RESEARCH REPORT
ANIMAL SCIENCE

Title: Genome-wide association meta-analysis of experimental populations to identify QTL for pork quality and validation in commercial populations – **NPB #11-042** **r**evised

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Industry Summary

Scientists working to better understand the underlying genetic control of pork quality traits; typically take very detailed measurements on animals in experimental herds, often called populations. These measurements typically are more informative than what could be gathered in commercial herds or high throughput packing plants. The results from experimental work provide a broad overview of where within the DNA of animals there are genes influencing important pork quality traits. However often the results reported from these experimental populations do not consistently report the same chromosomal regions that influence pork quality traits. Furthermore the regions identified are too broad so to find molecular markers that are very close to the genes controlling the traits of interest. For this project three experimental populations (1 from Michigan State University (MSU) and 2 from the U.S. Meat Animal Research Center (MARC)) that had similar meat quality data collected from the loin or longissimus muscle were pooled. The objective was to determine similar chromosomal locations across populations that were influencing these pork quality traits and identify the molecular markers that were significantly associated with the traits of interest. Each population was genotyped with Single Nucleotide Polymorphic (SNP) molecular markers. One population from MARC had 60,000 SNP markers genotyped for each animal. The second MARC and the MSU populations had 60,000 SNP markers genotyped on a subset of animals while the remainder were genotyped with approximately 9,000 SNP markers. This subset of markers was used to impute the 60,000 SNP genotypes with high accuracy (97%). Imputation is a mathematical procedure that uses the natural association of SNP markers that are very close together to predict the genotype of markers not directly genotyped. Ultimately each population had 60,000 SNP markers available for analysis. For pH taken 24 hours after slaughter, the combined analysis showed significant associations within a narrow region on swine chromosome 15 near the gene region of PRKAG3,which has been shown to significantly influence meat quality. In addition the combined analysis showed significant associations of SNP associations with shear force on swine chromosomes 2 and 15. The SNP associations on chromosome 2 are near the µ-calpain gene which has been shown to influence tenderness. Overall this project demonstrates that a larger number of markers can be predicted through imputation when only a smaller number of molecular markers have been genotyped. Thus reducing the genotyping cost. These imputed genotypes can be successfully used in pooling the results across populations to identify markers within relatively narrow chromosomal regions that significantly associate with pork quality traits.

The results of this project have these key findings;

- Imputation can be used to determine higher density SNP genotypes from lower density SNP genotypes thus reducing genotyping costs with only minor reductions in accuracy.

- Meta-analysis can be used to combine the results of multiple whole-genome association studies which will improve the understanding of important QTLs across populations.

- A significant QTL associated with ultimate pH was determined on SSC15 which will influence pork quality.

- There were two QTLs determined for shear force with one on SSC2 and the other on SSC15. These QTL will impact tenderness.

Keywords: Pig, genome-wide association, imputation, pork quality, meta-analysis

Scientific Abstract

In the current era of livestock genomic evaluation it is common practice to derive a genome-wide association analysis (GWA) from a genomic evaluation model of a single population. Analysis of multiple populations, however, is more difficult. An alternative to joint analysis could be the meta-analysis of several GWA from independent genomic evaluations. Meta-analysis of GWA allows combining results from individual studies, accounting for population substructure. The objectives of this research were: (a) to derive GWA from genomic evaluations for pork quality traits in three populations; and (b) to implement a Meta-analysis (MA) to find significant associations across populations. Data from two populations (MARC_Com and MARC_Res) were provided by Meat Animal Research Center and one population was provided by Michigan State University (MSUPRP). Population-specific GWA were derived from genomic evaluation models fit to each population for ultimate pH (n=1857 MARC_Com; n=530 MARC_Res; n=904 MSUPRP) and shear force (SF; n=1234 MARC_Com; n=1892 MARC_Res; n=911 MSUPRP). A MA was implemented by combining z-scores derived for each SNP in each population using two different weighting schemes: a) sample size (*N*) and b) estimated variance of SNP effects. For pH, one peak was identified for MSU and commercial populations on SSC15, (135Mb, p-value<1.21e-11 for MSUPRP and 134MB, p-value<9.26e-11 for MARC_Com). In the N-weighted MA, a peak was detected on SSC15 at position 134Mb (p-value < 2.13e-13). A virtually identical result was obtained using variance-weighted MA: a peak on SSC15, at 135Mb, p-value<5.18e-11. For shear force, GWA for MSUPRP showed one peak on SSC15 (135Mb, p-value<1.48e-8) and another peak on SSC2 (2.9Mb, p-value< 2.88e-8). For MARC_Com and MARC_Res, peaks on SSC2 were identified at positions 109Mb and 5.5Mb (p-value<1.83e-7 and 1.64e-7 respectively). The variance-weighted MA detected one peak on SSC2 (6.3Mb, p-value<7.82e-11) and another on SSC15 (135Mb, p-value<2.14e-7). In contrast, N-weighted MA, yielded two peaks on SSC2, at 5.9Mb and at 105Mb (p-value<6.73e-12 and 1.23e-6 respectively). According to our results, selecting a weighting scheme for MA-GWA is very important because it may influence the results. Regardless of the approach used to implement it, MA-GWA focused on peaks that were present in at least two populations. Thus, the presented MA-GWA methodology is an attractive alternative to synthesize results from multiple GWA derived from genomic evaluations and it can be used to elucidate the genetic architecture of economically relevant traits, when several populations are available.

