RENATA VERONEZE

LINKAGE DISEQUILIBRIUM AND HAPLOTYPE BLOCK STRUCTURE IN SIX COMMERCIAL PIG LINES

Dissertation presented to the Animal Science Graduate Program of the Universidade Federal de Viçosa, in partial fulfillment of the requirements for degree of *Magister Scientiae.*

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"I must endure the presence of two or three caterpillars if I wish to become acquainted with the butterflies"
The Little Prince - Antoine de Saint-Exupery

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BIOGRAPHY

Renata Veroneze, daughter of Rosivaldo Veroneze and Irene Nunes Veroneze, born on July 27, 1984, in Capivari, São Paulo, Brazil.

She began her studies in Animal Science at the *Universidade Federal de Vicosa* in 2004 and graduated in Animal Science in January 2009. In March 2009, she began s the master's degree in Animal Science at the same University.

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RESUMO

VERONEZE, Renata, M.Sc., Universidade Federal de Viçosa, fevereiro de 2011. **Desequilíbrio de ligação e blocos de haplótipo em seis linhas comerciais de suíno.** Orientador: Paulo Sávio Lopes. Co-orientadores: Simone Eliza Facioni Guimarães e Fabyano Fonseca e Silva.

O sucesso de estudos de associação e, consequentemente, a seleção genômica dependem da densidade de marcadores utilizados nas análises, a qual, por sua vez, é determinada pela extensão do desequilíbrio de ligação (LD) ao longo do genoma. O LD é organizado em blocos de haplótipos, separados por *hot spots* de recombinação. Essa organização do LD permite a seleção de um conjunto de SNPs que caracterizam o bloco, o que constitui uma forma adequada de escolher SNPs. O objetivo deste estudo foi estimar a extensão do desequilíbrio de ligação e o tamanho dos blocos de haplótipos de seis linhas comerciais de suínos. Foram genotipados 2050 animais com o SNP chip de 60K para suínos da Illumina. Os marcadores foram filtrados com base na MAF (>0,05) e Equilíbrio de Hardy-Weinberg (p valor > 0,001), o que resultou na utilização de, em média, 34021 SNPs para análises subsequentes. O programa Haploview foi usado no cáculo do LD de todos os pares de SNPs sintênicos, como também na construção dos blocos de haplótipo. O tamanho dos blocos de haplótipo das diferentes linhas foi comparado, utilizando-se o procedimento PROC MIXED do software SAS. Marcadores entre 105 – 175 Kb de distância apresentaram r^2 (correlação entre frequências gênicas) médio acima de 0,3 para todas as linhas, o qual é considerado um bom limiar para estudos de associação. Assim, mapas com um SNP, a cada 105 Kb, seriam adequados a esse tipo de análise. Teoricamente, o LD decresce com o aumento da distância entre os SNPs, entretanto, alguns cromossomos (1, 4, 5, 7, 9, 11, 12, 13, 14, 15 e 16) apresentaram r^2 elevado entre SNPs distantes em todas as linhas estudadas, o que poderia ser resultado de erros na distância e na posição dos marcadores no mapa utilizado. Em alguns cromossomos (2 e 18) alto r^2, entre SNPs distantes, foi observado apenas em algumas linhas, o que poderia ter sido causado por uma série de fatores que influenciam o LD. Entretanto, por tratar-se de linhas diferentes, provavelmente elas possuem histórico, endogamia e cruzamentos distintos. Dessa maneira, pode-se

pressupor que esse efeito teria sido causado pela seleção, uma vez que existem características de importância econômica que com certeza, em algum momento, foram selecionadas em mais de uma linha. O tamanho médio dos blocos de haplótipos foi de 287,81 Kb, com predominância de blocos pequenos com menos de 50 Kb. Nenhuma linha apresentou blocos maiores ou menores que as demais, em todos os cromossomos, não existindo, portanto, um padrão que possa discriminar as diferentes linhas. De acordo com a extensão do LD observado neste estudo, seriam necessários 22915 SNPs informativos (MAF > 0,05) para estudos de associação que abrangerem todo o genoma. O elevado desequilíbrio de ligação, observado entre pares de SNPs distantes, pode ter sido causado por erros no mapa e, em alguns casos, por seleção, entretanto para confirmação dessa última hipótese, seria necessário um estudo mais aprofundado das regiões onde esses SNPs se encontram.

ABSTRACT

VERONEZE, Renata, M.Sc., Universidade Federal de Viçosa, February 2011. **Linkage disequilibrium and haplotype block structure in six commercial pig lines.** Adviser: Paulo Sávio Lopes. Co-Advisers: Simone Eliza Facioni Guimarães and Fabyano Fonseca e Silva.

The success of association studies and genomic selection depends on marker density, which is determined by the linkage disequilibrium extended across the genome. The LD is organized into haplotypes blocks separated by recombination hot spots and this organization allows the selection of a set of SNPs that label the blocks. The objective of the present study was to estimate the linkage disequilibrium extent and haplotype block size of six commercial pig lines. Two thousand and fifty animals were genotyped using Illumina Porcine SNP60K. The MAF and Hardy-Weinberg equilibrium were used to filter the SNPs, which resulted, on average, in the use of 34021 markers for the subsequent analysis. The data were submitted to Haploview to calculate the LD for all SNP pairs and the haplotype blocks construction. The haplotype block size for all six lines was compared using the PROC MIXED procedure of SAS in a model with the number of SNPs per block as covariate. In markers distant 105 - 175 Kb the average r^2 was above 0.3 for all lines, which is considered a usable threshold for association studies; therefore maps with one SNP every 105 Kb would be suitable for this type of analysis. Following the theory, the LD decreases when the distance between SNPs increases, but high r^2 was observed between distant SNPs for some chromosomes (1, 4, 5, 7, 9, 11, 12, 13, 14, 15 and 16) in all lines that could be produced by errors in the marker distance and position of the map used. In some chromosomes (2 and 18) high r^2 between distant SNPs was observed only for some lines, which could be a result of a number of factors that influence the LD. However, the studied lines probably have different history and inbreeding. It could be argued that this is a selection effect, as these lines at a certain moment were certainly selected for traits of economic importance. Although the overall average haplotype block size was 287.81 Kb, a predominance of blocks with less than 50 Kb was observed for all lines. There is not a line that presents smaller or bigger blocks than the others in every chromosome; therefore there was no pattern that could

be used to discriminate the lines.. According to the LD extent observed in this study, 22915 informative SNPs (MAF > 0.05) would be necessary for whole genome association studies for the six lines analysed. The high linkage disequilibrium observed between distant SNPs may have been caused by map errors and in other cases by selection. Nevertheless, to confirm the last hypothesis a detailed study would be necessary of the regions where these SNPs are found.

CHAPTER 1

1. INTRODUCTION

Selection based on phenotype information has provided most of the pig genetic progress. Despite the success of this approach, the interest in the use of molecular information for selection is growing. In addition, considerable increase in the available molecular information has been experimented. The pig genome has been sequenced (www.ensembl.org/sus_scrofa) and the number of identified SNPs (Single Nucleotide Polymorphism) markers is growing fast which in turn enables an increase in porcine molecular genetic studies.

A successful association analysis and consequently the genomic selection depend on the marker density which is determined by the linkage disequilibrium (LD) extent across the genome (Khatkar, et al., 2008). LD is defined as the nonrandom association between alleles at different loci and is influenced by population history, breeding system and the pattern of geographic subdivision (Slatkin, 2008).

These allelic associations are mainly due to physical proximity; but distant SNPs pairs might be in complete LD. In addition, the LD extent can vary tremendously from one region to another. Despite this apparent complexity, the LD is organized into discrete blocks of haplotypes that show high LD, separated by putative hot spots of recombination (Daly, et al., 2001; Ardlie, et al., 2002; Jeffreys, et al., 2001). It is an important characteristic, because it makes it possible to select a set of SNPs in a rational way, so that SNPs that label a haplotype-block can be selected for association mapping (Johnson, et al., 2001).

Studies of linkage disequilibrium have shown that the LD extension in livestock is higher than in human populations, that can be explained by the small effective population size, selection and genetic drift, which are common features in livestock (McRae, et al. 2002).

According to Khatkar et al. (2008) significant LD extends to 40 Kb in Australian Holstein-Friesian cattle and the mean squared correlation of the alleles at two loci (r^2) is 0.024 among syntenic SNPs (Single Nucleotide Polimorfism) is 0.024. Qanbari et al. (2010) found 712 haplotype blocks in German Holstein cattle and the estimated average block size was 164 ± 177 Kb.

In pigs Du et al. (2007) used 4,500 SNPs markers and 6,000 pigs animals and identified lower LD than that previously reported using microsatellite markers, in this study for SNPs pairs 3 centiMorgan (cM) apart the average r^2 was equal to 0.1. Amaral et al.

(2008) genotyped three genomic regions using 371 SNP markers in several pig breeds, and reported that the LD extended up to 2 cM in European breeds and up to 0.05 cM in Chinese breeds. They also observed that the European breeds have larger haplotype blocks (>400kb) than the Chinese (10 kb). Using SNP markers, Uimari and Tapio (2011) reported an average r^2 of 0.47 and 0.49 for Finnish Landrace and Finnish Yorkshire, respectively, for SNPs 30 Kb apart.

LD studies elucidate the recombination history of a population, which is valuable information for selecting SNPs for association and genome selection studies.

2. REVIEW

2.1 Pig breeding

Pork is the most consumed meat around the world and it was estimated that 101 million tons of pork were produced in 2010 (http://www.abipecs.com.br/). In Brazil, the pork industry is very important and the country produces approximately 3 million tons of pork meat and its chain generates 630 thousand direct jobs (http://www.abipecs.com.br/). In addition, because of the physiological similarity with humans, the pig is an important animal model to study diseases (Lunney, 2007).

