

Single nucleotide polymorphisms for pig identification and parentage exclusion

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Summary

Single nucleotide polymorphisms (SNPs) have become an important type of marker for commercial diagnostic and parentage genotyping applications as automated genotyping systems have been developed that yield accurate genotypes. Unfortunately, allele frequencies for public SNP markers in commercial pig populations have not been available. To fulfil this need, SNP markers previously mapped in the USMARC swine reference population were tested in a panel of 155 boars that were representative of US purebred Duroc, Hampshire, Landrace and Yorkshire populations. Multiplex assay groups of 5–7 SNP assays/group were designed and genotypes were determined using Sequenom's MASSARRAY[®] system. Of 80 SNPs that were evaluated, 60 SNPs with minor allele frequencies >0.15 were selected for the final panel of markers. Overall identity power across breeds was 4.6×10^{-23} , but within-breed values ranged from 4.3×10^{-14} (Hampshire) to 2.6×10^{-22} (Yorkshire). Parentage exclusion probability with only one sampled parent was 0.9974 (all data) and ranged from 0.9594 (Hampshire) to 0.9963 (Yorkshire) within breeds. Sire exclusion probability when the dam's genotype was known was 0.99998 (all data) and ranged from 0.99868 (Hampshire) to 0.99997 (Yorkshire) within breeds. Power of exclusion was compared between the 60 SNP and 10 microsatellite markers. The parental exclusion probabilities for SNP and microsatellite marker panels were similar, but the SNP panel was much more sensitive for individual identification. This panel of SNP markers is theoretically sufficient for individual identification of any pig in the world and is publicly available.

Keywords identification, parentage, pig, single nucleotide polymorphism.

Introduction

Demand for genetic markers that are able to discriminate between lines of animals and potentially identify each animal has increased dramatically in recent years. Genetic identification of individual livestock animals is critical to determine farm of origin of animals that are diagnosed with important contagious diseases such as bovine spongiform encephalopathy, avian influenza or even foot and mouth disease (Heaton *et al.* 2005). In addition, as commercial pork production attempts to market a 'branded' product with specific eating qualities, tests that are able to accurately determine the origin of the pork product are needed to insure accurate product labelling. DNA-based markers work well for these applications as testing can be done on cooked

pork products (Meyer *et al.* 1994). Accurate and cheap animal and/or parental identification also has applications for animal forensics and in pedigreed swine production for determining accuracy of pedigrees and permitting multiple sire matings (Sherman *et al.* 2004).

To facilitate the use of single nucleotide polymorphisms (SNPs) in pigs, we selected the most informative SNP markers in the USMARC pig SNP map (B.A. Freking, J.W. Keele, D.J. Nonneman, G.A. Rohrer, W.M. Snelling & R.T. Wiedmann, unpublished data) and determined their allele frequencies within US purebred Duroc, Hampshire, Landrace and Yorkshire pig populations. In this study, we report the results for 60 SNP markers that are suitable for animal identification purposes in US commercial pigs.

Materials and methods

Animals

Blood or semen samples from 24 representative unrelated boars were obtained from the National Swine Registry for

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the four most common breeds in the United States (Duroc, Hampshire, Landrace and Yorkshire). Liver or semen samples for 49 additional animals from these four breeds were either purchased from commercial boar studs ($n = 8$), contributed by commercial pig breeding companies ($n = 13$) or purchased for other research studies at USMARC ($n = 28$). A total of 42 Landrace, 40 Duroc, 35 Yorkshire and 28 Hampshire animals were evaluated. In addition to the purebred animals, 21 pigs from a White Composite line developed at USMARC for a selection study on reproductive performance (Leymaster & Christenson 2000) were included. This population was developed in the mid-1980s, maintained as a closed population and contains 1/2 Yorkshire, 1/4 Landrace and 1/4 Chester White. Most animals sampled from each breed were males, but a small number of females were included. DNA was purified from biological tissues using standard phenol–chloroform extraction methods (Rohrer *et al.* 1996).

To have a measure of the accuracy of collected genotypes, the USMARC reference families were also genotyped for this study and the genotypes were compared with genotypes collected for the SNP markers with Sequenom's sME chemistry.

SNP genotyping

Seventy-three SNPs chosen for evaluation in this study were identified and mapped in a project outlined by Fahrenkrug *et al.* (2002). Seven additional SNPs were identified in other projects conducted at USMARC or from published literature (Nonneman & Rohrer 2004; Jacobs *et al.* 2006). The SNPs were selected for testing when the White Composite sire of the USMARC Reference Population was heterozygous or when the F1 Duroc-White Composite sow was heterozygous and the SNP was located in a unique region of the genome (more than 20 cM from other tested SNPs).

