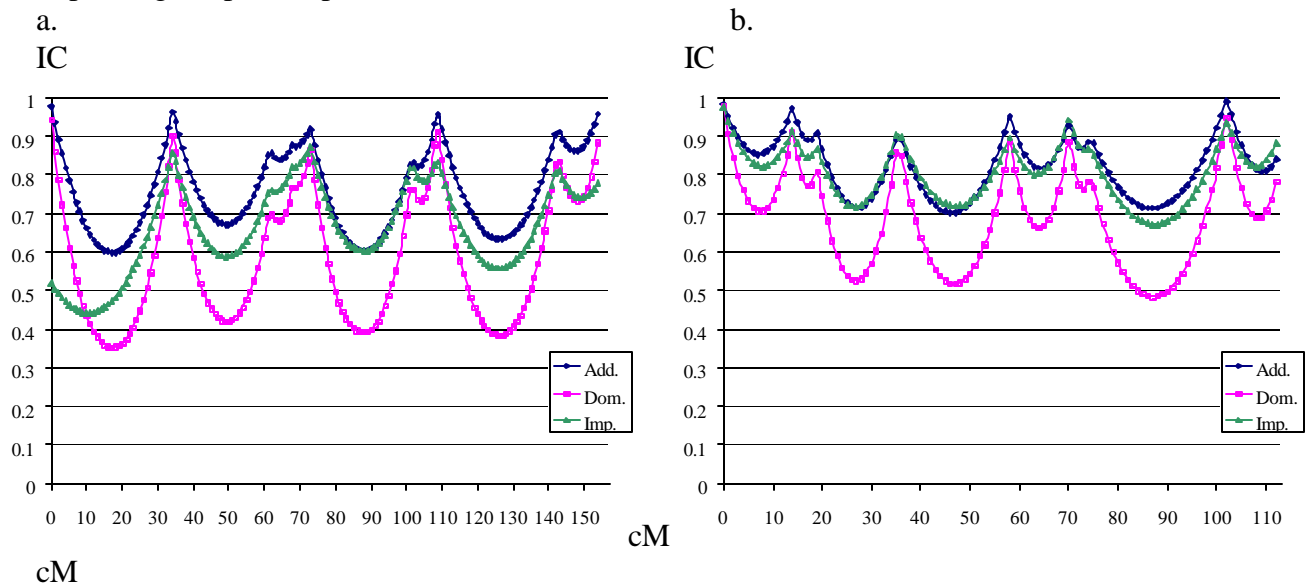
$$y_{ijkl} = \text{fixed effects}_i + c_a a_j + c_d d_k + c_i i_l + e_{ijkl}$$

where y_{ijkl} is the phenotypic record of the F₂ offspring with fixed effects level i , additive effect a_j , dominance effect d_k , and imprinting effect i_l . Twelve growth traits and 27 carcass and meat quality traits were studied. The fixed effects varied with trait and included sex, birth month-year (13 contemporary groups), parity (three levels), and covariates litter size, weight or age at slaughter. The fixed effects included in the model varied with the phenotype studied. For weight at birth, and d 21, 42, 63 and 84 the fixed effects were sex, parity of sow, litter size, and birth month-year. For weight at d 105, 126, 147, 168, 189, 210 and 240 fixed effects were as before including as covariates age at slaughter (on models for SSC six) or weight at slaughter (on models for SSC six and 13) and excluding parity and litter size. The carcass and meat quality traits evaluated

included pH at 45 m and 24 h postmortem, glycolitic potential, color, cooking loss, dressing percentage, drip loss, fat percentage, firmness, first rib, tenth rib, last lumbar, last rib and average backfat thickness, hot carcass weight, muscle color measurements L* (lightness), a* (redness), and b* (yellowness), loin eye area, carcass length, marbling, moisture, off-flavor, shear force, and tenderness.