To date, most of the pig genetic progress was obtained by selection using phenotypic information, without knowledge of the number of genes that affect the trait or the effects of each gene (Rothschild, 2008). Despite the success of phenotype based selection, there is a growing interest in the use of molecular information for selection, especially for traits with low heritability, that are difficult to measure or that can only be measured in one sex or late in life and also in traits that require the animal to be slaughtered (Dekkers and Rothschild, 2007).

Considerable increase in the available molecular information has been experimented, the pig genome has been sequenced (www.ensembl.org/sus_scrofa) and the number of identified SNPs markers is growing fast. SNP genotyping will allow for “whole genome association trials” and discovery of many significant associations (Rothschild, 2008), which are the basic information to perform genomic selection.

2.2 Single-nucleotide polymorphisms (SNPs) markers

A SNP marker is only a single base change in a DNA sequence, nevertheless for such change to be considered as a SNP the least frequent allele should have a frequency of

1% or greater (Vignal, et al., 2002). Most of the SNP markers are bi-allelic, because of the low probability of two independent base changes occurring in a single position.

Single-nucleotide polymorphisms are the most frequent type of variation found in DNA and they are valuable markers for high-throughput genetic mapping, genetic variation studies and association mapping. It was estimated that the human genome contains more than 10 million SNPs (Gunderson, et al., 2005), with one SNP every 1,000 bases or less (Weiner and Hudson, 2002). SNPs can be found in coding or regulatory regions, but in most cases they are found in intergenic spaces with no defined function (Caetano, 2009).

3. Linkage disequilibrium (LD)

Linkage disequilibrium (LD) is a nonrandom association between alleles at different loci. These allelic associations are mainly due to physical proximity but are also influenced by population history and evolutionary forces (Khatkar, 2008).

The LD extent within a population plays an important role in gene mapping and genome association studies (Bohmanova, 2010); it determines the number of markers that will be required for successful association mapping and genomic selection. The influence of the population history on LD extent results in differences in this measurement between populations and consequently in the effectiveness of genome association studies.

LD extent depends on the local recombination rates; therefore the LD extent is higher in regions with a low recombination rate, which include the Y chromosome, parts of the X chromosome and regions near the centromere in autosomes. On the other hand, regions with a high recombination rate, such as euchromatin and small regions known as hotspots (Jeffreys, et al., 2001) have small LD extent between two loci.

The population history, breeding system and pattern of geographic subdivision reflect the LD throughout the genome, while the history of natural selection, gene conversion, mutation and other forces that cause gene-frequency evolution reflect the LD in each genomic region (Slatkin, 2008).

Little information was found in the consulted literature about pig linkage disequilibrium estimated using SNP markers. Using SNPs Du et al. (2007) identified lower LD than that previously reported using microsatellite markers. In this study 6,000 pigs were genotyped with approximately 4,500 SNPs and for markers pairs 3 centiMorgan (cM) apart the average r^2 was equal to 0.1. Amaral et al. (2008) genotyped three genomic regions using 371 SNP markers in several pig breeds and reported that Chinese breeds have lower LD extending (0.05 cM) than European breeds (2 cM) and they also observed that the European breeds have larger haplotype blocks (>400kb) than the Chinese (10 kb).

4. Measurement of Linkage disequilibrium

The first linkage disequilibrium measurement (D) was proposed by Lewontin (1964) which quantifies the linkage disequilibrium as the difference between the observed frequency of a two-locus haplotype and the expected frequency if the alleles were segregating at random. So, it can be calculated as demonstrated below:

$$D_{ij} = P_{ij} - p_i \, q_j$$

where, P_{ij} is the observed frequency of the haplotype that consists of alleles i and j; p_i is the frequency of the allele i and q_j is the frequency of the allele j.

The D is of little use for LD measure, because of its dependence on allele frequencies (Ardlie, et al., 2002). Consequently, several alternative measures were developed, the two most common are D' (Lewontin, 1964) and r^2 (Hill and Robertson, 1968).

For any two biallelic loci, D' is defined as:

$$D' = \sum_{i=1}^{2} \sum_{j=2}^{2} p_i \, q_j \, \frac{|D_{ij}|}{D_{max}}$$

where,

$$D_{max} = \begin{cases} \min[p_i \, q_j \, , (1 - p_i)(1 - q_j)] \; if \; D_{ij} < 0 \\ min \, [p_i \, (1 - q_j), \; (1 - p_i) q_j] \; if \; D_{ij} > 0 \end{cases}$$

D' ranges from 0 to 1, D' equals 1 (complete LD) and means that there is no recombination between the two SNPs, in other words, one allele at each locus is completely associated with an allele at the other locus. Values $D' < 1$ does not have a clear interpretation (Du, et al., 2007).

The other LD measure (r^2) is the correlation of gene frequencies for alleles at two sites. It is defined as:

$$r^2 = \frac{D_{ij}^2}{p_1 p_2 q_1 q_2}$$

where, $p_1 p_2 q_1 q_2$ is the product of the four allele frequencies at the two loci.

For a pair of biallelic loci, $r^2 = 1$ if there are two haplotypes for two biallelic loci and the allele frequency at both loci are identical. Du et al. (2007) compared the effect of the minor allele frequencies (MAF) on the D' and r^2 measurements and demonstrated that D' suffers greater influence of the MAF and concluded that the r^2 is considerably more robust than D'. Bohmanova et al. (2010) verified that D' is strongly dependent on the allele frequency, in addition, they demonstrated that D' is inflated in small-sized samples.

5. Haplotype block structure

LD has a tendency to decrease over large distances; nevertheless distant SNPs pairs might be in complete LD. In addition, tremendous differences can occur in the extent of LD from one genomic region to another (Wall, et al. 2003).

Despite this apparent complexity of the observed LD patterns, some studies have demonstrated that the LD is organized into discrete blocks of haplotypes that show high LD, separated by possible hot spots of recombination (Daly, et al., 2001; Ardlie, et al., 2002; Jeffreys, et al., 2001). The fact that the LD is often discontinuous produces haplotypic profiles across the genome because of the variation in local recombination rates, mutation rates and genetic hitchhiking (Jeffreys, et al., 2001).

A haplotype block was defined by Reich et al. (2001) as a contiguous set of markers in which the average D' (the standardized coefficient of LD) is greater than some predetermined threshold. Another definition is given by Patil et al. (2001); based on the concept of “chromosome coverage,” with a haplotype block containing a minimum number of SNPs that account for a majority of common haplotypes.

In biological terms the haplotype block can be defined by examining the patterns of recombination across each region, since the haplotype blocks represent regions inherited without substantial recombination in the ancestors of the current population (Gabriel, et al., 2002).

Diverse approaches to define a LD block have been proposed but the simplest way is to establish a LD threshold to include the SNPs in a block without considering the information of the haplotype-phase (Tishkoff and Verrelli, 2003).

The approach proposed by Gabriel et al. (2002) is based on D' as a measure of allelic association. The authors considered that a pair of alleles is in “strong LD” when the one-sided upper 95% confidence bound on D' is 0.98 and the lower bound is above 0.7.

In addition, for these authors the haplotype block is a region over which a very small proportion (5%) of comparisons among informative SNP pairs show strong evidence of historical recombination, and the term “strong evidence for historical recombination” pairs where the upper confidence bound on D' is less than 0.9.

The haplotype-block has important implications for association mapping because it makes it possible to select a set of SNPs that label the haplotype-block, which is a rational way to choose SNPs for association studies (Johnson, et al., 2001). In addition, haplotype block distribution and structure may provide a wider comprehension of the distribution of genetic variation throughout the genome (Wang, et al., 2002).

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CHAPTER 2

Linkage disequilibrium and haplotype block structure in six commercial pig lines[1]

ABSTRACT: Linkage disequilibrium (LD) across the genome is critical information for association studies and consequently for genome selection, since it determines the number of SNPs that should be used for a successful association analysis. Some studies demonstrated that the LD is organized into discrete blocks of haplotypes that show high LD, separated by possible hot spots of recombination. These haplotype-blocks have important implications for association mapping because they make it possible to select a set of SNPs that label the haplotype-block, which is a coherent way of selecting useful SNPs. Only a few LD studies with pigs using SNPs markers are available and some of them are restricted to specific genomic regions. We estimated the LD at different marker distances and calculated the average haplotype block size for six pig lines; we also compared the lines block size. Six commercial pig lines (1, 2, 5, 6, 4 and 3) were genotyped using the Illumina PorcineSNP60K Beadchip; on average a panel of 34,021 SNPs with an average 0.285 MAF was included in the analysis. The linkage disequilibrium declined as a function of the distance, but high LD was observed between distant SNP pairs especially in chromosomes 1, 4, 5, 7, 9, 11, 12, 13, 14, 15 and 16. All lines had an average r^2 above 0.3 in markers 105 -175 Kb apart. The estimated average block size was 287.81 Kb. However, a predominance of blocks with less than 50 Kb in all lines was observed. Except in two cases, no pig line showed higher or smaller block size than any of the other lines for all chromosomes. At least one SNP every 105 Kb is required for whole genome association studies, giving a total requirement of 22,915 informative SNPs (MAF > 0.05) in the analysed lines. The high linkage disequilibrium between distant SNP pairs could be produced in some chromosomes by errors in the marker distance and position and in other cases by selection. Nevertheless, to confirm the last hypothesis a detailed study would be necessary of the regions where these SNPs are found.

Keywords: Linkage Disequilibrium, Haplotype Blocks, SNP, pig

[1] Article written in the Animal Science journal format

INTRODUCTION

There has been a considerable increase in the molecular information available. The pig genome has been sequenced (www.ensembl.org/sus_scrofa) and the number of identified SNPs markers is growing fast. SNP genotyping will allow for "whole genome association trials" and discovery of many significant associations (Rothschild, et al., 2007), which are the basic information to perform genomic selection. A successful association analysis and consequent genomic selection depend on the marker density which is determined by the linkage disequilibrium (LD) extent across the genome (Khatkar, et al., 2008).