Multiplex assays for use in the Sequenom MASSARRAY[®] system were designed using MASSARRAY[®] Assay Design software. A minimum of five and a maximum of eight assays per plex group were used as criteria. Assays were designed for 80 unique SNPs. Each amplification primer had a 10-base tag added to ensure that the amplification primer masses were outside the range of SNP allele masses. Amplicon lengths were approximately 120 bp. Information on amplicons, oligonucleotides and polymorphisms are given in Table S1. Reaction conditions were as suggested by Sequenom for the hME chemistry.

Flanking SNP discovery

The amplicon for each SNP was resequenced (Fahrenkrug *et al.* 2002) in 16 animals (three Duroc, three Landrace, three Yorkshire and one each of Berkshire, Chester White, Hampshire, Meishan, Pietrain, Poland China and Spot) and evaluated for additional SNPs. Particular attention was given to

regions that contained assay primers to ensure robust assay systems in commercial pig populations. All SNPs were submitted to GenBank's dbSNP database (Table S3).

Microsatellite genotyping

To compare the utility of these SNP markers vs. more informative microsatellite markers, 10 microsatellites that were used in a previous genome scan project of a Duroc-Landrace population (Rohrer *et al.* 2006) were genotyped across the panel of purebred pigs. The selected markers were highly informative and easily scored in the previous study. Reaction conditions were as described (Rohrer *et al.* 1996). The markers used were SW21, SW818, SW1370, SW1824, SWR1829, SW1891, SW1904, SW2156, SW2519 and SW2527.

Analyses

Genotypic data were inspected for inconsistencies based on expected genotypic frequencies. In addition, genotypes for the USMARC Reference Population from the mapping project obtained with sME chemistry were compared with genotypes collected for the current project using hME chemistry. The third requirement for the panel of markers was that the minor allele frequency of all markers is >0.15 .

The average probability of two animals having an identical genotype for a marker is equal to the summation of the square of each genotypic frequency (Holt *et al.* 2000; Heaton *et al.* 2005). To determine the probability of two animals having the same genotype for all markers, the multiple product of each individual marker probability was computed. Parental exclusion probabilities when both suspected parents' genotypes were known and parental exclusion probabilities when only one suspected parent was genotyped were computed as described (Jamieson & Taylor 1997).

Results

SNP marker panel

The summary values of the 60-SNP marker panel in each of the four major breeds and in the entire set of genotyped animals are presented in Table 1. As the world swine population is around one billion animals, the probability that two animals share a common genotype for all 60 loci is unlikely as the probability of this occurrence ranged from 4.3×10^{-14} (Hampshire) to 2.6×10^{-22} (Yorkshire). In addition, this panel of markers is powerful enough to exclude 99.9% of sires assuming that the dams' genotypes are available. However, the exclusion probabilities are much lower if only one parent is available, i.e. the exclusion probabilities in this situation for Duroc and Hampshire were $<99.0\%$. In general, the power of this panel of markers was only marginally better when the allele frequency for each

Table 1 Exclusion probabilities for SNP and microsatellite marker panels within each population.

	60-SNP panel			10-microsatellite panel		
	One-parent exclusion ¹	Two-parent exclusion ²	ID power ³	One-parent exclusion ¹	Two-parent exclusion ²	ID power ³
Duroc	0.985684	0.999758	1.29×10^{-17}	0.954885	0.996823	7.84×10^{-9}
Hampshire	0.959369	0.998676	4.32×10^{-14}	0.931317	0.993637	4.02×10^{-8}
Landrace	0.994942	0.999955	4.42×10^{-21}	0.988423	0.999558	1.04×10^{-10}
Yorkshire	0.996287	0.999975	2.60×10^{-22}	0.990433	0.999641	6.78×10^{-11}
White Composite	0.996746	0.999979	1.09×10^{-22}	0.981871	0.999073	5.30×10^{-10}
Average allele frequency ⁴	0.997391	0.999982	4.55×10^{-23}	0.998199	0.999964	5.41×10^{-13}

¹One-parent exclusion is the power to eliminate an animal as a possible parent when DNA is only available from the suspected parent and the offspring.

²Two-parent exclusion is the power to eliminate an animal as a possible parent when DNA is available on the suspected parent, a known parent and the offspring.

³ID power is the probability that two animals will have identical genotypes for all markers. Exclusion probability for animal identification = 1-ID power.

