# A Directed Search for Quantitative Trait Loci on Chromosomes 4 and 7 in Pigs[1]

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**ABSTRACT:** Improvements in the porcine genetic map and availability of resource families to study performance traits in pigs have made it possible to re-examine previous findings that linked certain traits to genes or chromosomal regions. Previous studies suggested that chromosomes 4 and 7 may be associated with growth and performance traits. To confirm these previous results, an interval mapping-regression approach was used to determine whether quantitative trait loci (QTL) exist in the Iowa State University reference/resource families. Traits measured were birth weight; body weight at 21 d; weaning weight (weight at 42 d); average daily gain; backfat at the first, 10th, lumbar, and last ribs and average backfat thickness; loin eye area; meat color; marbling; and firmness. The total number of F2 pigs used ranged from 241 to 330 and came from five Chinese × American resource families. Five markers (S0001, SW871, S0175, S0214, and SW445) were genotyped and mapped on chromosome 4, and so were 10 markers (S0064, tumor necrosis factor $\alpha$ [TNF$\alpha$], S0102, S0078, S0158, S0066, SW304, SW1083, S0101, and S0212) on chromosome 7. Data were analyzed for each family (breed cross) separately and were also pooled. Experiment-wise thresholds were used to determine significance. Suggestive evidence of QTL on chromosomes 4 and 7 was observed for several traits in pooled and individual family analyses. Suggestive evidence of a QTL with a relatively large effect for average daily gain was detected on chromosome 4 in the pooled analysis. Significant ($P < .05$) evidence for QTL was seen on chromosome 7 for 10th-rib, last-rib, and average backfat thickness in the pooled data set in a region of the chromosome that was near TNF$\alpha$. These results verify in part that chromosomes 4 and 7 contain QTL for growth and carcass traits.

Key Words: Pigs, Quantitative Trait Loci, Genetic Markers, Gene Mapping

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## Introduction

In contrast to the usual assumptions of many genes with small effects, Lande (1981) suggested that a few genes may account for a relatively large proportion of the genetic variation for quantitative traits. These loci are known as *quantitative trait loci* (**QTL**) and can be identified through the use of linked molecular markers in certain experimental crosses. One of the major goals of genomic research in pigs has been the mapping and identification of QTL. At present, the combined swine genetic linkage map spans approximately 2,300 cM and provides approximately 1,800 genetic markers, among which there are approximately 250 genes (Archibald et al., 1994 and personal communication; Marklund et al., 1996a; Rohrer et al., 1996). The search for QTL can use the entire genome (Andersson et al., 1994) or focus on individual candidate genes (Rothschild et al., 1996) or chromosomes (Clamp et al., 1992; Rothschild et al., 1995).

There is evidence of QTL in a Wild Boar and Large White three-generation family on chromosome 4 for growth from birth to 70 kg, average backfat depth, and abdominal fat percentage (Andersson et al., 1994). Subsequent generations also have QTL on chromosome 4 for fatness traits and growth rate (Andersson-Eklund et al., 1996; Marklund et al., 1996b). The swine leucocyte antigen (SLA) complex and linked genes, including blood groups C and J (Andresen and Baker, 1964), are associated with birth and weaning weights, growth, backfat, and

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Table 1. Number of animals and F test thresholds

| Trait[a] | MED[b] | S[c] | T[d] | MEH | S | T | MEL | S | T | MZH | S | T | Overall[e] | S | T |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BWT | 99 | 4.1 | 8.2 | 111 | 4.1 | 8.2 | 46 | 4.4 | 9.2 | 69 | 4.2 | 8.6 | 330 | 4.0 | 7.7 |
| WT21 | 98 | 4.1 | 8.2 | 111 | 4.1 | 8.2 | 46 | 4.4 | 9.2 | 69 | 4.2 | 8.6 | 329 | 4.0 | 7.7 |
| WT42 | 98 | 4.1 | 8.2 | 111 | 4.1 | 8.2 | 46 | 4.4 | 9.2 | 69 | 4.2 | 8.6 | 329 | 4.0 | 7.7 |
| ADG | 83 | 4.2 | 8.4 | 100 | 4.1 | 8.2 | 34 | 4.6 | 9.9 | 61 | 4.3 | 8.7 | 283 | 4.0 | 7.8 |
| Carcass | 77 | 4.2 | 8.5 | 77 | 4.2 | 8.4 | 32 | 4.7 | 10.1 | 51 | 4.4 | 9.0 | 241 | 4.0 | 7.8 |