Introduction

As we progress from using a few genetic markers in breeding programs to tens of thousands, determining the consistency of marker associations, across populations, with traits of economic importance will be critical. Particularly as breeding programs begin to define the magnitude and significance of the SNP regression estimates on traits within the selection objective to calculate genome-wide breeding values. This will be particularly cumbersome for traits that are expressed later in life (e.g. reproductive traits or longevity) or those that require animal harvest (i.e. meat quality) due to limited DNA resources of animals with extensive phenotypic data collected. This critical resource is needed before robust prediction equations can be developed for genomic breeding values.

Utilization of experimental populations that have maintained the necessary DNA resources and judicially gathered extensive meat quality phenotypes can aid in the determination of pork quality Quantitative Trait Loci (QTL) using high density SNP markers. These results can then be combined across populations to ascertain QTL regions that consistently demonstrate significant association with pork quality. The results of which should provide to the pork industry a more inclusive set of high density SNP markers to be used to improve pork quality and consumer appeal.

Objectives

1. Complete genome-wide association analyses in three populations for meat quality traits using imputed SNP genotypes in two of the three populations. The populations include the Michigan State University Pig Resource Population (MSUPRP) and two from the U.S. Meat Animal Research Center (MARC), Clay Center, NE.

2. Conduct a meta-analysis to detect QTL for pork quality traits, combining results determined in the MSUPRP and the two MARC populations.

Materials and Methods

Populations. Information from three pig populations was used in this study. The MSUPRP is an F2 resource population that consists of four Duroc boars and 15 Pietrain females, normal for the RYR1 gene (stress gene), which served as founders (Edwards et al; 2008). The 954 pig F_2 generation, produced from 6 F_1 boars and 51 F_1 females, had 60 growth, carcass merit, meat, cooking and eating quality traits recorded. The second population is the MARC ½ Landrace- ¼ Duroc- ¼ Yorkshire resource population (MARC_Res) in which meat quality phenotypes were collected on pigs from the fourth, sixth and seventh generations. The third population consists of information collected by MARC personnel from a three-breed cross commercial population (MARC_Com). Meat quality data were collected on 1,920 Duroc sired pigs.

Meat quality traits The novelty of this work is combining data from several populations which had common information collected. For this study, each population had common measurements taken on the longissimus muscle. This included; pH recorded at 24 hours after slaughter (pHu), CIE L* a* and b*, intramuscular fat percentage (IMF), percentage fluid loss (FLOSS), percentage cook loss (CLOSS) and a measure of shear force. The two MARC population had slice shear force (SSF) recorded while Warner-Bratzler Shear Force (WBSF) was measured in the MSUPRP. Table 1 includes the statistics for these characteristics for these populations.

Genotypes
All populations had Single Nucleotide Polymorphism (SNP) genotypes scored. Quality control procedures were used to assess all SNP genotypes. Individuals with low genotyping rate (<0.9), SNPs with low minor allele frequency (MAF< 0.01) and SNPs with more than 10% missing data were discarded. For the MSUPRP, the F0

and F1 generations had high density SNP genotypes completed with approximately 60,000 SNP genotypes (60K_SNP). Within the F2 generation, 336 animals were genotyped in high density while the rest were SNP genotyped in low density with a commercial SNP panel that contained ~ 9K SNPs (9KSNP; GeneSeek, Lincoln, NE). Subsequently 60K_SNP genotypes were imputed for the rest of the 935 MSUPRP F2 animals with 97% accuracy (Gualdron et al., 2013).