The LD is a nonrandom association between alleles at different loci. These allelic associations are mainly due to physical proximity but are also influenced by population history and evolutionary forces (Khatkar, et al., 2008). The influence of the population history on LD extent results in differences in this measurement between populations and consequently in the effectiveness of genome association studies.

The LD tends to decrease over large distances; nevertheless distant SNPs pairs might be in complete LD. In addition, tremendous differences can occur in the extent of LD from one genomic region to another (Wall and Pritchard, 2003). Despite this apparent complexity of the observed LD patterns, some studies have demonstrated that the LD is organized in discrete blocks of haplotypes that show high LD, separated by putative hot spots of recombination (Daly, et al., 2001; Ardlie, et al., 2002; Jeffreys, et al., 2001). Thus, the LD is often discontinuous and produces haplotypic profiles across the genome because of the variation in local recombination rates, mutation rates and genetic hitchhiking (Ardlie, et al., 2002).

The haplotype structure has important implications for association mapping and genomic selection because it makes it possible to select a set of SNPs that label the haplotype-block, which is a rational way to choose SNPs (Johnson, et al., 2001).

Du et al. (2007) used 4,500 SNPs markers and 6,000 pigs and observed, in the studied populations, that for SNPs pairs 3 centiMorgan (cM) apart the average r^2 was equal to 0.1. Amaral et al. (2008) genotyped three genomic regions using 371 SNP markers in several pig breeds. These authors reported that the LD extended up to 2 cM in European breeds and up to 0.05 cM in Chinese breeds and they also observed that the European breeds have larger haplotype blocks (>400kb) than the Chinese (10 kb).

The present paper presents linkage disequilibrium and haplotype block structure in six commercial pig lines.

MATERIALS AND METHODS

Data and haplotype reconstruction

The data consisted of 2050 animals from commercial pig sire lines (1, n=1008; 2, n=316 and 5, n=241) and dam lines (4, n=208; 6, n=108 and 3, n=169) that were genotyped using the Illumina Porcine SNP60K Beadchip. The marker position used was derived from Build 10, avaible at http://www.animalgenome.org/repository/pig/. Markers with minor allele frequency (MAF) <0.05 and/or with P-value for Hardy-Weinberg equilibrium (HWE) <0.001 were discarded. This editing resulted in an average of 34,021 useful SNPs for each line which were used for further analysis.

Measure of LD

The correlation of gene frequencies (r^2) (Hill and Robertson,1968) was used as LD measure and it is defined as:

$$r^2 = \frac{D_{ij}^2}{p_1 p_2 q_1 q_2}$$

where, $D_{ij} = P_{ij} - p_i\, q_j$, is the LD measure purposed by Lewontin (1964), being P_{ij} the observed frequency of the haplotype that consists of alleles i and j; p_i the frequency of the allele i and q_j the frequency of the allele j and $p_1 p_2 q_1 q_2$ is the product of the four allele frequencies at the two loci.

The r^2 was calculated using the Haploview v. 4.2 software (Barrett, et al., 2005) for every SNP pair and the R v.2.10.1 software was used to edit the Haploview outcome and construct LD graphics.

Haplotype blocks

D' (Lewontin, 1964) was used as LD measurement to define the blocks and for any two biallelic loci it is defined as:

$$D' = \sum_{i=1}^{2} \sum_{j=2}^{2} p_i\, q_j\, \frac{|D_{ij}|}{D_{max}}$$

where,

$$D_{max} = \begin{cases} \min[p_i\, q_j\, , (1 - p_i)(1 - q_j)]\; if\; D_{ij} < 0 \\ min\,[p_i\,(1 - q_j),\; (1 - p_i)q_j]\; if\; D_{ij} > 0 \end{cases}$$

The haplotype blocks were estimated using the algorithm suggested by Gabriel et al. (2002). It considers that a pair of SNPs is in strong LD when the upper 95% confidence bound of D' is between 0.7 and 0.98. For these authors the haplotype block is a region over which a very small proportion (5%) of comparisons among informative SNP pairs show strong evidence of historical recombination, and the term "strong evidence for historical recombination" pairs for which the upper confidence bound on D' is less than 0.9. Genotypes were inserted into Haploview v. 4.2 (Barret, et al., 2005) to calculate LD statistics and construct the haplotype blocks.

The average block size was compared among the six lines, and between sire (1, 2 and 5) and sow (3, 4 and 6) lines in each chromosome using the PROC MIXED procedure from SAS v. 9.1 following the model:

$$Y_{ij} = \mu + L_i + b\,(G_{ij} - \bar{G}\,) + \varepsilon_{ij}$$

where,Y_{ij} is the observed block size; μ is the general constant; L_i is the *ith* level of genetic group *i*= 1, 2, 3, 4, 5 or 6; *b* is the linear regression coefficient of the block size in function of the number of SNPs of the block *j* and genetic group *i* and G_{ij} is the number of SNPs of block *j* and genetic group i and $\overline{G}$ the average number of SNPs. ε_{ij} is the random error, normally and independent distributed.

RESULTS

Data description

Each pig line was genotyped for 41,785 SNPs. On average, 34,021 SNPs remained for filtering on MAF (≥0.05) and HWE (P>0.001) and they had an overall MAF mean of 0.285. The number of SNPs on the different lines is summarised in Table1. It ranged from 32,706 on line 4 to 34,937 on line 6. There were small differences in the number of SNPs after filtering and average MAF for each line in every chromosome (see Data Supplements).

Table 1: Number of animals, the final number of SNPs used, average MAF and average distance between SNPs for each line

Line	Number of animals	Final number of SNPs	Average MAF	Average distance between SNPs
1	1,008	34138	0.279	70.481
2	316	33081	0.286	72.733
3	169	34438	0.289	69.283
4	208	32706	0.278	73.567
5	241	34828	0.291	69.085
6	108	34937	0.285	68.869

Linkage Disequilibrium

In theory, the linkage disequilibrium is higher in short distances and it decreases when the distance between markers increases. Nevertheless, a different behaviour was observed in chromosome 1 for all lines. Figure 1 shows high LD between distant SNP pairs in similar regions for all studied lines. Chromosomes 4, 5, 7, 9, 11, 12, 13, 14, 15 and 16 performed similarly, at a lesser intensity (Data Supplements). Figure 2 shows the LD behaviour in chromosome 2. There were differences in the LD decrease across the lines, the r^2 (LD measure) was particularly higher between distant SNPs in lines 1 and 6. Chromosome 3 (figure 3) has a linkage disequilibrium decrease comparable to the theory, the same was observed in chromosomes 6, 8 and 17 (Data Supplements).

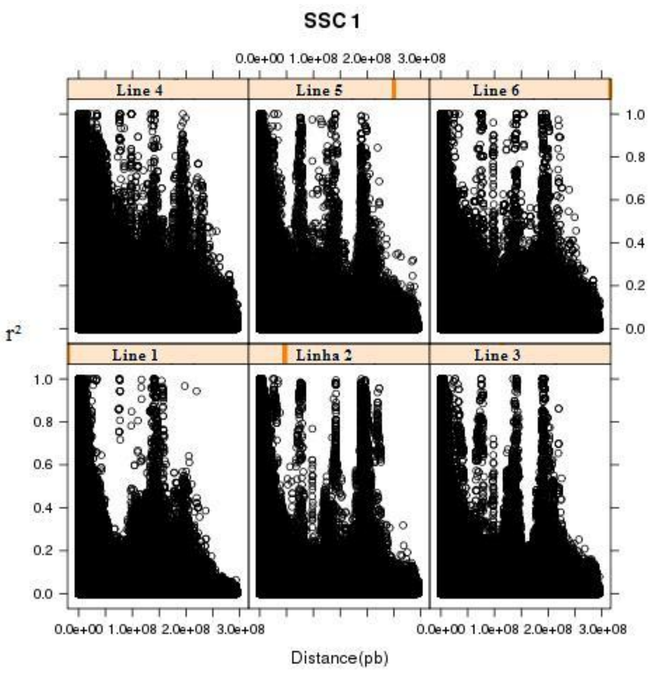


Figure 1
Linkage Disequilibrium between SNP pairs in relation to physical distance between SNPs in pig chromosome 1 for six commercial lines.

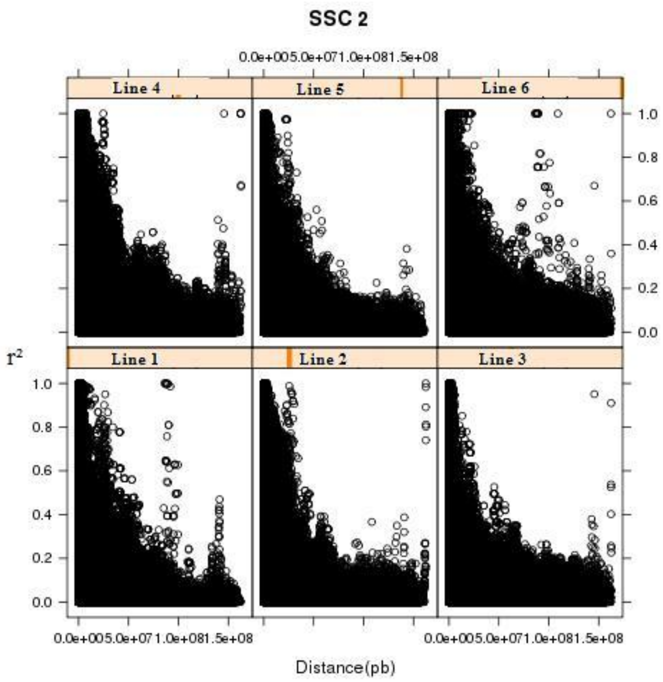


Figure 2
Linkage Disequilibrium (r^2) between SNP pairs in relation to physical distance between SNPs in pig chromosome 2 for six commercial lines.