[a]BWT: birth weight (kg); WT21: 21-d weight (kg); WT42: 42-d weight (weaning weight) (kg); ADG: average daily gain (kg/d); Carcass: carcass traits for each breed cross and overall data sets all had the same observation numbers, including: meat color, meat marbling, meat firmness, first-rib backfat thickness, last-rib backfat thickness, lumbar-rib fat thickness, 10th-rib fat thickness, average backfat thickness, and loin eye area.
[b]MED: Meishan × Duroc; MEH: Meishan × Hampshire; MEL: Meishan × Landrace; MZH: Minzhu × Hampshire.
[c]S: Suggestive linkage (Lander and Kruglyak, 1995).
[d]T: Significant linkage, an experiment-wide probability of .05, following Lander and Kruglyak (1995).
[e]Overall: Minzhu × Landrace was included with four observations for carcass traits and five for the others.

carcass traits (Rothschild et al., 1986, 1990; Warner and Rothschild, 1991; Rothschild et al., 1995). Evidence for QTL has also been detected for 12 performance traits, including backfat and loin eye area, on chromosome 7 in a Meishan × Pietrain family (Moser et al., 1998) and in other populations (Wilkie et al., 1996; Milan et al., 1998; Rohrer and Keele, 1998). The objective of this study was to use a directed chromosome scan with expanded marker information to confirm previously detected associations of genetic markers on chromosomes 4 and 7 with growth and carcass traits in our resource families of pigs.

## Materials and Methods

### *Animals and Management*

Five three-generation reference/resource families were established at Iowa State University (**ISU**) for gene mapping and QTL identification. These families were created with diverse crosses of two Chinese breeds, Meishan and Minzhu, and three American breeds, Duroc, Hampshire, and Landrace. The Chinese pigs were imported in 1989 from the People's Republic of China to Iowa State University under a cooperative project that also involved the USDA/ARS and the University of Illinois. The five Chinese × American breed cross families were Meishan × Duroc, Meishan × Hampshire, Meishan × Landrace, Minzhu × Hampshire, and Minzhu × Landrace. Each family originated from matings of two males (Chinese breeds) and two females (American breeds), producing 35 F1 animals. By intercrossing F1 animals within each of the breed cross families, a total of 330 F2 animals were generated for QTL analyses.

During gestation, F1 sows were kept in outside lots with a large shelter and fed a 15% crude protein diet. Sows were moved to a farrowing house with a solid concrete floor just before farrowing. Litters were born in individual farrowing pens that were bedded with straw and contained a creep area. Three to 4 d after farrowing, sows were moved to 4.8- × 5.5-m lactation pens and fed a 16% crude protein diet. Pigs were kept warm in 1.8- × 5.5-m pens bedded with straw and were creep-fed at 21 d old. Pigs were weaned at 42 d of age. At weaning, pigs were moved to a 2.4- × 3.6-m indoor pen with a flush gutter. They remained in these pens until they reached a market weight of approximately 105 kg. The weaned pigs had free access to a diet that contained 18% crude protein until they reached approximately 34 kg and then were given free access to a 16% crude protein diet until market weight. Water was freely available. All conditions were consistent with proper animal care.

### *Traits*

The traits measured on the young F2 animals were birth weight, 21-d body weight, and 42-d body weight or weaning weight. Other traits measured were average daily gain from weaning to marketing; loin eye area; meat color (score, 1–5); marbling (score, 1–5); firmness (score, 1–5); backfat thickness at the first, 10th, lumbar, and last ribs; and average backfat thickness on the carcass. The number of F2 animals measured for each trait in each family (breed) cross is given in Table 1.