The terms c_a , c_d and c_i represent the additive, dominance and imprinting coefficients, and e_{ijkl} is the residual. The additive, dominance and imprinting coefficients were calculated as $c_a = pr(QQ) - pr(qq)$, $c_d = pr(Qq) + pr(qQ)$ and $c_i = pr(Qq) - pr(qQ)$ where $pr(QQ)$ is the probability of being homozygous for the Berkshire origin and $pr(qq)$ is the probability of being homozygous for the Duroc origin, $pr(Qq)$ and $pr(qQ)$ are the probability of being heterozygous. The probability of each genotype was calculated every one cM, and an F test was used to assess the evidence of a QTL. Chromosome-wide significance thresholds were calculated using 1000 permutations within sex, birth month-year and slaughter group.

Figure 2. Marker information content (IC) for additive (Add.), dominance (Dom.) and imprinting (Imp.) components across SSC 6 (a) and 13 (b).



Results and Discussion

Table 2. Carcass and meat quality traits with significant QTL effects when age at slaughter was the covariate for chromosome six.

<i>Trait</i> ¹	<i>Loc.</i> ²	<i>CI</i>	<i>F</i>	<i>LOD</i>	<i>Add.</i>	<i>Dom.</i>	<i>Imp.</i>	<i>F</i> <.05	<i>F</i> <.01
Last_Rib	63	SW1841-SW492	5.35	3.45	0.017	-0.061	-0.083**		
	5.123								
Avg_Bfat	64	SW1841-SW492	4.63	2.99	0.033	-0.057	-0.080**		
	4.413								
Dressing	56	SW1841-SW492	6.50	4.19	-0.158	-0.643**	0.216*		
	4.697								
LEA	92	SW1129-SW1473	9.58	6.13	-1.521***	-0.041	0.732*		
	5.413								
Moisture	20	S0035-SW1841	5.77	3.72	-0.195**	-0.175	-0.049		
	5.095								

¹ Dressing=dressing percentage; Last_Rib=last rib fat in cm; Lea=loin eye area in cm²; Moisture=moisture percentage; Avg_Bfat=average backfat in cm.

² Loc.= QTL location; CI=markers flanking the putative location; F=F value; LOD=Log of odds; Add.=additive effect; Dom.=dominance effect; Imp.=imprinting effect; F<.05=F value corresponding to P-value < 0.05; F<.01=F value corresponding to P-value < 0.01. Bolded F values surpassed the Bonferroni-adjusted P < 0.05 or P < 0.01 values.

* P < 0.05, ** P < 0.001, *** P < 0.0001

Table 3. Carcass and meat quality traits with significant QTL effects when weight at slaughter was the covariate for chromosome six.

<i>Trait</i> ¹	<i>Loc.</i> ²	<i>CI</i>	<i>F</i>	<i>LOD</i>	<i>Add.</i>	<i>Dom.</i>	<i>Imp.</i>	<i>F</i> <.05	<i>F</i> <.01
Last_Rib	64	SW1841-SW492	6.94	4.46	0.022	-0.064	-0.087	3.893	4.918
Rib_10	62	SW1841-SW492	3.97	2.57	0.014	-0.083	-0.080	3.954	5.319
Avg_Bfat	65	SW1841-SW492	5.80	3.74	0.039	-0.058	-0.083	3.841	5.116
LEA	90	SW1129-SW1473	7.38	4.75	-1.277	-0.287	0.637	4.224	6.028
Length	92	SW1129-SW1473	6.47	4.17	0.392	-0.352	0.065	4.149	5.359
Moisture	21	S0035-SW1841	4.99	3.22	-0.182	-0.167	-0.046	3.881	5.006

¹ Length=carcass length in cm; Last_Rib=last rib fat in cm; Lea=loin eye area in cm²; Moisture=moisture percentage; Avg_Bfat=average backfat in cm; Rib_10=tenth rib fat in cm.

² Loc.= QTL location; F=F value; LOD=Log of odds; Add.=additive effect; Dom.=dominance effect; Imp.=imprinting effect; F<.05=F value corresponding to P-value < 0.05; F<.01=F value corresponding to P-value < 0.01. Bolded F values surpassed the Bonferroni-adjusted P < 0.05 or P < 0.01 values.