The MARC_Res population had 60K_SNP genotypes available from previous work. The MARC_Com was not a pedigreed population and had not been genotyped. A random sample of 480 animals was genotyped with the 60K_SNP panel while the remainder was SNP genotyped with the 9KSNP chip. From the animals genotyped with the 60K_SNP chip, haplotype panels were constructed. For animals genotyped with the 9KSNP chip, high density haplotype panels were used to impute the rest of the 60K_SNP genotypes with 97% accuracy. Table 1 provides the summary SNP statistics for each population and Table 2 provides the correlation of phase between SNP genotypes across populations. Results in Table 2 illustrate the closeness of the MARC_Res and MARC_Com populations compared to MSUPRP.

Data Analyses For each population genomic animal models were fit to the data to estimate variance components for each trait within each population. The genomic relationship matrix was assembled for each population using the methodology outlined by (VanRaden, 2008). For each population the models were developed to account for the fixed (e.g. year-season, sex, pen, etc.) and random (e.g. animal, litter, etc) and residual effects appropriate for each population. From these variance components, heritabilities were estimated for each trait within each population. These were used to determine if the data could be combined for whole-genome association analyses or if a meta-analysis would need to be used to determine SNP association across populations.

Preliminary assessment of heterogeneity across population involved comparison of posterior distribution of genetic parameters: heritabilities, genetic variances and residual variances. When estimates of genetic parameters differed across populations, this indicated heterogeneous variances. Genomic selection models exploit linkage disequilibrium (LD) between causative variants and markers. Consequently presence of genetic substructure (e.g., heterogeneous minor allele frequencies, heterogeneous haplotype phase, etc.) prevented combining the populations into a single genomic model. We assessed population structure through estimation of persistence of phase (Badke et al., 2012), analysis of heteroskedasticity and by estimating accuracy of phenotype prediction across populations. There was evidence of population structure and heterogeneity between the variance components and linkage phase (Figure 1), suggesting a meta-analysis should be conducted (Evangelou et al., 2007).

For whole genome association analyses (GWA), the estimated animal genomic breeding values, or GEBVs, were then transformed into regularized marker effects using a linear transformation to determine individual SNP effects (Wang et al., 2012). Manhattan plots of marker effects were then constructed by plotting the estimated marker effects divided by the square-root of their variance versus the genomic position.

Meta-analyses were conducted using an approach similar to what has been used in human genetic epidemiology (Willer et al., 2010). This methodology averages out estimates of marker (j) effects across populations (k). This methodology suggests evaluating two-different weighing schemes. One uses a sample size based approach, in which case, the effect and p-value observed in each study are converted to a signed Z-score such that very negative Z-scores indicate a small P-value. The second approach uses an inverse-variance based approach, which requires the same trait scale across populations. The across population averaged z-value was then used to assemble a Manhattan plot as described previously.

Results

The phenotypic statistics for the traits evaluated, by population are provided in Table 3. For the most part, these three populations were similar for these traits. The summary of the genetic statistics for these populations is provided in Table 4. Heritabilities were similar across populations for these traits except for the objective color traits of CIE L* and CIE a*. The heritability for CIE L* was similar for both the MSUPRP and MARC_Res populations (0.36 and 0.31, respectively). However the heritability for CIE L* was nearly twice as large as for the MARC_Com population. A different situation occurred for CIE a*. The heritability for CIE a* for MARC_Res population was relatively low (0.16) while the heritabilities for the other two population were much larger (0.46 and 0.61 for MARC_Com and MSUPRP, respectively).

The results from the individual population GWA for pHu can be seen in Figure 2. For the MARC_Res population no significant Quantitative Trait Loci (QTL) were determined. However for both MSUPRP and MARC_Com significant QTLs were found on SSC15. The significant SNPs for each QTL region for each population can be found in Tables 5 and 6. The SNPs that were significant within the QTL region were different across these two populations but were in proximately of each other, with more significant SNPs downstream and upstream in the MSUPRP population compared to the MARC_Com population. This region of SSC15 contains the gene PRKAG3, which has been shown to significantly associate with measures of meat quality (Ciobanu et al., 2001).

The GWA for shear force for each population can be found in Figure 3. There were significant QTL peaks for each population and the significant SNPs within each QTL region are reported in Tables 7, 8 and 9. A QTL was found on SSC2 in a similar position within each population. However, within the MSUPRP a significant QTL was found on SSC15 that was not found in either of the other two populations. This QTL is in close proximity to the gene PRKAG3.