### *Marker Information*

Microsatellite markers were chosen in order to span regions of chromosomes 4 and 7 that had been found to be significant in past studies. In a previous study with these animals (Rothschild et al., 1995), no markers were genotyped for chromosome 4. For this analysis, a total of five microsatellite markers were selected on chromosome 4: S0001, SW871, S0175, S0214, and SW445. In the previous study, five markers had been genotyped for chromosome 7. In the present project, a total of 10 markers of which five were new, were chosen on chromosome 7: S0064, tumor necrosis factor $\alpha$ (TNF$\alpha$), S0102, S0078, S0158, S0066, SW304, SW1083, S0101, and S0212. The five new markers were chosen to increase density

and to extend the coverage on chromosome 7. All markers are microsatellites except that TNF$\alpha$ is a gene within the pig MHC (Chardon et al., 1991). All animals in the three-generation pedigrees were genotyped for all markers. Standard molecular biology techniques were applied for microsatellite genotyping, and Southern analysis was used for TNF$\alpha$ (Rothschild et al., 1995). In part, the primers were kindly provided by the U.S. Pig Genome Coordination Program. The number of alleles for each marker varied from 2 (TNF$\alpha$) to 13 (S0064).

### *Statistical Analyses*

*Linkage Maps.* Linkage analysis was performed using CRIMAP version 2.4 (Green et al., 1990). The CHROMPIC option was used to identify errors and potential double-crossovers. Pairwise analysis of linkage was performed with the TWOPOINT option under the assumption of equal recombination rates in the two sexes. A LOD score of 3.0 was used as the significance threshold for pairwise comparisons. Multipoint maps of chromosomes 4 and 7 were built with BUILD, FLIPS, and FIXED options. The best maps were determined based on highest log 10 likelihoods, and these were used for QTL analyses.

*QTL Analysis.* Even though the phenotypic data used for this study were the same as those previously published by Rothschild et al. (1995), the QTL analyses differed greatly. As has been stated previously, the past study did not include any marker data on chromosome 4, and five new microsatellite markers were also added for chromosome 7. Furthermore, the simple single point analysis used in the previous study was replaced by an interval regression mapping approach for QTL mapping and detection (Haley et al., 1994). Marker information was used to calculate the probabilities that each F2 animal would inherit none, one, or two alleles from each breed for a putative QTL at a given position on chromosome 4 and 7. Additive and dominance coefficients for a QTL were calculated for each F2 animal from the genotypic probabilities under the assumption that the two breeds were fixed for alternative QTL alleles. The effects that are found, however, depend on the difference in these gene frequencies. In the pooled analyses, the Chinese breeds were combined as one origin and the American breeds as the other when the additive and dominant coefficients were calculated. Additive and dominance effects of a QTL at a given position were defined as deviations from the mean of the two homozygotes for the QTL. Trait measurements were regressed on the additive and dominance coefficients for each animal. This procedure was repeated at 1-cM intervals across the linkage map. A curve of F-ratio values along the chromosome was drawn, and the highest point represented the most likely position of a QTL. Models involving multiple QTL were also tested.

The following formula was used to compute the expected number of false-positives in the experiment for a given F-ratio threshold value F: $\mu(F) = [C + 2G\rho F(dfn)][\alpha(F, dfn, dfd)]$. The terms dfn and dfd are the numerator and denominator degrees of freedom, respectively, and $\alpha(F, dfn, dfd)$ is the pointwise significance probability value for this F-value, which was derived from standard statistical tables. The number of chromosomes (C) and morgans (G) covered in the experiment were C = 2 and G = 2.08, and $\rho$ is a crossover rate parameter, which was set equal to 1.5, following Lander and Kruglyak (1995) for an intercross design with two degrees of freedom. The experiment-wise significance level for this F-statistic was then computed as $\alpha^*(F, dfn, dfd) = 1 - e^{-\mu(F)}$ following Lander and Kruglyak (1995). For each trait, experiment-wise F-ratio threshold values for suggestive evidence of a QTL were derived as the threshold values that resulted in one expected false-positive ($\mu(F) = 1$) (Lander and Kruglyak, 1995). Experiment-wise F-ratio threshold values for significant evidence for a QTL were derived as the threshold values that resulted in an experiment-wise probability of false-positives equal to .05 ($\alpha^*(F, dfn, dfd) = .05$). Significance threshold values for different traits and various data sets are listed in Table 1.