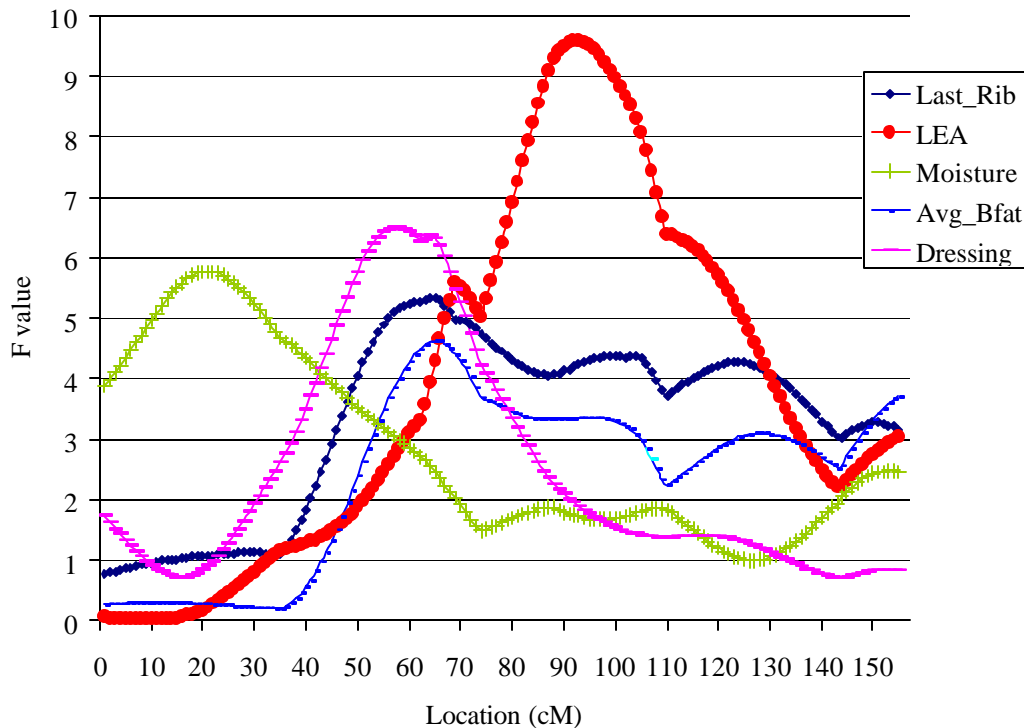
Table 4. Growth traits with significant QTL effects.

<i>Trait</i> ¹	<i>Loc.</i> ²	<i>CI</i>	<i>F</i>	<i>LOD</i>	<i>Add.</i>	<i>Dom.</i>	<i>Imp.</i>	<i>F<.05</i>	<i>F<.01</i>
42d_wt	101	SW1473-SW1647	4.00	2.59	-0.415	-0.077	0.112	3.980	5.300

¹ Loc.= QTL location; F=F value; LOD=Log of odds; Add.=additive effect; Dom.=dominance effect; Imp.=imprinting effect; F<.05=F value corresponding to P-value < 0.05; F<.01=F value corresponding to P-value < 0.01. Bolded F values surpassed the Bonferroni-adjusted P < 0.05 or P < 0.01 values.

² 42d_wt=live weight at d 42 in kg.

Figure 3. F-values along chromosome 6 for five traits using age as covariate.



Chromosome 6 results

The estimates from the models using age or weight at slaughter as covariate were consistent (Tables 2, 3 and 4). The results suggest the presence of multiple QTL on SSC 6 influencing weight and carcass yield. In the case of dressing percentage, average backfat and last rib fat, there may be one QTL with pleiotropic effects or multiple QTL in between 55 and 65 cM influencing these traits (Figure 2). The genotypic means for the QTL detected suggested additive mode of action for loin eye area and moisture with Berkshire alleles producing pigs with less moisture and smaller loin eye area. Substantial imprinting effects were found for last rib fat and average backfat. Confidence intervals exceeded the marker interval, thus the markers surrounding the estimated QTL location are provided as confidence interval limits.