⁴The average of allele frequencies of Duroc, Hampshire, Landrace and Yorkshire were used for these calculations.

marker was the average of the four purebred allele frequencies. These values would be representative of a four-breed composite population.

The Hampshire breed had the least amount of within-breed genetic variation of the four major breeds studied. Nine of the 60 markers were fixed for one allele (Table 2) leading to lower identity and exclusion probabilities. Six of the 60 loci were fixed in the Duroc sample, while Landrace and Yorkshire breeds were segregating at all loci included in the final panel (Table 2).

Assessment of assay robustness

Resequencing STS amplicons in 16 animals representing 10 breeds revealed approximately 40% more SNPs than were previously identified in the eight parents of the USMARC Reference Population. As not all amplicons were sequenced in both groups of animals, a direct comparison of only 46 of the 57 total amplicons was conducted. The eight reference parents had a total of 336 tagged SNPs and sequences from the 16 other animals detected 134 additional SNPs. The increased number of SNPs was due to a more diverse population and longer sequence reads. Only one SNP was detected in a region where the probe primer annealed, but the polymorphism was towards the 5' end of the probe and did not appear to affect the accuracy of genotypes. No SNPs were detected in amplification primer sites.

A comparison of genotypes collected in the USMARC Reference Population using sME chemistry vs. the current study using the hME chemistry was conducted for 49 SNP markers included in this panel. Three SNP assays had a considerable number of discrepancies; however, the genotypes collected in the current study (hME chemistry) appear to be accurate based on Mendelian segregation and linkage analysis. For the remaining 46 markers, 0.6% of the genotypes differed. The primary difference between these

chemistries is purification of the final product. Both procedures rely on the addition of one or two bases to the probe primer and mass spectrometry for discrimination of extended products.

Microsatellite marker panel

The average number of alleles in the 10 microsatellites was 10.6 and ranged from six alleles for *SW21* to 13 alleles for *SW2156* (Table 3). *SW21* was the only marker with <10 alleles. The probability of two animals having identical genotypes for all 10 loci ranged from 7.4×10^{-9} for Hampshire to 6.4×10^{-12} for Yorkshire (Table 1). Parental exclusion probabilities when both parents were genotyped were all >99% and ranged from 99.6% (Hampshire) to 99.98% (Landrace and Yorkshire). Parental exclusion probabilities when only one parent was genotyped ranged from 94.8% (Hampshire) to 99.4% (Yorkshire).

The power of the microsatellite marker panel was increased when the average allele frequencies across the four purebred populations were used in the calculations. The probability of two animals having identical genotypes for all 10 loci was 5.4×10^{-13} . Parental exclusion with both parents available was 99.996% and 99.8% when one parent was available. The allele frequencies for microsatellite markers within breeds are provided in Table S2.

Discussion

The current panel of 60 SNP is sufficient for identification in pigs, even after factoring in the need for two inconsistent genotypes for exclusion as proposed by Weller *et al.* (2006). The exclusion probabilities computed for this panel of SNP markers were similar to those reported in cattle for a similar number of SNP markers (Heaton *et al.* 2002; Werner *et al.* 2004). These 10 microsatellite markers produced similar

Table 2 Genetic map position and allele frequency of the most common allele in each population for the 60 SNP markers included in the identity panel.