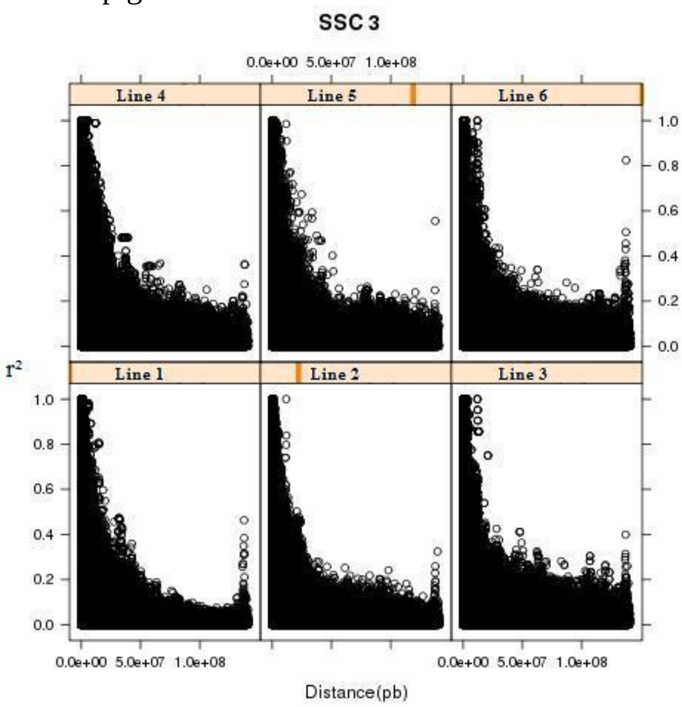


Figure 3
Linkage Disequilibrium (r^2) between SNP pairs in relation to physical distance between SNPs in pig chromosome 3 for six commercial lines.

Figure 4 shows the average correlation between gene frequencies (r^2) in different marker distances for all lines. As expected, LD as a function of distance declined rapidly. It can be observed that all lines presented similar average r^2 in the different distances.

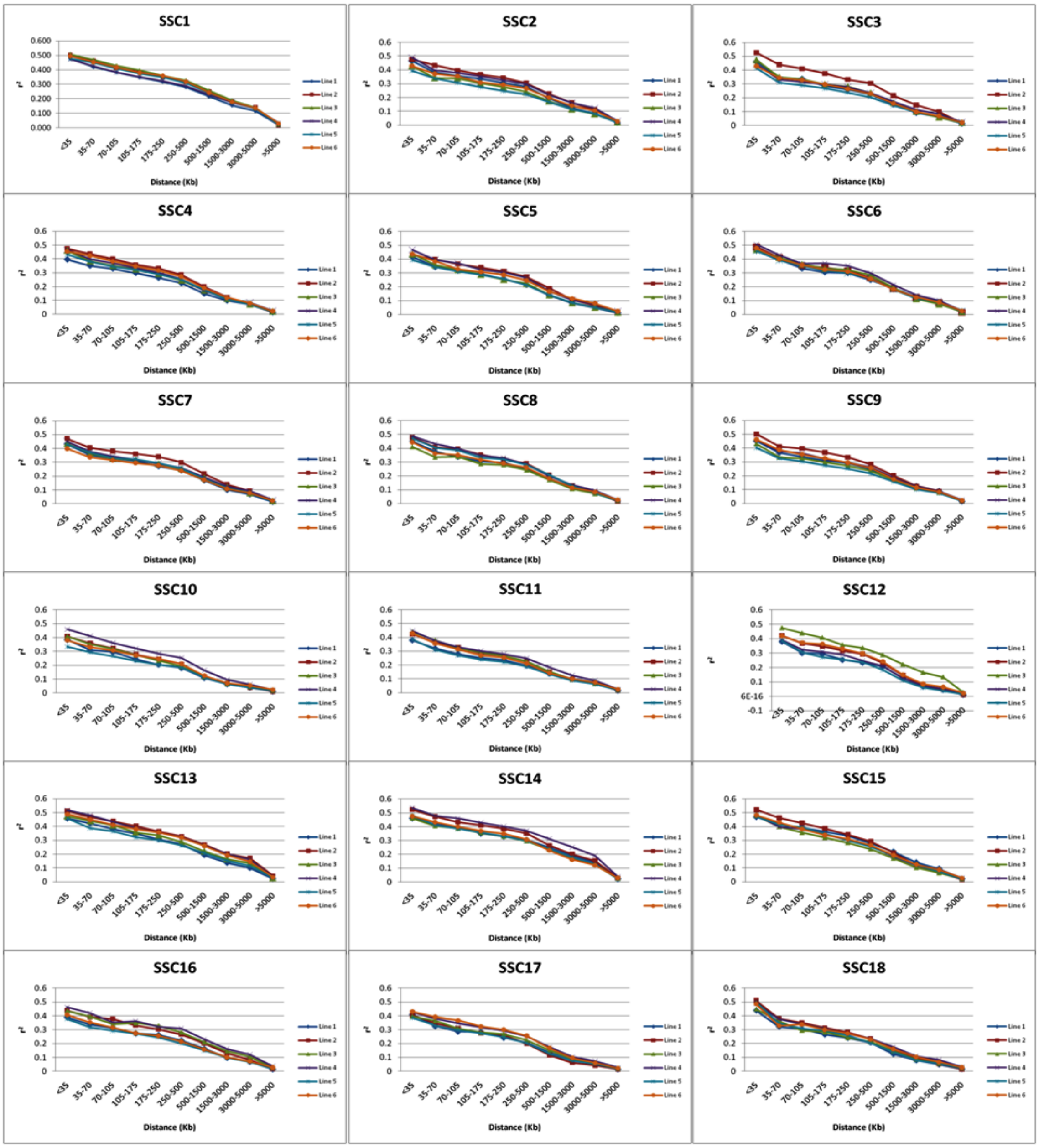


Figure 4
Average r^2 across lines at different marker distance for all chromosomes

Haplotype block structure

Information about haplotype blocks is critical for association studies. The number of haplotype blocks in all autosomes, the number of SNPs captured by the blocks and the proportion of captured SNPs for each line are shown in Table 2. The number of haplotype blocks ranged from 3,917 on line 1 to 3,343 on line 6 and the proportion of the genome captured by haplotype blocks ranged from 46.98 % on line 4 to 36.76 % on line 5. Line 1 had the highest number of SNPs captured by blocks (21,298), but line 4 had the highest proportion (63.87%) of captured SNPs in relation to the SNPs used. Line 5 had the lowest number (19,156) and proportion (55.00%) of captured SNPs. This descriptive analysis by each autossome was done and is exhibited in Data Supplements.

In general, the number of blocks differed between lines and chromosome, only the SSC9 the lines 3 and 5 had the same number of blocks (265) but they differed in the number of SNPs in the blocks and average block size. The same occurred with lines 2 and 4 and 5 and 6 on autossome 10 and on autossome 16 with lines 3 and 4. Smaller or higher block size did not predominate in a specific line, the average block size depended on the line and chromosome. Generally, all lines and chromosomes had a higher standard deviation regarding block size (Data Supplements).

Figure 5 illustrates the block size frequency considering all autosomes. The six lines show a higher frequency of blocks with less than 50 Kb and blocks with more than 800 Kb occur at low frequency in all lines.

Table 2: Total number of blocks, genome proportion captured by haplotype blocks, total number of SNPs in the haplotype blocks, proportion of the used SNPs captured by haplotype blocks, average number of SNPs per block and average block size.

Line	Total Number of blocks	Genome proportion captured by haploblocks (%)	Total number of SNPs in the haploblocks	Proportion of the used SNPs captured by haploblocks (%)	Average number of SNP per block	Average block Size (Kb)
1	3,917	43.94	21,298	62.39	5.44	269.91
2	3,515	43.25	20,420	61.73	5.81	296.04
3	3,582	41.77	20,196	58.15	5.64	280.61
4	3,370	46.98	20,890	63.87	6.20	335.43
5	3,726	36.76	19,156	55.00	5.14	237.43
6	3,343	42.71	20,364	58.29	6.09	307.42