The results for the meta-analysis for pHu can be found in Tables 10 and 11. For pHu, using sample size as a weighting mechanism found different SNPs to be significant than the method using the inverse SNP variance as a weight. Nonetheless, the interval that spanned the significant SNPs was virtually the same for each method.

The results for the meta-analysis for shear force can be found in Tables 12 and 13. The two MARC populations had slice shear force measured, while Warner-Bratzler shear force was evaluated in the MSUPRP. These different methods to quantify shear force have dramatically different means and standard errors (Table 3). Shackelford and Wheeler (2009) had reported that slice shear force could be transformed to Warner-Bratzler shear force using the following equation;

Warner-Bratzler shear force =(0.1063x slice shear force) +2.2718.

The inverse of the MSUPRP SNP variance for shear force was multiplied by $(0.1063)^2$ to transform this weight to a slice shear force equivalent to conform units of measure of shear force across the three populations.

Similar to the meta-analysis for pHu, the weighting method using sample size found more SNPs to be significant; though the chromosomal interval in which these SNPs were found is similar. However, the method which used the inverse weights of the SNP variance also found a significant SNP on SSC 15. This SNP was highly significant in the MSUPRP while not significant in the two MARC populations. Yet, the meta-analysis determined this SNP did associate with shear force across the three populations. This suggests that this SNP may have been approaching significance in the two MARC populations while significant in the MSUPRP which culminated in this SNP being significant across all three populations.

Discussion

Heritabilities reported in Table 4, were found to be moderate to large in magnitude. Heritabilities ranged from 0.161 to 0.633. For the most part, heritabilities reported for the meat quality traits summarized in the study were within the range of literature values reported for these traits (Ciobanu et al, 2011). However within the summary of literature reported by Ciobanu et al., (2011) heritability values for CIE a* and b* were not reported. Within the present study the heritabilities for CIE a*, a measure of the redness spectrum, ranged from 0.161 to 0.613. This is similar to the range of heritabilities for CIE a* reported for the Finish Landrace and Large White breeds (0.17 to 0.56; Sevon-Aimonen et al., 2007), as well as the heritabilities for CIE a* reported for the Norwegian Landrace and Duroc breeds (0.46 and 0.43, respectively; Gjerlaug-Enger et al., 2010). The heritabilities for CIE b*, a measure of the yellow spectrum, were more consistent across populations, compare to CIE a*, and ranged from 0.182 to 0.375. The heritabilities reported in this study were somewhat larger than the range of heritabilities reported for the CIE b* for the Finnish Landrace and Large White breeds (0.00 to 0.28; Seveon-Aimonen et al., 2007) but similar to the heritabilities reported for CIE b* in the Norwegian Landrace and Duroc breeds (0.31 and 0.33, respectively; Gjerlaug-Enger et al., 2010).

There were SNPs on SSC15 that did significantly associate with pHu in the MSUPRP and MARC_Com populations but no significant SNP associations were found in the MARC_Res population with ultimate pH. These significant SNP associations were located within the chromosomal region of the major gene PRKAG3. This gene has been shown to influence pHu (Ciobanu et al., 2001; Otto et al., 2007; Rohrer et al., 2012). The meta-analysis combining the results from the three populations (Tables 10 and 11) reported significant SNPs that were either significant in one or both populations as well as some that were not reported to be significant in either population. In Table 10, for the meta-analysis using the number of animals from each population as weights determine two SNPs (MARC0082467 and ALGA0087491) that were not reported significant in either population. The meta-analysis method that used the inverse SNP variance as the weighing scheme reported only one SNP (ALGA0087491) that was significantly associated with pHu in the combined analysis, but not significant in either population.

For shear force, significant SNPs were found on SSC2 and SSC15 in the MSUPRP, while for the MARC_Res population significant SNP associations with shear force were found with SNPs on SSC2. Within the MARC_Com population significant SNP associations were found on SSC2 and SSC11. Within SSC2, there were similar regions in which significant SNP associations were found but there were also differences. The significant SNPs for shear force within the MARC_Res population were within a narrow region from 5.479 MB to 6.2.4 MB. The significant SNPs within the MSUPRP did overlap with the MARC_Res population but also had significant SNPs upstream from the significant SNPs found in MARC_Res. The converse was true for MARC_Com. The MARC_Com population had significant SNPs within the same region as did MARC_Res but also had significant SNPs downsteam for the SNPs reported significant in MARC_Res.