The data were analyzed for each breed cross separately for the four breed crosses with the most number of pigs and pooled together for all five breed crosses. Models for the pooled data included sex, year-season, and breed cross as fixed effects for all traits and a relevant covariate for each of the traits except for average daily gain. Total born, total born alive, and weaning number were used as covariates for birth weight, 21-d weight, and 42-d (weaning) weight, respectively. For backfat and loin eye area traits, carcass weight was used as the covariate. Models for the single breed cross data were similar to those for the pooled data. The regression approach used here allows systematic environmental effects to be estimated simultaneously with the QTL effects. This removes noise from environmental factors and increases accuracy for detecting QTL. Different additive and dominance effects for each breed cross were examined by including interactions of additive and dominance coefficients with breed crosses. These interactions were not significant, so breed crosses were assumed to have the same additive and dominance effects for the pooled analyses.

## Results

### *Linkage Maps*

The distance covered by the linkage map of chromosome 4 using the five markers was approximately 60 cM, and the average distance between markers was approximately 12 cM. This distance is

Table 2. Summary of maximum F ratios and their map positions (cM) for QTL on chromosome 4

| Trait[a] | MED, cM[b] | MED, F | MEH, cM | MEH, F | MEL, cM | MEL, F | MZH, cM | MZH, F | Overall, cM | Overall, F |
|---|---|---|---|---|---|---|---|---|---|---|
| BWT | 6 | 1.36 | 59 | 1.16 | 32 | 3.72 | 5 | 3.13 | 32 | 1.48 |
| WT21 | 0 | 1.42 | 37 | 1.90 | 33 | 2.02 | 59 | 1.26 | 59 | 1.58 |
| WWT | 1 | 1.82 | 33 | 3.29 | 33 | 3.98 | 0 | 2.74 | 10 | 4.18 |
| ADG | 27 | 1.33 | 41 | 3.65 | 13 | .97 | 12 | 1.20 | 25 | 5.72 |
| C | 56 | 1.71 | 48 | 4.59 | 39 | 2.31 | 5 | 2.41 | 49 | 2.58 |
| M | 14 | 3.63 | 21 | 1.05 | 41 | 1.74 | 2 | 2.10 | 0 | .88 |
| F | 14 | .31 | 51 | 2.23 | 18 | 1.92 | 0 | 3.14 | 13 | 1.84 |
| FRIB | 5 | 1.31 | 44 | 1.39 | 34 | 2.84 | 5 | 1.57 | 42 | 2.22 |
| LRIB | 48 | .77 | 59 | 1.09 | 30 | 2.43 | 3 | 4.71 | 10 | 1.42 |
| LUMBAR | 5 | 1.19 | 7 | 1.53 | 59 | 1.17 | 2 | 3.07 | 59 | 1.08 |
| TENTH | 26 | 1.19 | 44 | 1.68 | 0 | 2.30 | 4 | 3.40 | 32 | .82 |
| LEA | 14 | 1.48 | 19 | 4.58 | 0 | .59 | 6 | 2.72 | 59 | 2.96 |
| ABF | 5 | .80 | 7 | .77 | 32 | 2.16 | 4 | 3.24 | 59 | .86 |

[a]BWT: birth weight (kg); WT21: 21-d weight (kg); WT42: 42-d weight (weaning weight) (kg); ADG: average daily gain (kg/d); C: meat color (score, 1–5); M: meat marbling (score, 1–5), F: meat firmness (score 1–5); FRIB: first-rib backfat thickness (cm); LRIB: last-rib backfat thickness (cm); LUMBAR: lumbar-rib fat thickness (cm); TENTH: 10th-rib fat thickness (cm); LEA: loin eye area ($cm^2$); ABF: average backfat thickness (cm).
[b]MED: Meishan × Duroc; MEH: Meishan × Hampshire; MEL: Meishan × Landrace; MZH: Minzhu × Hampshire.