The detection of QTL influencing backfat depth is of substantial economic importance for the pork industry because it is a key determinant of market hog price. Malek et al. (2001a,b) reported QTL for the tenth rib backfat (128 cM), carcass length (141 cM) and Hormel ham pH (53 cM) on SSC 6. A QTL mapping study by Bidanel et al. (2001) based on 1000 F₂ pigs from a cross between Meishan and Large White identified a QTL for growth and backfat thickness on SSC 6. Suggestive linkage was found for weight at 10 and 13 wk at approximately 133 cM, weight at 17 and 22 wk at approximately 76 cM, average daily gain from birth to three wk at 55 cM, from 3 wk to 10 wk at 130 cM, from 10 to 22 wk at 81 cM. Backfat at 13 and 17 wk, at 40 and 60 kg was detected at approximately 60 cM. Ovilo et al. (2002) studied 577 F₂ cross between Iberian and

Landrace breeds and found a QTL for intramuscular fat at 101 cM (95 to 106 cM) on SSC 6. The gene action was partially dominant with the heterozygote being closer to the Landrace genotype. Ovilo et al. (2002) postulated the gene H-FABP as positional candidate gene for the QTL influencing intramuscular fat because of its role on cellular fatty acid transport and its location, 84 cM on SSC 6 fat content on the long arm and a maternally expressed QTL on the short arm of SSC 6 in a cross between Meishan and commercial Dutch pig. Grindfleck et al. (2001) showed a significant association between a QTL on SSC 6 and intramuscular fat and meat tenderness.

Chromosome 13 results

One region on SSC 13 has been associated with significant variation in cooking loss, fat percentage, first rib backfat and moisture percentage at a significance level $P < 0.05$ or higher (Table 5, Figure 4). The genotypic means for the QTL detected indicated a significant additive mode of action for moisture and less significant for cooking loss, fat percentage and first rib backfat with Berkshire alleles producing pork with more moisture and more cooking loss. Imprinting effects at $P < 0.05$ were found for the fat and moisture traits. These results are consistent with the literature. Bidanel et al. (2001) identified a QTL for weight and backfat thickness on SSC 13. A QTL for weight at 10, 13 and 22 wk was detected at approximately 75 cM, and one for average daily gain from 3 to 10 wk was detected at 74 cM. A candidate gene is PIT1, regulator of the transcription of growth hormone and prolactin among others that has been located between markers S0068 (62.2 cM) and SW398 (79.3 cM) on SSC 13 by Archibald et al. (1995) and Yu et al. (1999). Wimmers et al. (2002) identified the hepatic enzyme homogenisate 1,2-dioxygenase close to marker S0075 (64.8 cM). Another candidate gene was reported by Harbitz et al. (1999) who identified the hormone-sensitive lipase gene LIPE (approximately 75 cM). These authors reported that this region was associated to backfat thickness, lean and fat content of muscles.

Table 5. Carcass and meat quality traits with significant QTL effects when age at slaughter was the covariate for chromosome 13.

<i>Trait</i> ¹	<i>Loc.</i> ² <i>F<.01</i>	<i>CI</i>	<i>F</i>	<i>LOD</i>	<i>Add.</i>	<i>Dom.</i>	<i>Imp.</i>	<i>F<.05</i>	
Cook_Loss	70	SW1495-SW225	4.86	3.14	0.608*	-0.238	-0.588	3.833	5.461
Fat	70	SW1495-SW225	4.27	2.76	-0.186*	0.040	0.062*	3.950	5.380
Fir_Rib	75	SW1495-SW225	4.76	3.08	-0.075*	0.140*	0.050*	3.849	4.928
Moisture	70	SW1495-SW225	5.06	3.27	0.166***	-0.026	-0.045*	4.063	5.071