Assay	SSC	Position (cM)	STS accession no. ¹	SNP ss no. ¹	Duroc allele frequency	Hampshire allele frequency	Landrace allele frequency	Yorkshire allele frequency	White Composite allele frequency
10723.179h	1	122	BV680481	52052014	0.988	1.000	0.940	0.544	0.500
12059.2h	4	99	BV677906	48398212	0.607	0.500	0.469	0.595	0.625
12303.1h	17	52	BV102818	23129578	0.526	0.946	0.650	0.703	0.575
12775.1h	12	94	BV677907	48398221	0.825	0.607	0.619	0.721	0.775
12891.1h	10	52	BV677908	48398224	0.363	0.929	0.821	0.929	0.810
13438.1h	7	50	BV103643	23130590	0.684	0.963	0.987	0.733	0.853
13631.1h	16	33	BV677910	48398232	0.538	0.964	0.732	0.258	0.625
13687.2h	14	56	BV677911	48398239	0.050	0.963	0.298	0.788	0.789
13739.1h	10	90	BV103636	23130238	0.400	0.583	0.542	0.545	0.816
13741.1h	5	51	BV677912	48398241	0.788	0.852	0.440	0.532	0.275
14325.1h	7	69	BV103461	23130318	0.500	0.875	0.763	0.567	0.700
14367.1h	12	0	BV677913	48398254	0.276	0.554	0.571	0.694	0.600
14585.1h2	6	125	BV677914	48398263	0.350	0.667	0.679	0.281	0.553
14753.2h	6	111	BV677916	48398106	0.838	0.018	0.905	0.647	0.700
14757.1h	8	143	BV677917	48398459	0.829	0.750	0.417	0.843	0.700
14757.2h2	8	143	BV677917	48398457	0.888	0.741	0.631	0.817	0.700
15241.1h	7	148	BV677918	48398465	0.050	0.444	0.524	0.514	0.575
15289.2h	6	41	BV677919	48398481	0.650	0.019	0.512	0.621	0.550
16045.1h	9	135	BV677920	48398548	0.038	0.339	0.537	0.788	0.600
16297.2h	15	98	BV103337	23131234	0.838	0.375	0.774	0.629	0.700
16307.1h	7	71	BV677922	48398517	0.705	0.389	0.405	0.594	0.525
16655.2h	18	2	BV677878	48398297	0.568	0.089	0.413	0.804	0.737
16871.2h	1	104	BV103218	23130675	0.429	0.481	0.720	0.810	0.800
16873.1h	8	12	BV103219	23130679	0.853	0.955	0.729	0.731	0.538
16873.2h	8	12	BV103219	23130680	0.825	0.981	0.750	0.697	0.525
16951.1h	6	98	BV677881	48398316	0.526	0.946	0.464	0.781	0.700
16961.1h	2	127	BV677882	48398332	0.770	0.815	0.560	0.468	0.425
16963.2h2	3	33	BV677883	48398346	0.970	0.043	0.719	0.304	0.750
17187.1h	17	38	BV103260	23131937	0.413	0.036	0.571	0.629	0.875
17191.1h	3	88	BV103262	23131976	1.000	1.000	0.619	0.500	0.800
17379.2h	14	33	BV102798	23131808	0.558	0.688	0.712	0.324	0.300
17429.1h	10	57	BV677895	48398424	0.956	1.000	0.581	0.813	0.667
21195.1h	8	18	BV677885	48398357	0.525	1.000	0.427	0.667	0.700
21351.2h2	7	69	BV102746	23131826	0.700	0.760	0.513	0.621	0.452
21726.2h	2	63	BV677886	48398363	0.913	0.286	0.857	0.486	0.550
23321.05h	17	60	BV677888	48398372	0.675	0.286	0.595	0.543	0.762
23811.1h	13	112	BV677889	48398381	0.575	0.518	0.902	0.814	0.650
2535.1h2	7	59	G72967	16337617	0.171	0.205	0.539	0.794	0.526
26047.2h	2	22	BV677890	48398386	0.750	0.731	0.538	0.406	0.395
26106.1h	6	181	BV677891	48398402	0.397	0.250	0.705	0.765	0.781
26113.1h	13	96	BV677892	48398412	0.684	1.000	0.794	0.773	0.947
27514.1h	3	33	BV102888	23132881	1.000	0.125	0.756	0.371	0.725
2928.3h	5	90	BV677897	48398268	0.938	0.981	0.524	0.721	0.725
3819.2h	12	26	BV677898	48398278	1.000	0.696	0.750	0.486	0.475
39683.2h	5	100	BV677924	48398449	0.385	0.630	0.905	0.758	0.225
39683.3h	5	100	BV677924	48398454	0.963	0.667	0.607	0.656	0.775
41061.649h	15	84	BV677833	48398045	0.538	0.056	0.359	0.071	0.381
44017.483h	5	58	BV677835	48398049	0.236	0.563	0.878	0.444	0.632
44360.103h	5	60	BV677837	48398059	0.767	0.433	0.152	0.588	0.625
4899.2h	12	6	BV677899	48398150	0.850	0.250	0.563	0.607	0.250
6711.1h	9	8	BV677900	48398153	0.388	1.000	0.738	0.914	0.675
6711.2h	9	8	BV677900	48398157	0.661	0.929	0.765	0.726	0.639
7637.1h	3	31	BV677901	48398169	0.527	0.963	0.690	0.379	0.750

Table 2 Continued

Assay	SSC	Position		SNP ss no.	Duroc allele frequency	Hampshire allele frequency	Landrace allele frequency	Yorkshire allele frequency	White Composite allele frequency
		(cM)	STS accession no.						
7637.2h	3	31	BV677901	48398164	0.696	1.000	0.821	0.688	0.816
7843.2h	7	104	BV677902	48398179	1.000	1.000	0.964	0.534	0.553
7907.1h	3	18	BV677903	48398185	1.000	0.444	0.923	0.574	0.667
8109.1h	17	92	BV677904	48398193	1.000	1.000	0.738	0.328	0.600
9501.1h	10	124	BV677905	48398196	0.375	0.944	0.750	0.804	0.675
MAN-12P1h	8	7	BV680482	52052035	0.167	0.607	0.939	0.682	0.643
PGC1X8.2h	8	33	BV680483	52052039	0.554	0.788	0.500	0.379	0.619

¹<http://www.ncbi.nlm.nih.gov/Genbank/index.html>.