The sample size weighted meta-analysis reported significant SNPs over a much broader range than the inverse weighting method on SSC2. The inverse variance weighting method only reported significant SNPS within 5.8 to 6.25 MB while SNPs within the range of 5.8 to 10.5 MB were found to be significant for the sample size weighting method. The SNPs reported to be significant for the inverse variance weighting method are near the gene µ-calpain which has been shown to influence tenderness in pork (Melody et al., 2004). It has been reported that the SSC2 SNP H3GA0005672 was significantly associated with shear force in the MARC_Res population (Nonneman et al., 2013). However this SNP was not significantly associated with shear force in either of the other two populations nor was it significant in the meta-analysis. One SNP on SSC15 did significantly associate with shear force. This SNP is within the region of PRKAG3.

Summary This project demonstrates that a large number of markers can be predicted through imputation with a high accuracy (97%) when a smaller number of molecular markers have been genotyped. Thus reducing the genotyping cost. This will lower the cost of future studies using SNP markers to determine QTL and regions for further fine mapping. In addition, imputed genotypes can be successfully used in pooling the results (meta-analysis) across populations to narrow chromosomal regions that significantly associate with traits of interest. Though the method used in meta-analysis can influence the resulting set of markers that are determined to be significant. Ultimately this project demonstrates the methodology needed to pool pedigreed and non-pedigreed as well as experimental and non-experimental populations to improve our understanding of chromosomal regions controlling traits of interest.

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Table 1. Summary SNP statistics by population

	Population[a]		
Item	MSUPRP	MARC_Res	MARC_Com
Number of markers included	61565	61565	61565
Number of animals with high density SNP genotypes	336	1237	480
Number of animals with low density SNP genotypes	948	0	1440
Animals removed for low genotyping call rate (>0.10)	11	3	6
Number of failed SNPs	2897	2898	3624
Number of SNPs will low MAF (<0.01)	11360	8127	6618
Final number of SNP markers	47308	53228	53794
Imputation Accuracy	0.97	0.97	0.97

[a] MSUPRP- MSU DurocxPietrain F2 Population; MARC_Res – US MARC DurocxLandrace F2 population; MARC_Com – US MARC non-pedigreed commercial population

Table 2. Pearson correlation between SNPs at the same location across populations

	Population[a]		
Population	MSUPRP	MARC_Res	MARC_Com
MSUPRP	1.00	0.78	0.85
MARC_Res	0.78	1.00	0.89
MARC_Com	0.85	0.89	1.00

[a]MSUPRP- MSU DurocxPietrain F2 Population; MARC_Res – US MARC DurocxLandrace F2 population; MARC_Com – US MARC non-pedigreed commercial population

Table 3. Meat Quality Traits Common to three populations

			Average	Std Err	Minimum	Maximum
Population[a]	**Trait[b]**	**Number**				
MSUPRP	pHu	927	5.51	0.139	5.09	6.35
MARC_Res		531	5.81	0.168	5.40	7.0
MARC_Com		1885	5.65	0.166	5.18	6.5
MSUPRP	CIE L*	874	53.79	2.239	46.65	62.59
MARC_Res		704	56.13	3.756	41.75	69.18
MARC_Com		1780	57.67	3.344	44.36	68.53
MSUPRP	CIE a*	874	17.26	1.827	13.23	23.55
MARC_Res		704	6.75	1.428	2.525	10.96
MARC_Com		1780	14.49	1.496	9.238	19.36
MSUPRP	CIE b*	874	9.107	1.603	4.72	14.24
MARC_Res		704	12.92	1.686	6.97	17.20
MARC_Com		1780	21.03	2.068	14.41	26.52
MSUPRP	IMF	936	3.18	1.398	0.34	9.66
MARC_Res		1237	2.28	1.048	0.58	10.61
MARC_Com		712	2.15	0.772	0.50	5.74
MSUPRP	FLOSS	946	1.85	1.177	0.00	7.97
MARC_Res		531	3.15	1.176	0.78	9.33
MARC_Com		1807	0.88	0.769	-0.49	5.69
MSUPRP	CLOSS	936	22.74	2.826	12.72	31.81
MARC_Res		1237	20.18	3.062	12.24	29.55
MARC_Com		1807	17.25	2.256	8.48	24.97
MSUPRP	WBSF	935	3.21	0.689	1.83	6.54
MARC_Res	SFF	1237	13.79	3.431	6.43	30.15
MARC_Com		1920	16.79	5.616	6.38	47.05