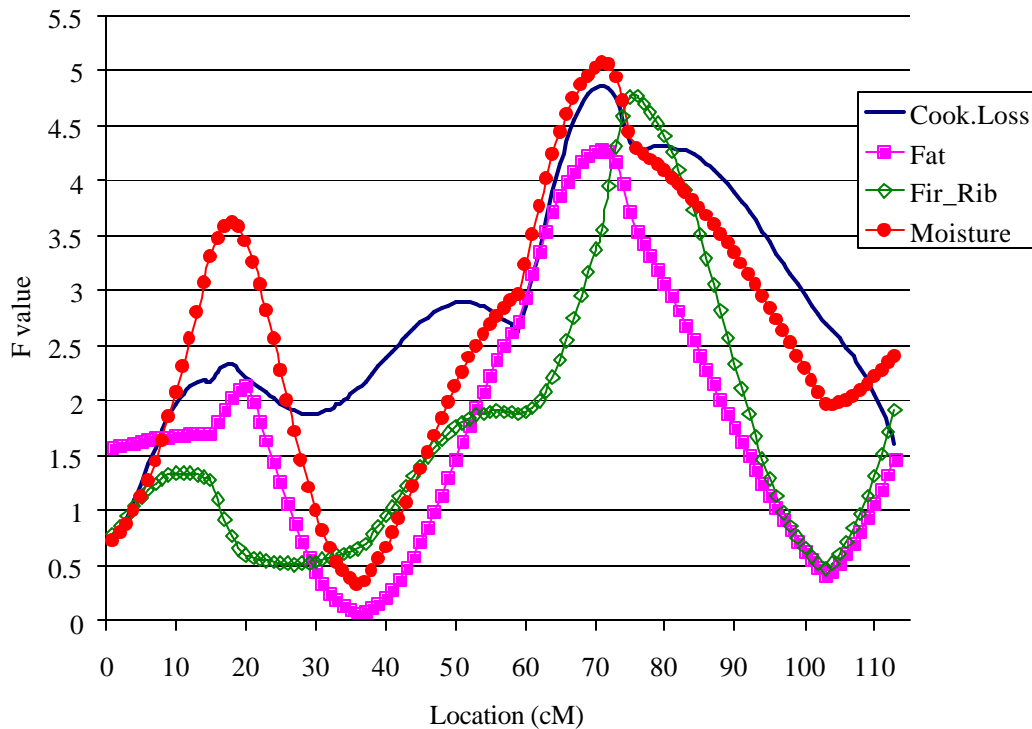
¹ Cook_Loss=cooking loss; Fat=fat percentage; Fir_Rib=first rib fat in cm; Moisture=moisture percentage.

² Loc.= QTL location; CI=markers flanking the putative location; F=F value; LOD=Log of odds; Add.=additive effect; Dom.=dominance effect; Imp.=imprinting effect; F<.05=F value corresponding to P-value < 0.05; F<.01=F value corresponding to P-value < 0.01.

Bolded F values surpassed the Bonferroni-adjusted $P < 0.05$ or $P < 0.01$ values.

$P < 0.05$, ** $P < 0.001$, *** $P < 0.0001$.

Figure 4. F values along chromosome 13 for five traits using age as covariate.



Conclusions

Genome regions with QTL influencing weight, carcass and meat quality traits in pigs were located on SSC 6 and 13 using a reference population created at the University of Illinois. The estimated confidence intervals were wide and additional information is required to confine the estimated positions and improve the estimates of additive, dominance and imprinting effects.

The Iowa State University and University of Illinois F₂ populations can be used to cross-validate the findings in the other population. Alternative, a combined analysis of these data sets could confirm the results and may be increase the power to detect QTL. Once the interval containing the QTL has been narrowed, comparative mapping could suggest positional candidate genes to be tested.

The results from this study augment the understanding of the inheritance of growth, carcass and meat quality traits in pigs. This study helped to assess the effect of using a Berkshire-Duroc crossbreeding system toward the improvement of economically important traits.

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