similar to the 64 cM from a previous map (Rohrer et al., 1996). The chromosome 4 map from our data was, with centimorgan distance in parentheses, S0001-(4.6)-SW871-(9.0)-S0175-(18.5)-S0214-(27.8)-SW445. The linkage map of chromosome 7 spanned approximately 148 cM, and the average distance between markers was approximately 15 cM. This is comparable to the previously published map length of 137 cM obtained by Archibald et al. (1994). The chromosome 7 map was S0064-(19.6)-TNF$\alpha$-(26.5)-S0102-(21.4)-S0078-(4.2)-S0158-(10.8)-S006(14.9)-SW304-(13.2)-SW1083-(25.4)-S0101-(11.7)-S0212.

### *QTL on Chromosome 4*

Maximum F ratios and their map positions for QTL on Chromosome 4 for the pooled analyses and the individual breed cross analyses are presented in Table 2.

*Pooled Data Sets.* There was suggestive evidence (F = 4.18) of a QTL for weaning weight in the region of between SW871 and S0175 (Table 2). Suggestive evidence was also seen for a QTL for average daily gain with a relatively large effect in the region between S0175 and S0214. The F ratio was 5.72 (a nominal *P*-value of .01) and the *P*-value was .24 for the experiment-wide multipoint test. All other traits had small peak F values below suggestive levels (Table 2).

*Individual Data Sets for Each Breed Cross.* There was suggestive evidence of QTL for loin eye area (F = 4.6) and meat color (F = 4.6) in the Meishan × Hampshire family (Table 2). The region close to S0001 and SW871 showed suggestive evidence of QTL for last-rib backfat (F = 4.7) in the Minzhu × Hampshire family.

### *QTL on Chromosome 7*

Maximum F ratios and their map positions for QTL on Chromosome 7 for the pooled and individual breed cross analyses are presented in Table 3.

*Pooled Data Sets.* Suggestive evidence of QTL was found in the region between TNF$\alpha$ and S0078 for all backfat measurements (F = 4.9 to 6.4) (Table 3). No other effects were significant or suggestive for the pooled analyses.

*Individual Data Sets for Each Breed Cross.* The region from TNF$\alpha$ to S0078 showed suggestive evidence of QTL for some of the backfat traits in each of the families (Table 3). There was suggestive evidence of a QTL for meat firmness (F = 5.4) in the region near S0212 in the Meishan × Duroc family. Suggestive evidence was observed for color (F = 6.0) between SW304 and SW1083 in the Meishan × Landrace family. Suggestive evidence for an association of the region between S0064 and TNF$\alpha$ with loin eye area (F = 7.2) was detected, and S0212 was suggestively associated with birth weight (F = 4.4) and weight at 21 d (F = 5.0) in the Minzhu × Hampshire family.

*Significant Linkage Results.* Significant linkage results on chromosome 7 for the pooled data are presented in Figure 1 and Table 4. Significant QTL were found on chromosome 7 with large effects for 10th-rib, last-rib, and average backfat thickness. Models with two QTL were tested but did not provide a significantly better fit than the single QTL model. The genetic effect of these QTL seemed to be mainly

Table 3. Summary of maximum F ratios and their map positions (cM) for QTL on chromosome 7