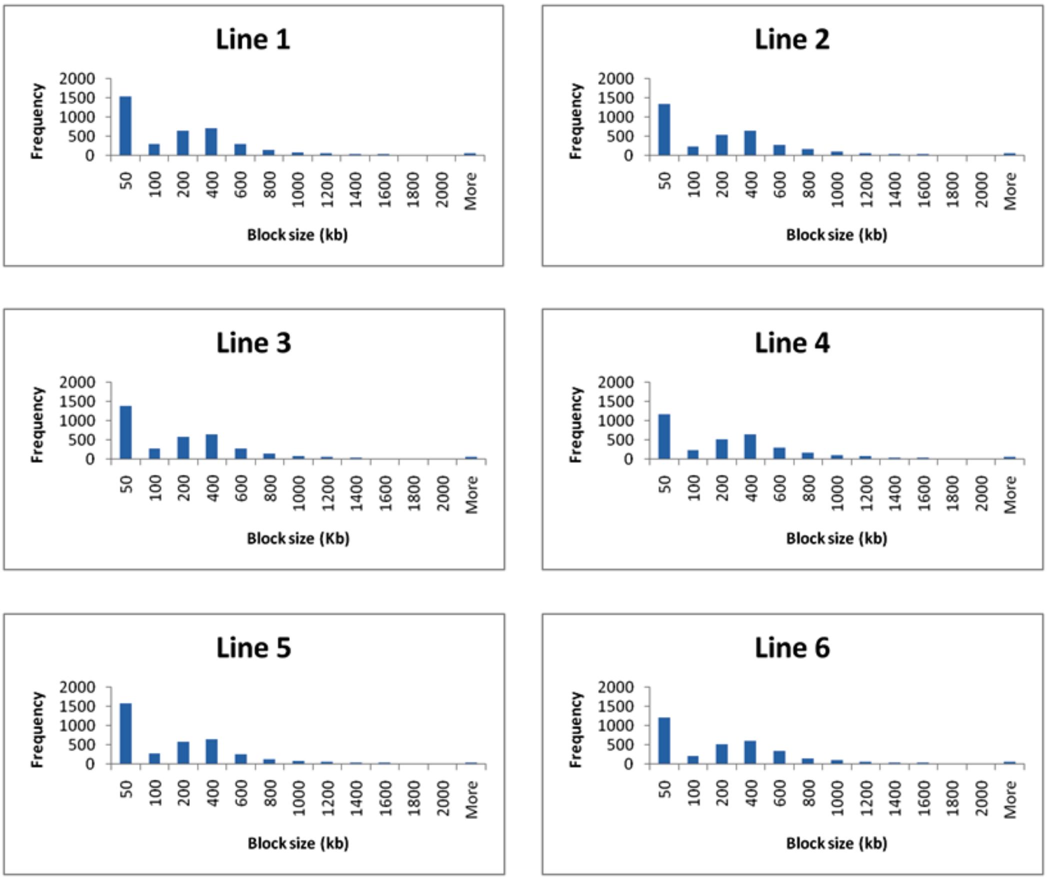
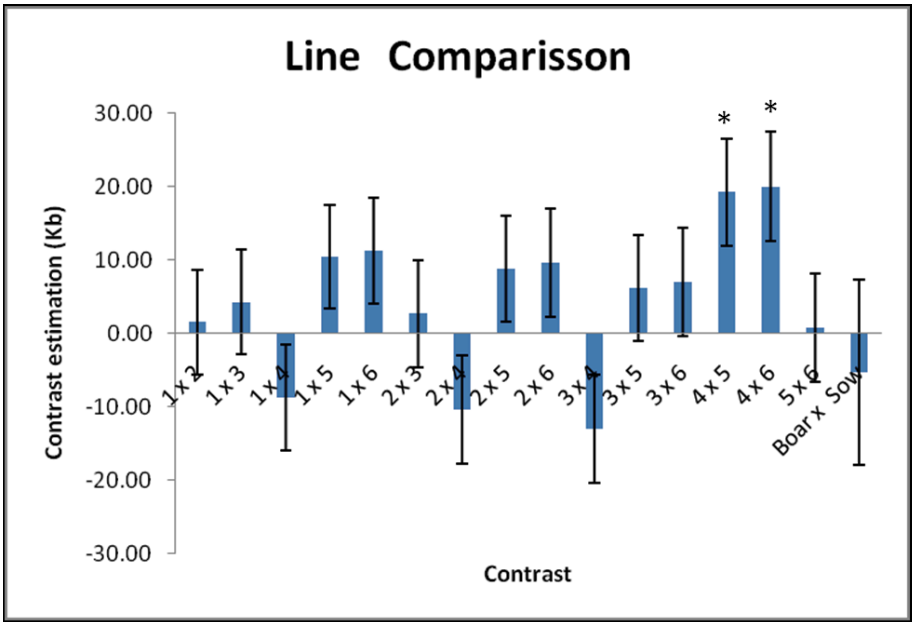


Figure 5
Block Size frequency in six pig lines considering all autossomes.

Table 1 shows that there were small dissimilarities in SNP density between lines; therefore to eliminate these differences the lines were compared using the number of SNP per block as covariate. The average block size of all lines was compared using the PROC MIXED procedure of SAS v.9.1. Figure 6 shows the comparison results considering all autossomes. Only the contrasts between lines 4 and 5 and 4 and 6 were significant ($P<0.01$).



*Significant comparison (p-value<0.05)
Figure 6
Contrasts between pig lines considering all autossomes evaluated using the t-test.

There was no common behaviour regarding average block size in all autossomes (Data Supplements), so it was important to make a line comparison by chromosome. The significant line comparisons by chromosome are presented in Table 3. The average block size adjusted for number of SNPs in the blocks for each line by autossome and all comparisons between lines are shown in the Data Supplements.

Table 3: Contrast estimate, standard error and P-value of the significant line comparisons by autossome.

Autossome	Contrast	Contrast Estimate	Standard Error	P-value
1	3 vs 5	45.731	25.028	0.068
1	3 vs 6	41.908	25.077	0.095
2	4 x 6	61.174	31.539	0.053
3	1 vs 5	33.650	20.178	0.096
3	3 vs 5	36.148	20.413	0.077
5	1 vs 4	-49.159	25.067	0.050
5	2 vs 4	-46.215	24.876	0.063
5	4 vs 6	47.498	25.617	0.064
7	3 vs 4	-45.122	22.748	0.048
7	4 vs 6	37.591	22.666	0.097
9	1 vs 3	37.622	18.857	0.046
9	1 vs 5	39.640	18.861	0.036
9	3 vs 6	-35.140	19.931	0.078
9	5 vs 6	-37.158	19.966	0.063
10	4 vs 5	45.977	23.889	0.055
15	1 vs4	-79.789	41.770	0.056
18	2 vs 3	44.580	19.738	0.024
18	3 vs 5	-49.339	19.895	0.013
18	3 vs 6	-33.225	19.477	0.089
18	Boar vs Sow	70.509	33.887	0.038

There were significant block size differences in autossomes 1, 2, 3, 5, 7, 9, 10, 15 and 18 (Table 3). Autossomes 9 and 18 had the largest number of significant comparisons, and in chromosome 18 the lines 2, 5 and 6 had greater block size than line 3, in addition the contrast in this chromosome between boar lines (1, 2 and 5) and sow lines (3, 4 and 6) was significant. A similar situation was observed in chromosome 5 where lines 1, 2 and 6 had smaller block sizes than line 4.

DISCUSSION

The LD extent within a population determines the number of markers that will be required for successful association mapping and genomic selection. The major attraction of haplotype block estimation is the idea that most of the genetic variation is captured by common haplotypes and a small number of SNPs (tag SNPs) can be used to characterize the block. This report presents an LD analysis of six pig commercial lines covering all autossomes.

The number of genotyped animals diverges considerable among the lines, and line 1 had practically half of the genotyped animals (1008). It is well known that D' is inflated with small sample sizes as demonstrated by Bohmanova et al. (2010), but the influence of this factor on the haplotype block estimation is reduced, since in the Gabriel et al. (2002) approach a narrow D' confidence bound is used. In addition, the correlation of gene frequencies (r^2) was used as linkage disequilibrium measurement to avoid the influence of small sample size and lower allele frequency, since it is considered a more robust linkage disequilibrium appraisal than D' (Du, et al., 2007; Johnson, et al., 2001; Amaral, et al., 2008; Bohmanova, et al., 2010).

In theory, the concept of linkage disequilibrium is quite simple; it refers to the nonrandom segregation of markers that are closely linked. The expected behaviour is to observe a decrease in the LD with increase in distance, consequently high levels of linkage disequilibrium occur between SNPs in close proximity and a lower LD is expected for distant SNP pairs. However, a range of factors affect the recombination measurement such as genetic drift, demographic population history, selection and other factors which make the linkage disequilibrium highly variable even between closely linked markers (Ardlie, et al., 2002; Kruglyak, 1999; Pritchard and Przeworski, 2001).

Although a decrease in the LD with increase in distance was expected and observed in some chromosomes (3, 6, 8 and 17), high linkage disequilibrium was observed between SNPs at large distances for all lines in chromosomes 1, 4, 5, 7, 9, 10, 12, 13, 14, 15 and 16. It could be caused by the many factors that affect the LD as cited above. Nevertheless, the fact that high LD was observed in all the different lines studied leads us to suppose that it was caused by the accuracy of the genome assembly (Sscrofa10). Thus, the LD peaks observed in some chromosomes could be caused by mistakes in the order and distance between markers. The same problem was cited by Uimari and Tapio (2011), in a LD study using Sscrofa 9.

It is known that these lines have been submitted to diverse selection objectives mainly sire (1, 2 and 5) and sow lines (3, 4 and 6) and they had differences regarding effective population size factors, inbreeding ratio, crossing and others that can affect the LD. In chromosomes 2 and 18 high LD was observed between distant SNPs for some lines, that could be explained by any factor cited above. Nevertheless, maybe factors such as genetic drift and population demography could be discarded, because they are characteristic of each population, and in this case, the SSC 18 and SSC 2 showed a similar pattern for more than one line.

There are some important traits for the pig chain, that could be a selection objective for any line, that can make different pig lines present a similar LD behavior. In this way, the high linkage disequilibrium over markers at large distances could be explained by a selection effect. However, to confirm this hypothesis it would be necessary to identify which are the distant SNPs that are in linkage disequilibrium and to investigate the QTLs present at these regions.

In the current study marker pairs separated by 1500 – 3000 Kb had an average r^2 of 0.12, which was similar to that reported by Du et al. (2007) for pigs that estimated an average r^2 of 0.1 in a distance of 3 cM. In cattle, Qanbari et al. (2010) reported an average r^2 of 0.3 between markers distant 25 kb and Bohmanova et al. (2010) found an average r^2 of 0.2 between markers 40-60 Kb apart for North American Holstein cattle, both studies found lower r^2 than that reported in the present study. Uimari and Tapio (2011) reported an average r^2 of 0.47 and 0.49 for Finnish Landrace and Finnish Yorkshire, respectively, for SNPs 30 Kb apart. In the present study, an average r^2 of 0.43, 0.47, 0.45, 0.47, 0.42 and 0.45 was observed for the lines 1, 2, 3, 4, 5 and 6, respectively for SNPs with less than 35 Kb apart.

An average r^2 above 0.3 was found for all lines in markers between 105-175 Kb distance. This level of LD is suitable for association studies and genomic selection and considering that the pig genome size is 2.41 Gb (www.ensembl.org/sus_scrofa), it implies the use of 22,915 informative SNPs (MAF > 0.05) for whole genome studies.

The recommendation above is supported by Meuwissen et al. (2001) who reported in a simulation study that the required LD level for genomic selection was 0.2; Qanbari et al. (2010) considered that a threshold of 0.25 was a useful LD for association studies and Ardlie et al. (2002) defined an $r^2 > 1/3$ as high values of LD. In pigs, Du et al. (2007) recommended marker spacing between 0.1 and 1 cM for whole association studies, in addition the authors considered an r^2 of 0.3 as a threshold of “usable” LD for association studies.