[a]MSUPRP- MSU DurocxPietrain F2 Population; MARC_Res – US MARC DurocxLandrace F2 population; MARC_Com – US MARC non-pedigreed commercial population

[b]pHu – ultimate pH; CIE L* - longissimus muscle (LM) measure of lightness; CIE a* - LM measure of redness; CIE b* - LM measure of yellowness; IMF – LM intramuscular fat percentage; FLOSS – LM fluid loss percentage; CLOSS – LM cook loss percentage; WBSF – cooked LM Warner-Bratzler shear force, kg; SFF – LM slice shear force, kg.

Table 4. Heritability and genetic and residual variance estimates for three populations

			Genetic Variance (S.E.)	**Residual Variance (S.E.)**	**Heritability ($h^{2)}$**
Population[a]	**Trait[b]**	**Number**			
MSUPRP	pHu	904	0.003 (0.002)	0.013 (0.001)	0.188
MARC_Res		530	0.007 (0.002)	0.019 (0.002)	0.269
MARC_Com		1857	0.011 (0.002)	0.016 (0.002)	0.407
MSUPRP	CIE L*	874	1.67 (0.325)	2.949 (0.204)	0.362
MARC_Res		704	2.832 (0.701)	6.363 (0.535)	0.308
MARC_Com		1780	3.817 (0.634)	6.706 (0.425)	0.633
MSUPRP	CIE a*	874	0.57 (0.77)	0.36 (0.031)	0.613
MARC_Res		704	0.131 (0.049)	0.687 (0.05)	0.161
MARC_Com		1780	0.957 (0.13)	1.121 (0.079)	0.46
MSUPRP	CIE b*	874	0.108 (0.029)	0.408 (0.026)	0.209
MARC_Res		704	0.188 (0.065)	0.847 (0.063)	0.182
MARC_Com		1780	1.20 (0.194)	2.005 (0.128)	0.375
MSUPRP	IMF	910	0.937 (0.137)	0.791 (0.061)	0.542
MARC_Res		1237	0.442 (0.054)	0.362 (0.028)	0.55
MARC_Com		910	0.287 (0.137)	0.337 (0.041)	0.46
MSUPRP	FLOSS	927	0.291 (0.067)	0.801 (0.050)	0.266
MARC_Res		673	0.526 (0.116)	0.805 (0.082)	0.395
MARC_Com		1780	0.186 (0.031)	0.33 (0.021)	0.360
MSUPRP	CLOSS	912	2.236 (0.483)	5.358 (0.344)	0.295
MARC_Res		1234	1.241 (0.204)	2.17 (0.139)	0.364
MARC_Com		1780	1.637 (0.274)	2.929 (0.185)	0.359
MSUPRP	WBSF	911	0.107 (0.025)	0.297 (0.019)	0.265
MARC_Res	SFF	1237	3.275 (0.606)	7.553 (-.46)	0.302
MARC_Com		1892	10.38 (0.025)	19.982 (1.19)	0.342

[a]MSUPRP- MSU DurocxPietrain F2 Population; MARC_Res – US MARC DurocxLandrace F2 population; MARC_Com – US MARC non-pedigreed commercial population

[b]pHu – ultimate pH; CIE L* - longissimus muscle (LM) measure of lightness; CIE a* - LM measure of redness; CIE b* - LM measure of yellowness; IMF – LM intramuscular fat percentage; FLOSS – LM fluid loss percentage; CLOSS – LM cook loss percentage; WBSF – cooked LM Warner-Bratzler shear force, kg; SFF – LM slice shear force, kg.

Table 5. SNPs associated with ultimate pH in the MSUPRP population[a]

SNP_ID	SSC	Position	Effect	P-value[b]
DIAS0004560	15	122991614	-0.0125	7.5465E-07
H3GA0054872	15	122998623	-0.0125	7.5272E-07
ASGA0083809	15	125240941	-0.0124	1.1796E-06
SIRI0000158	15	129798767	-0.0129	6.9069E-07
ALGA0087078	15	133108407	0.0116	3.4437E-07
DIAS0000678	15	134531546	-0.0133	8.2119E-09
MARC0047188	15	135199210	0.0164	1.2091E-11
H3GA0052416	15	135234539	-0.0164	1.2088E-11
MARC0093624	15	135538479	-0.0140	4.7846E-09
ALGA0087403	15	135895297	0.0102	1.2115E-06
ALGA0087227	15	138208768	0.0123	6.0690E-07
ALGA0087207	15	138593445	-0.0122	8.0871E-07
ASGA0070725	15	138715882	0.0122	8.6060E-07

[a]MSUPRP is the MSU F2 resource population.
[b]After Bonferroni correction, SNPs with $P < 1.2874\ e^{-6}$ are considered significant.