Table 3 Number of alleles identified for each microsatellite marker used within each population.

Marker	Duroc (n = 40)	Hampshire (n = 28)	Landrace (n = 42)	Yorkshire (n = 35)	Total unique
SW1370	5	6	10	7	10
SW1824	6	5	8	6	10
SW1891	7	3	6	5	10
SW1904	5	6	8	8	12
SW21	4	4	4	4	6
SW2156	6	7	10	9	13
SW2519	4	5	7	6	11
SWR2527	5	5	9	7	10
SW818	6	7	9	6	12
SWR1829	9	6	9	9	12

results both within and across breeds as those found by Nechtelberger *et al.* (2001) in swine and similar to those found for cattle microsatellites by Sherman *et al.* (2004).

The difference in power of SNPs vs. microsatellite markers for specific applications was evident in these data. The panel of 60 SNPs was clearly superior to the 10 microsatellite markers for individual identification. Generally, it would require approximately 20 microsatellite markers, similar in information content to these 10 microsatellites, to have a similar identity exclusion probability as was calculated for the 60 SNP markers. However, the parentage exclusion probabilities were only marginally better for the SNP markers due to differences in the number of alleles.

To determine the relative number of unlinked SNPs required to equal a microsatellite marker, the exclusion probability for a SNP with allele frequency of 0.50 was compared with the exclusion probabilities of the average of the 10 microsatellite markers for the 'theoretical' crossbred population (average of four purebred population allele frequencies), as well as the single most exclusive probability computed for a breed-marker combination (best-case scenario). The exclusion probability for the identification of one SNP was 0.625, for two-parent exclusion was 0.1875 and for one-parent exclusion was 0.125. For identification, three SNPs were required to exceed the average microsatellite

marker in a crossbred population, while four SNPs would exceed the best-case scenario for a single microsatellite marker. For either parentage scenario, five SNPs were required for parentage exclusion relative to the average microsatellite marker, and seven SNPs were required to exceed the best-case scenario for a single microsatellite marker.

One assumption for the calculations was that all markers were independent, thus requiring >50 cM distances between all markers. This is not possible for more than 50 markers in the pig genome as it is only approximately 2500 cM in length (Rohrer *et al.* 1996). Minor violations of the unlinked assumption (markers 20–50 cM apart) will likely have little effect on the exclusion probabilities. However, within this panel of markers, there were three pairs of SNPs within 1000 bases of each other. The most conservative estimate of the exclusion power would be to eliminate one of these markers from the computations. However, these pairs of loci were not in complete linkage disequilibrium, so the additional SNP adds to the exclusion power of the panel. The exclusion probabilities computed for this study did not take this close linkage into consideration.

As SNPs are typically biallelic and those selected for this marker panel were informative in most breeds, there was little improvement of exclusion power in the theoretical crossbred population (average of the four breeds' allele frequencies) or in the White Composite population. However, microsatellite markers were more powerful in crossbred populations (theoretical or White Composite) than in purebred populations because different alleles were present in each breed. Thus, crossbred populations generally had a greater number of alleles segregating than did any individual purebred population and allele frequencies were closer to $1/n$ (where n equals the number of alleles), which is when the greatest power to discriminate would be achieved.

Markers in this panel were selected based on their informativity in all four breeds, and so this panel does not have the characteristics required to predict breed composition of an animal. Furthermore, development of such a panel of SNP markers would be difficult due to their bi-allelic

nature. Breed discrimination is another area where microsatellite markers or possibly haplotyped groups of SNP markers would be more suitable, especially if the objective was to predict an animal's percentage of a specific breed.

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Supplemental Material

The following supplementary material is available for this article online from <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2052.2007.01593.x>

Table S1 Primer sequences and marker information for the 60 SNP markers included in the identity panel.

Table S2 Allele frequencies for microsatellite markers genotyped within each population.

Table S3 Complete GenBank STS accession numbers and ss numbers for amplicons containing SNP markers in the identity panel.