| Trait[a] | MED, cM[b] | MED, F | MEH, cM | MEH, F | MEL, cM | MEL, F | MZH, cM | MZH, F | Overall, cM | Overall, F |
|---|---|---|---|---|---|---|---|---|---|---|
| BWT | 16 | 2.2 | 17 | 3.3 | 4 | 1.9 | 147 | 4.2 | 16 | 2.8 |
| WT21 | 9 | 3.0 | 124 | 3.6 | 68 | 3.5 | 147 | 4.7 | 46 | 2.3 |
| WWT | 109 | 2.1 | 7 | 2.4 | 134 | 2.5 | 147 | 2.0 | 13 | 2.7 |
| ADG | 111 | 1.3 | 137 | 3.2 | 98 | .9 | 1 | 2.4 | 83 | 2.2 |
| C | 147 | 1.5 | 90 | 3.9 | 103 | 6.0 | 0 | 1.2 | 83 | 3.7 |
| M | 10 | 1.5 | 79 | 2.3 | 131 | 2.7 | 0 | 1.7 | 110 | .7 |
| F | 147 | 5.4 | 34 | 4.1 | 98 | 3.3 | 11 | 1.8 | 97 | 3.1 |
| FRIB | 20 | 4.0 | 67 | 4.5 | 0 | 2.7 | 39 | 2.9 | 57 | 4.9 |
| LRIB | 17 | 5.7 | 33 | 4.6 | 147 | 2.5 | 32 | 5.0 | 24 | 8.7 |
| LUMBAR | 15 | 4.4 | 34 | 3.5 | 147 | 4.9 | 46 | 3.3 | 53 | 6.4 |
| TENTH | 9 | 3.2 | 67 | 3.1 | 58 | 5.0 | 46 | 3.8 | 58 | 7.9 |
| LEA | 147 | 1.8 | 147 | 2.0 | 83 | 2.5 | 11 | 7.2 | 67 | 2.1 |
| ABF | 17 | 6.0 | 67 | 5.0 | 147 | 3.1 | 37 | 4.5 | 27 | 7.9 |

[a]BWT: birth weight (kg); WT21: 21-d weight (kg); WT42: 42-d weight (weaning weight) (kg); ADG: average daily gain (kg/d); C: meat color (score, 1–5); M: meat marbling (score, 1–5), F: meat firmness (score 1–5); FRIB: first-rib backfat thickness (cm); LRIB: last-rib backfat thickness (cm); LUMBAR: lumbar-rib fat thickness (cm); TENTH: 10th-rib fat thickness (cm); LEA: loin eye area ($cm^2$); ABF: average backfat thickness (cm).
[b]MED: Meishan × Duroc; MEH: Meishan × Hampshire; MEL: Meishan × Landrace; MZH: Minzhu × Hampshire.

additive. However, there was an indication of a dominance effect for 10th-rib backfat thickness. The QTL on chromosome 7 had estimated genetic effects for backfat thickness accounting for approximately 6 to 7% of the error variance in the F2 population of the ISU resource families. Our results indicated that Chinese breeds had the leaner alleles for the backfat traits.

## Discussion

Research can be organized to look for QTL on a genome-wide basis, on a chromosomal basis, or even on a candidate gene basis. Our approach was to try to verify several earlier findings for QTL on chromosomes 4 and 7 (reviewed in Rothschild, 1998). Debate exists among researchers as to what significance level should be set in these "verification studies." We used significance threshold values based on the formula of Lander and Kruglyak (1995) for an experiment-wise test with two chromosomes. Markers on chromosome 4 did not show significant linkage with QTL for the traits studied, but there were some indications of suggestive linkages with growth and carcass quality traits in individual ISU resource families. Lander and Kruglyak (1995) defined suggestive linkage as statistical evidence that a false-positive QTL would be expected to occur one time at random in a genome scan. They further suggested that researchers report results as significant when a multipoint *P*-value of .05 is seen. In our case, two chromosomes were scanned, and we applied their formula accordingly. We have discussed QTL results only when F values exceeded approximately 4.1 because this fits their criterion as suggestive.