Table 6. SNPs associated with ultimate pH in the MARC_Com population[a]

SNP_ID	SSC	Position	Effect	P-value[b]
ASGA0070625	15	133677385	0.0782	9.7370E-11
MARC0083357	15	133738342	-0.0786	9.9399E-11
M1GA0020450	15	133929898	0.0628	1.9571E-07
MARC0039273	15	133964455	0.0788	9.9384E-11
ASGA0070646	15	133970166	0.0785	9.2641E-11
DIAS0002965	15	134006845	-0.0778	1.2865E-10
DIAS0003382	15	134123978	-0.0716	6.4320E-09

[a]MARC_Com is the US MARC non-pedigreed commercial population.
[b]After Bonferroni correction, SNPs with $P < 1.2874\ e^{-6}$ are considered significant.

Table 7. SNPs associated with shear force in the MSUPRP population[a]

SNP_ID	SSC	Position	Effect	P-value[b]
M1GA0002229	2	2921459	0.1135	2.885E-08
ASGA0008534	2	3571211	0.1081	1.496E-07
M1GA0025499	2	5486683	0.1247	2.571E-07
ASGA0084492	2	6331738	0.1140	1.242E-06
ALGA0087078	15	133108407	0.0899	2.884E-07
DIAS0000678	15	134531546	-0.0895	5.605E-07
MARC0047188	15	135199210	0.1060	1.588E-08
H3GA0052416	15	135234539	-0.1062	1.479E-08
MARC0093624	15	135538479	-0.0960	2.194E-07

[a]MSUPRP is the MSU F2 resource population.
[b]After Bonferroni correction, SNPs with $P < 1.2873\ e^{-6}$ are considered significant.

Table 8. SNPs associated with shear force in the MARC_Res population[a]

SNP_ID	SSC	Position	Effect	P-value[b]
H3GA0055977	2	5479542	-0.7642	1.640E-07
ASGA0008680	2	5817132	-0.5730	3.248E-05
H3GA0005672	2	5903796	-0.6440	1.778E-06
ALGA0011566	2	5939643	0.6580	1.489E-06
ALGA0011623	2	6254385	0.5784	2.652E-05
SIRI0000872	5	11095982	0.6084	2.749E-05

[a]MARC_Res is the US MARC resource population
[b]After Bonferroni correction, SNPs with $P < 1.2873\ e^{-6}$ are considered significant.

Table 9. SNPs associated with shear force in the MARC_Com population[a]

SNP_ID	SSC	Position	Effect	P-value[b]
ASGA0008695	2	5956519	-1.4696	8.450E-06
M1GA0002408	2	5984348	-1.5577	5.197E-06
DRGA0003281	2	109366164	-1.6829	1.827E-07
DRGA0003319	2	111514339	-1.5725	1.332E-06
H3GA0032368	11	75204064	-0.9900	2.153E-06
MARC0081433	11	75298434	-0.9541	7.908E-06

[a]MARC_Com is the US MARC non-pedigreed commercial population.
[b]After Bonferroni correction, SNPs with $P < 1.2873\ e^{-6}$ are considered significant.

Table 10. GWA Meta-analysis of SNPs associated with ultimate pH using sample size for the weighting scheme

SNP_ID	SSC	Position	Z	P-value[a]
H3GA0054274	15	133220838	-5.07459	3.88E-07
MARC0082467	15	133269167	-5.95208	2.65E-09
ASGA0070625	15	133677385	5.691983	1.26E-08
MARC0083357	15	133738342	-5.55051	2.85E-08
M1GA0020450	15	133929898	7.340468	2.13E-13
ASGA0070646	15	133970166	5.031581	4.86E-07
ALGA0087491	15	135375798	-5.47605	4.35E-08

[a]After Bonferroni correction, SNPs with $P < 1.2874\ e^{-6}$ are considered significant.