In the current study, all the pig autossomes were included in the investigation with an average marker density of one SNP every 70.67 Kb. The blocks covered on average 42.57 % of the pig genome and included 59.91 % of the used SNPs. These values were much higher than the coverage described by Qanbari et al. (2010) which found that the blocks covered 4.7% of the bovine genome and included only 8% of all SNPs.

Although the average block size was 287.81 Kb, small blocks with less than 50 Kb predominated in the six evaluated pig lines. Amaral et al. (2008) analyzed three regions of the chromosomes 18 and 3 and observed that in Chinese pig breeds LD is mostly organized in blocks of up to 10 Kb and in European breeds the LD extents over haplotype blocks up to 400 kb. Although these results diverged from the current study, it is complex to compare the outcome from these studies, since in Amaral et al. (2008) the investigation was limited to three high density marked regions.

LD studies from humans and cattle can be used to make inferences about pigs, since it was reported that haplotype block structure is conserved across mammals (Guryev, et al., 2006). Qanbari et al. (2010) used 40,854 SNPs covering the whole bovine genome and observed 712 haplotype blocks with an average size of 164 Kb. Villa-Angulo et al. (2009) evaluated high density marker regions (on average one SNP per 4 Kb) of the bovine genome and reported haplotype blocks with an overall mean size of 10.3 Kb across 19 breeds, which according to the authors was similar to the block size observed in humans. An average block size of 7.3, 13.2, and 16.3 kb were observed in three human populations when ten 500 Kb regions with a density of approximately one SNP every 5 kb were analyzed (International HapMap Consortium, 2005).

It was expected that the average block size in pigs would be higher than in humans because of the natural aspects of livestock, such as small effective number, selection, crossing and genetic drift which contribute to increase the block size. The comparison with cattle studies is complicated because they have diverse outcomes, as showed above.

Some differences in SNP density between the lines were observed in this study, which can influence their haplotype block pattern. As a result, the block size was compared using the number of SNPs per block as covariate, in order to eliminate the influence of the marker density on the block size.

In chromosome 18 line 3 had smaller block size than most of the analyzed lines (2, 5 and 6). It could not be caused by SNP density, MAF or numbers of genotyped animals because these measurements were similar to the other lines and no differences were observed for them. This difference is difficult to understand, it could be caused by a range of factors such as selection, genetic drift, inbreeding and population history and only an in-depth study of these haplotype blocks could give a better understanding of this divergence.

The significant differences between lines regarding block size are difficult to explain, because they could be caused by many factors. An investigation of the regions where the lines disagree regarding the haplotype blocks and their selection history might provide greater understanding of the significant differences and it would permit a solid explanation of this divergence.

CONCLUSIONS

According to the LD extent observed at this study, 22,915 informative SNPs (MAF > 0.05) would be necessary for whole genome association studies in the present lines. The high linkage disequilibrium observed in some chromosomes between distant SNPs may be caused by mistakes in the position and distance of the SNP marker. In addition, for some chromosomes (SSC2 and SSC18), the high LD may be caused by selection; but a in-depth study on the regions where these SNPs are found would be necessary to confirm this hypothesis. A concrete explanation for the divergences in haplotype block size can be made only with a more detailed study of the blocks.

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DATA SUPPLEMENTS

Table 1. Number of SNPs in the beginning of analysis, the final number of SNPs used, average MAF and average distance between SNPs by chromosome

All Chromossomes				
Line	Initial number of SNPs	Final number of SNPs	Average MAF	Average distance between SNPs
1	41,785	34,138	0.279	70.481
2	41,785	33,081	0.286	72.733
3	41,785	34,438	0.289	69.283
4	41,785	32,706	0.278	73.567
5	41,785	34,828	0.291	69.085
6	41,785	34,937	0.285	68.869
SSC1				
Line	Initial number of SNPs	Final number of SNPs	Average MAF	Average distance between SNPs
1	5,386	4,183	0.269	70.812
2	5,386	4,326	0.281	68.472
3	5,386	4,054	0.285	73.066
4	5,386	4,156	0.276	71.272
5	5,386	4,404	0.303	67.259
6	5,386	4,515	0.290	65.605
SSC2				
Line	Initial number of SNPs	Final number of SNPs	Average MAF	Average distance between SNPs
1	2,656	2,217	0.285	73.556
2	2,656	2,168	0.291	75.219
3	2,656	2,273	0.294	71.744
4	2,656	2,078	0.278	78.477
5	2,656	2,332	0.292	69.929
6	2,656	2,362	0.285	69.041
SSC3				
Line	Initial number of SNPs	Final number of SNPs	Average MAF	Average distance between SNPs
1	2,238	1,750	0.260	81.483
2	2,238	1,759	0.289	81.066
3	2,238	1,898	0.279	75.129
4	2,238	1,908	0.282	74.735
5	2,238	1,977	0.289	72.127
6	2,238	1,914	0.288	74.501

Cont. Table 1. Number of SNPs in the beginning of analysis, the final number of SNPs used, average MAF and average distance between SNPs by chromosome

SSC4				
Line	Initial number of SNPs	Final number of SNPs	Average MAF	Average distance between SNPs
1	2,964	2,552	0.279	54.274
2	2,964	2,211	0.285	62.644
3	2,964	2,435	0.290	56.881
4	2,964	2,292	0.277	60.430
5	2,964	2,456	0.305	56.395
6	2,964	2,300	0.283	60.220
SSC5				
Line	Initial number of SNPs	Final number of SNPs	Average MAF	Average distance between SNPs
1	1,915	1,546	0.270	71.502
2	1,915	1,590	0.291	69.524
3	1,915	1,463	0.286	75.559
4	1,915	1,453	0.261	76.079
5	1,915	1,623	0.293	68.110
6	1,915	1,565	0.278	70.634
SSC6				
Line	Initial number of SNPs	Final number of SNPs	Average MAF	Average distance between SNPs
1	2,411	2,050	0.294	76.834
2	2,411	1,953	0.293	80.650
3	2,411	2,070	0.293	76.092
4	2,411	1,913	0.257	82.337
5	2,411	1,989	0.285	79.191
6	2,411	2,038	0.295	77.287
SSC7				
Line	Initial number of SNPs	Final number of SNPs	Average MAF	Average distance between SNPs
1	2,780	2,125	0.271	63.097
2	2,780	2,203	0.287	60.863
3	2,780	2,152	0.296	62.306
4	2,780	2,070	0.271	64.774
5	2,780	2,288	0.281	58.602
6	2,780	2,419	0.280	55.429

Cont. Table 1. Number of SNPs in the beginning of analysis, the final number of SNPs used, average MAF and average distance between SNPs by chromosome

SSC8				
Line	Initial number of SNPs	Final number of SNPs	Average MAF	Average distance between SNPs
1	2,177	1,825	0.284	80.919
2	2,177	1,652	0.288	89.393
3	2,177	1,887	0.294	78.260
4	2,177	1,634	0.272	90.377
5	2,177	1,439	0.272	102.624
6	2,177	1,834	0.288	80.522
SSC9				
Line	Initial number of SNPs	Final number of SNPs	Average MAF	Average distance between SNPs
1	2,578	2,074	0.284	73.322
2	2,578	2,120	0.278	71.731
3	2,578	2,264	0.284	67.169
4	2,578	2,128	0.276	71.461
5	2,578	2,279	0.302	66.727
6	2,578	2,153	0.263	70.632
SSC10				
Line	Initial number of SNPs	Final number of SNPs	Average MAF	Average distance between SNPs
1	1,299	1,100	0.278	73.278
2	1,299	1,054	0.284	76.476
3	1,299	1,084	0.287	74.360
4	1,299	1,065	0.278	75.687
5	1,299	1,137	0.291	70.894
6	1,299	1,151	0.284	70.031
SSC11				
Line	Initial number of SNPs	Final number of SNPs	Average MAF	Average distance between SNPs
1	1,561	1,328	0.293	63.386
2	1,561	1,226	0.286	68.660
3	1,561	1,265	0.262	66.543
4	1,561	1,163	0.283	72.379
5	1,561	1,328	0.287	63.386
6	1,561	1,278	0.268	65.866

Cont. Table 1. Number of SNPs in the beginning of analysis, the final number of SNPs used, average MAF and average distance between SNPs by chromosome

SSC12				
Line	Initial number of SNPs	Final number of SNPs	Average MAF	Average distance between SNPs
1	1,247	1,009	0.284	63.707
2	1,247	1,024	0.294	62.773
3	1,247	1,089	0.292	59.027
4	1,247	1,071	0.277	60.019
5	1,247	1,138	0.301	56.485
6	1,247	1,074	0.307	59.851
SSC13				
Line	Initial number of SNPs	Final number of SNPs	Average MAF	Average distance between SNPs
1	2,966	2,315	0.279	91.962
2	2,966	2,355	0.285	90.400
3	2,966	2,416	0.285	88.118
4	2,966	2,258	0.298	94.284
5	2,966	2,526	0.298	84.280
6	2,966	2,470	0.284	86.191
SSC14				
Line	Initial number of SNPs	Final number of SNPs	Average MAF	Average distance between SNPs
1	3,292	2,785	0.279	55.180
2	3,292	2,661	0.290	57.752
3	3,292	2,896	0.315	53.065
4	3,292	2,653	0.300	57.926
5	3,292	2,804	0.284	54.806
6	3,292	2,685	0.291	57.235
SSC15				
Line	Initial number of SNPs	Final number of SNPs	Average MAF	Average distance between SNPs
1	2,270	1,945	0.286	78.535
2	2,270	1,726	0.282	88.499
3	2,270	1,810	0.271	84.392
4	2,270	1,689	0.273	90.438
5	2,270	1,805	0.266	84.626
6	2,270	1,887	0.281	80.949