Our results, therefore, confirm those found by Andersson et al. (1994) only in a limited way. Differences may exist in part because the two studies used different breeds and perhaps QTL did not segregate in our families. In the individual breed cross data sets for chromosome 4, the region between S0214 and SW445 was suggestive for an association with meat color. The region between S0001 and SW871 had a suggestive association with last-rib backfat thickness and the region near S0175 for an association with loin eye area. These results were in some agreement with those from the previous studies (Andersson et al., 1994; Andersson-Eklund et al., 1996; Marklund et al., 1996b; Wilkie et al., 1996). It was worth noting that there was suggestive evidence of a QTL with a

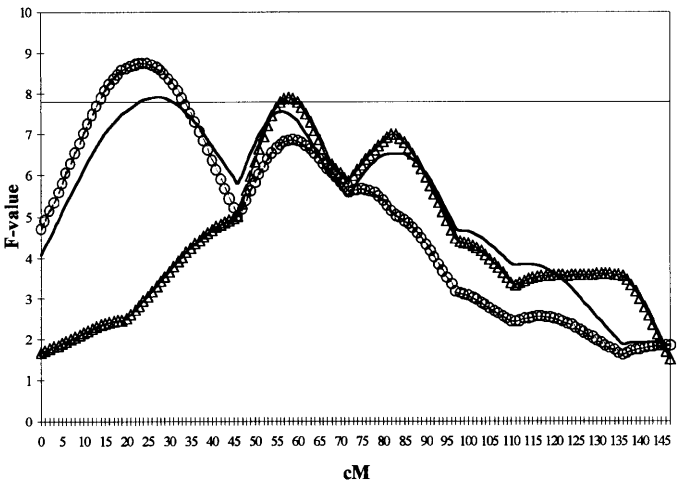


Figure 1. Evidence of QTL for backfat thickness on chromosome 7. Traits are last-rib backfat thickness (cm), circled line with peak of 8.7 at 24 cM; 10th-rib fat thickness (cm), triangled line with peak of 7.9 at 58 cM; average backfat thickness (cm), solid line with peak of 7.9 at 27 cM; the 5% significant threshold, horizontal straight line.

Table 4. Summary of significant QTL effects on chromosome 7 for backfat thickness

| Trait[a] | F value[b] | *P*-value[c] | dfn, dfd[d] | Estimated map position[e] | Additive effect[f] | Dominance effect | Percentage of F2 residual variance[g] |
|---|---|---|---|---|---|---|---|
| LRIB | 8.7 | .025 | 2, 229 | 24 | –.37 ± .089 | .07 ± .164 | 6.7 |
| TENTH | 7.9 | .047 | 2, 229 | 58 | –.23 ± .083 | –.41 ± .137 | 6.0 |
| ABF | 7.9 | .047 | 2, 229 | 27 | –.31 ± .078 | –.02 ± .144 | 6.0 |

[a]LRIB: last-rib backfat thickness (cm); TENTH: 10th-rib backfat thickness (cm); ABF: average backfat thickness (cm).
[b]The test statistics represent the highest F ratio for a given chromosome.
[c]Experiment-wide *P*-values.
[d]Degrees of freedom for numerator and denominator, respectively.
[e]The map position is the one that gives the highest F ratio on that chromosome estimated in centimorgans from the proximal end marker.
[f]Estimates are presented as mean ± SE.
[g]The reduction in the residual variance of the F2 animals affected by inclusion of a QTL at the given position.

relatively large effect on average daily gain in the region between S0214 and S0175 on chromosome 4 based on the pooled data set. The F ratio for this evidence was 5.7, and the *P*-value was approximately .24 under the experiment-wide multipoint test. The association of the region between S0214 and S0175 on chromosome 4 with average daily gain was significant at the nominal *P*-level of .01, which implies that this result was a confirmation of one of the findings of Andersson et al. (1994) for growth rate.

Suggestive linkages were also detected on chromosome 7 with many of the growth and carcass traits in our ISU resource families. In the Minzhu × Hampshire family, the evidence for a QTL for loin eye area between S0064 and TNF$\alpha$ was detected with an F value of 7.2 at $P < .15$ for the experiment-wide multipoint test. This region near TNF$\alpha$ may be important for lean growth. The indications of these suggestive linkage results on chromosome 7 agreed well with those of Wilkie et al. (1996).