Table 11. GWA Meta-analysis of SNPs associated with ultimate pH using the inverse variance for the weighting scheme

SNP_ID	SSC	Position	Z	P-value[a]
H3GA0054274	15	133220838	-4.90656	9.27E-07
M1GA0020450	15	133929898	5.77640	7.63E-09
MARC0047188	15	135199210	6.56565	5.18E-11
H3GA0052416	15	135234539	-4.94232	7.72E-07
ALGA0087491	15	135375798	-5.63802	7.72E-07
MARC0093624	15	135538479	-4.84587	1.26E-06

[a]After Bonferroni correction, SNPs with $P < 1.2874\ e^{-6}$ are considered significant.

Table 12. GWA Meta-analysis of SNPs associated with shear force using sample size for the weighting scheme

SNP_ID	SSC	Position	Z	P-value[a]
ASGA0008680	2	5817132	-6.50911	7.56E-11
ASGA0008662	2	5849903	-5.46866	4.53E-08
H3GA0005676	2	5888217	-6.86337	6.73E-12
ASGA0008746	2	6222845	5.072601	3.92E-07
ALGA0011623	2	6254385	6.812087	9.62E-12
ASGA0084492	2	6331738	5.083193	3.71E-07
ASGA0089651	2	105072899	-4.85142	1.23E-06

[a]After Bonferroni correction, SNPs with $P < 1.2873\ e^{-6}$ are considered significant.

Table 13. GWA Meta-analysis of SNPs associated with shear force using the inverse variance for the weighting scheme.

SNP_ID	SSC	Position	Z	P-value[a]
ASGA0008680	2	5817132	-6.17789	6.50E-10
H3GA0005676	2	5888217	-6.36972	1.89E-10
ALGA0011623	2	6254385	6.504022	7.82E-11
MARC0047188	15	135199210	5.18666	2.14E-07

[a]After Bonferroni correction, SNPs with $P < 1.2873\ e^{-6}$ are considered significant.

Figure 1. Correlation of phase between populations over genomic distance

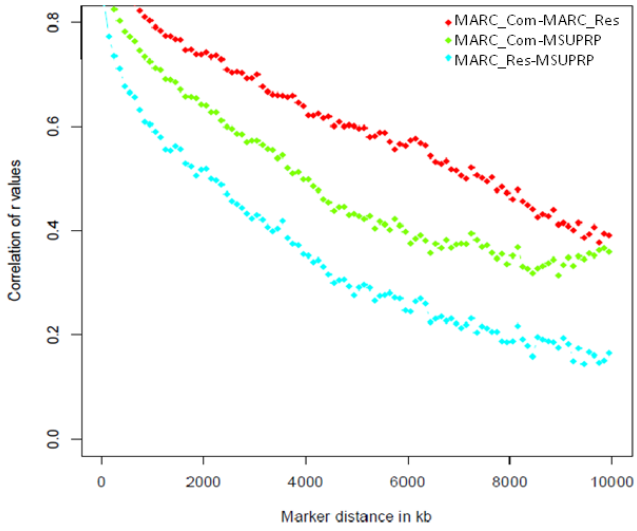

Figure 2. GWA for ultimate pH in: a) MARC_Com; b) MARC_Res; c) MSUPRP

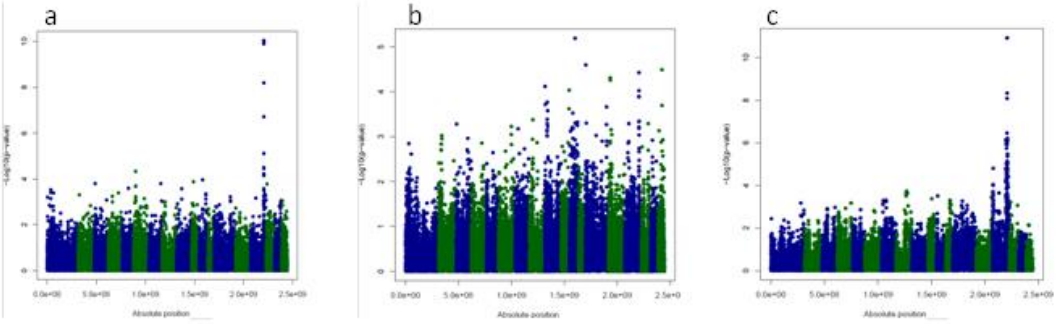

Figure 3. GWA for shear force in: a) MARC_Com; b) MARC_Res; and c) MSUPRP