Cont. Table 1. Number of SNPs in the beginning of analysis, the final number of SNPs used, average MAF and average distance between SNPs by chromosome

Line	Initial number of SNPs	Final number of SNPs	Average MAF	Average distance between SNPs
SSC16				
1	1,554	1,320	0.285	65.149
2	1,554	1,198	0.298	71.783
3	1,554	1,263	0.293	55.374
4	1,554	1,227	0.281	70.087
5	1,554	1,332	0.296	64.562
6	1,554	1,249	0.294	68.852
SSC17				
Line	Initial number of SNPs	Final number of SNPs	Average MAF	Average distance between SNPs
1	1,399	1,108	0.271	62.646
2	1,399	1,083	0.274	64.092
3	1,399	1,183	0.277	58.675
4	1,399	1,089	0.278	63.739
5	1,399	1,190	0.291	58.329
6	1,399	1,165	0.297	59.581
SSC18				
Line	Initial number of SNPs	Final number of SNPs	Average MAF	Average distance between SNPs
1	1,092	906	0.294	66.248
2	1,092	772	0.260	77.747
3	1,092	936	0.299	64.125
4	1,092	859	0.269	69.873
5	1,092	781	0.259	76.851
6	1,092	878	0.268	68.361

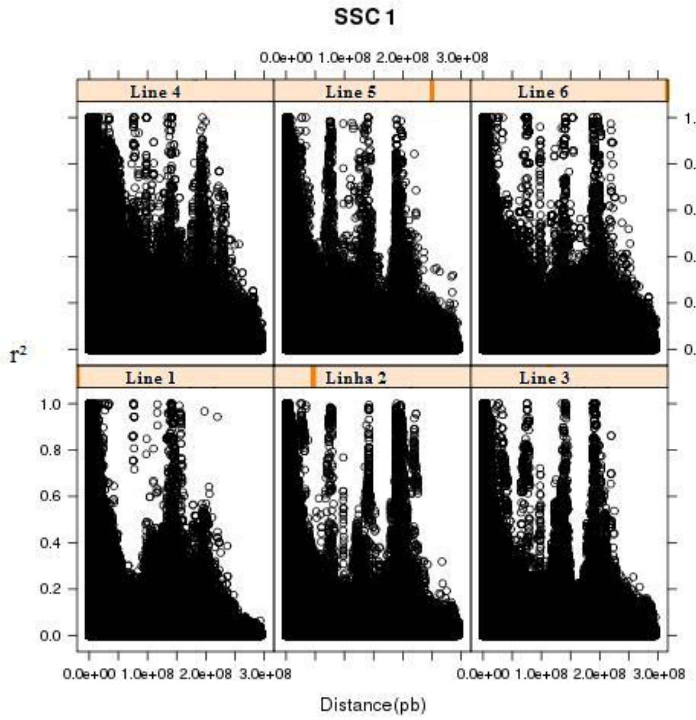

Figure 1
Linkage Disequilibrium between SNP pairs in relation to physical distance between loci in pig chromosome 1 for six commercial lines.

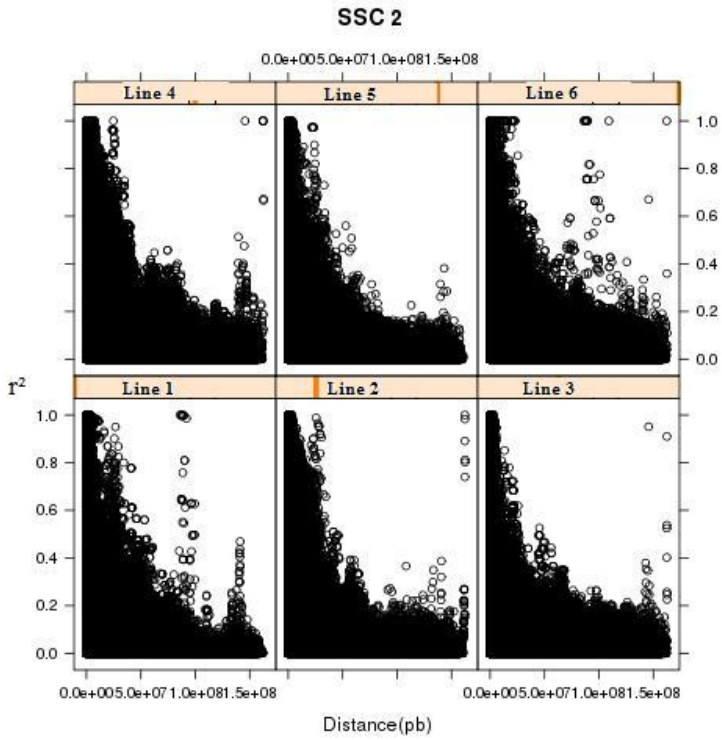

Figure 2
Linkage Disequilibrium between SNP pairs in relation to physical distance between loci in pig chromosome 2 for six commercial lines.

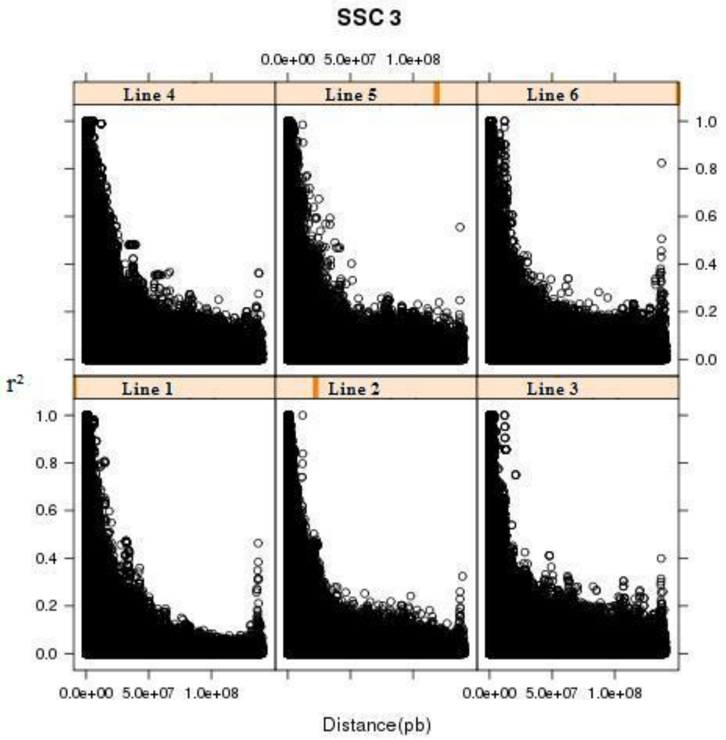

Figure 3
Linkage Disequilibrium between SNP pairs in relation to physical distance between loci in pig chromosome 3 for six commercial lines.

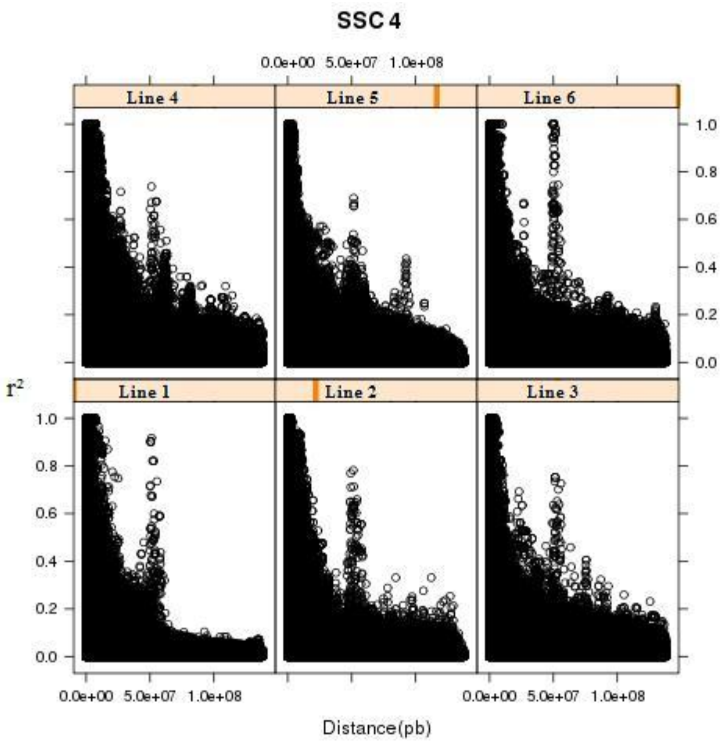

Figure 4
Linkage Disequilibrium between SNP pairs in relation to physical distance between loci in pig chromosome 4 for six commercial lines.

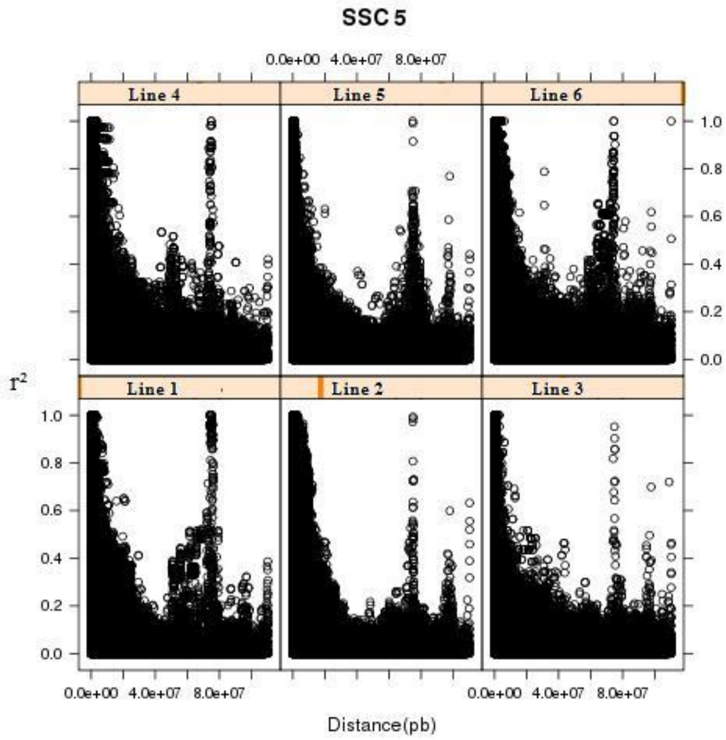

Figure 5
Linkage Disequilibrium between SNP pairs in relation to physical distance between loci in pig chromosome 5 for six commercial lines.