Significant evidence at the 5% level in a two-chromosome scan for QTL was found on chromosome 7 with marked effects for last-rib, 10th-rib, and average backfat thickness. The gene action at these QTL seemed to be primarily additive. However, a dominance effect was observed for 10th-rib backfat thickness. The negative additive effect was explained by the fact that individuals with the Chinese breed alleles had the leaner allele. This evidence for a cryptic allele for backfat thickness was in a good agreement with findings of Milan et al. (1998), Moser et al. (1998), and Rohrer and Keele (1998). The negative dominance effect indicated that individuals that had received one allele from the Chinese breeds and the other allele from the American breeds had a smaller mean than the mean of the homozygotes. The estimated difference between homozygotes for the Chinese alleles and homozygotes for the American alleles for the last-rib, 10th-rib, and average backfat deposition were .74, .46, and .63 cm, respectively. When additive genetic effects are discussed in terms of QTL detection, effects of .5 to $1.0\sigma_p$ are considered large (Falconer and Mackay, 1996). The additive effects for the last-rib, 10th-rib, and average backfat were $.48\sigma_p$, $.30\sigma_p$, and $.48\sigma_p$, respectively, and they explained approximately 6 to 7% of the total residual variance in the F2 population in the ISU resource families. The effects of QTL for these backfat thickness traits can therefore be considered moderate to large. Estimated QTL on chromosome 7 for the last-rib backfat and average backfat thickness were located near TNF$\alpha$ in the region between S0064 and S0102, and the QTL for the 10th-rib back fatness was between S0102 and S0066. The QTL identified here may be a single locus with a large effect or a cluster of linked loci each with smaller effects. The multiple peaks in the graph may be due to recombination events near the typed markers and not due to multiple QTL because our test of such effects was not significant. This could be studied in further experiments using subsequent generations. The analysis done here used more information on additional markers and linkage information than that of Rothschild et al. (1995) and should have increased the accuracy of the QTL detection.

Previous research has shown that the SLA complex and linked genes were significantly associated with birth and weaning weights, growth, backfat, and carcass traits (Andresen and Baker, 1964; reviewed in Warner and Rothschild, 1991). The TNF$\alpha$ gene belongs to the SLA complex (Chardon et al., 1991). The significant evidence for QTL for backfat thickness near TNF$\alpha$ and the possibilities of QTL for loin eye area close to TNF$\alpha$ in some of the ISU resource families seem to confirm the important role of TNF$\alpha$ in relation to performance of the pig. Recent evidence (Norman et al., 1995) suggests that TNF$\alpha$ plays a role in fat deposition in humans. Another possible candidate gene affecting fat deposition, *Colipase*, has also been found in this region (Baskin and Pomp, 1998). These results together suggest possible explanations for the QTL for backfat in this region of chromosome 7.

Our present results were in some agreement with previous findings, confirming that chromosomes 4 and 7 may contain QTL for growth and carcass traits in

pigs. Increased accuracy of the analysis and significance of the results could be obtained with more F2 animals per family and additional markers. With small sample sizes, only QTL with large effects can be detected, so very large sample sizes are required to detect QTL with moderate to smaller effects. Falconer and Mackay (1996) indicated that some "significant" QTL may be false-positives, and QTL responsible for significant variation within and between populations cannot be detected if the tested strains are fixed by chance for alleles with similar effects. Hence, QTL should be confirmed by several experiments. Our project now is one of several recent ones that have confirmed previous findings and that will help in the search for the actual genes involved in the traits of economic interest.

## Implications

Evidence of quantitative trait loci was found for some growth and carcass traits on chromosomes 4 and 7 at the suggestive linkage level. These results should be interpreted with caution. The suggestive quantitative trait loci evidence for average daily gain on chromosome 4 confirmed previous observations. The significant evidence for quantitative trait loci for backfat deposition found on chromosome 7 near tumor necrosis factor $\alpha$ (TNF$\alpha$) indicates that TNF$\alpha$ or a closely linked gene may be associated with backfat thickness in pigs. These chromosome 7 results clearly add to the growing body of evidence of at least one backfat quantitative trait locus in this region. Further research to find the individual genes responsible is now necessary. These genes, when discovered, can be eventually used to select for faster growing and lean pigs.

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