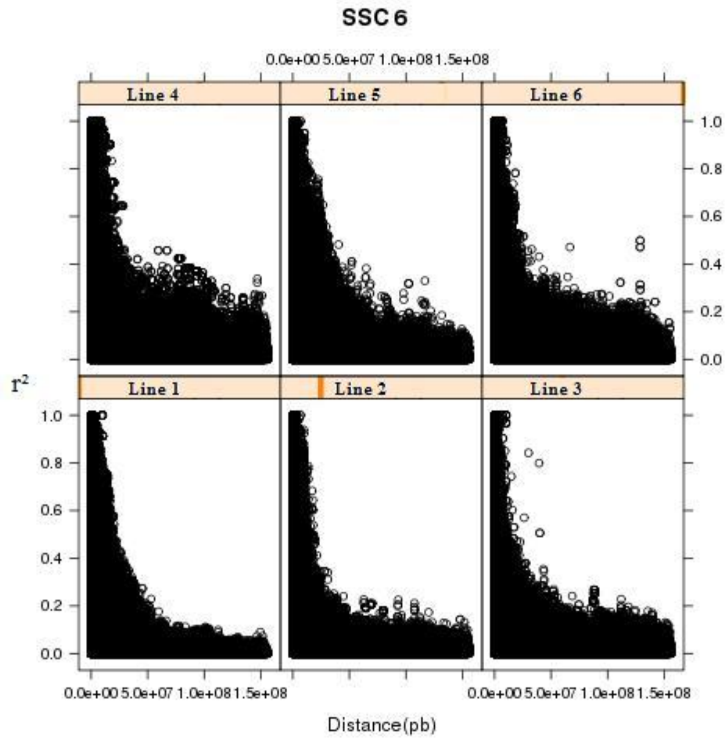

Figure 6
Linkage Disequilibrium between SNP pairs in relation to physical distance between loci in pig chromosome 6 for six commercial lines.

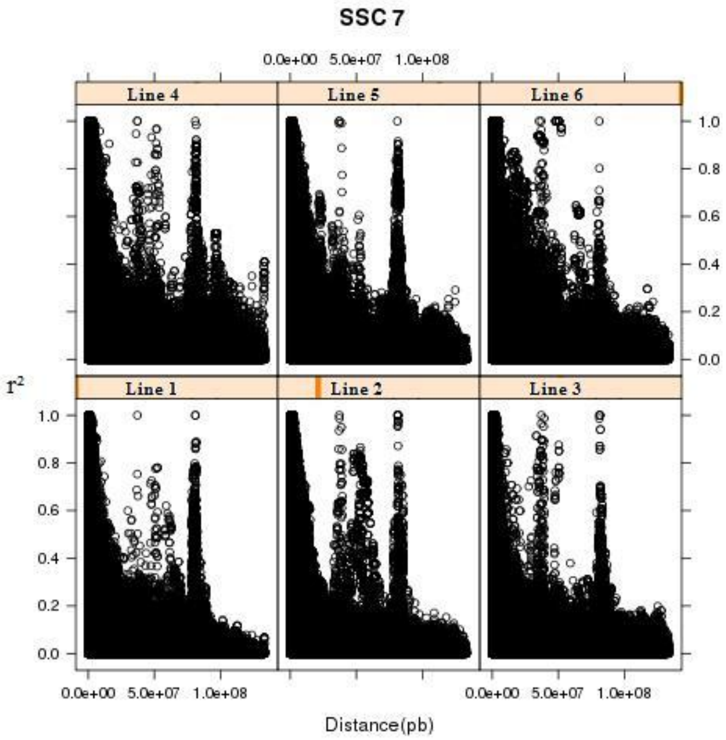

Figure 7
Linkage Disequilibrium between SNP pairs in relation to physical distance between loci in pig chromosome 7 for six commercial lines.

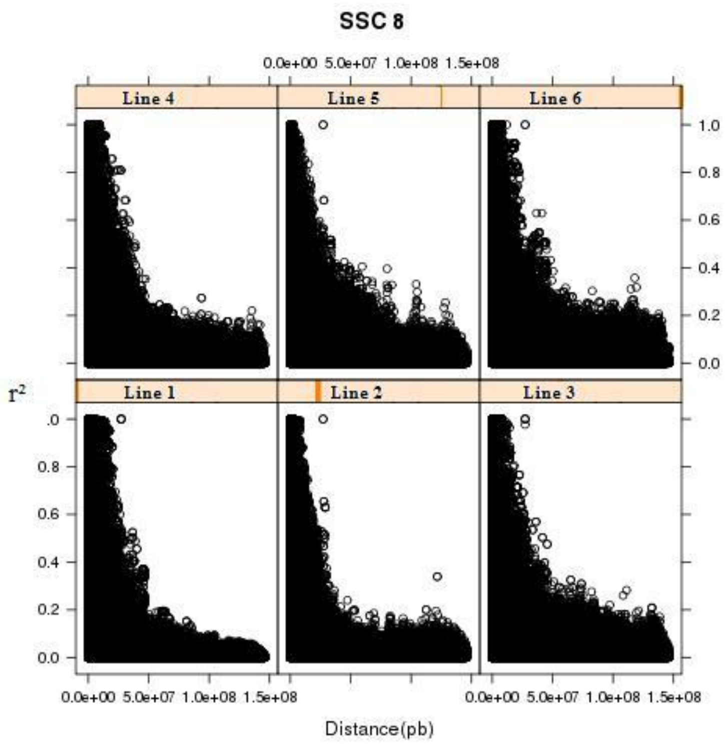

Figure 8
Linkage Disequilibrium between SNP pairs in relation to physical distance between loci in pig chromosome 8 for six commercial lines.

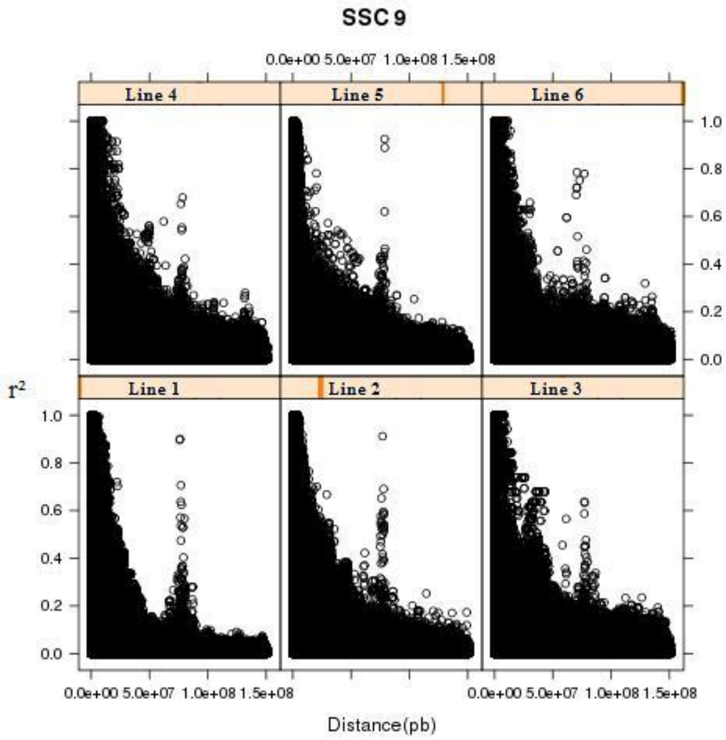

Figure 9
Linkage Disequilibrium between SNP pairs in relation to physical distance between loci in pig chromosome 9 for six commercial lines.

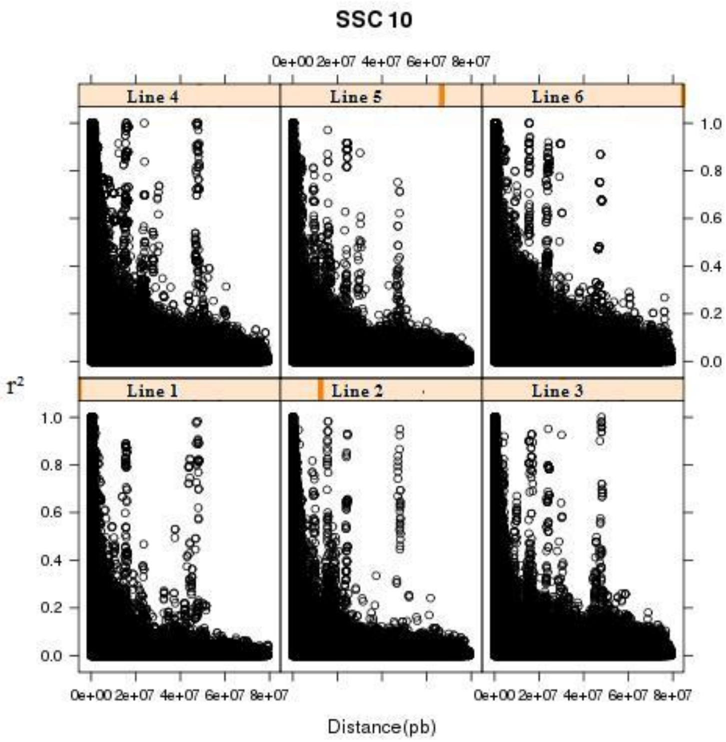

Figure 10
Linkage Disequilibrium between SNP pairs in relation to physical distance between loci in pig chromosome 10 for six commercial lines.

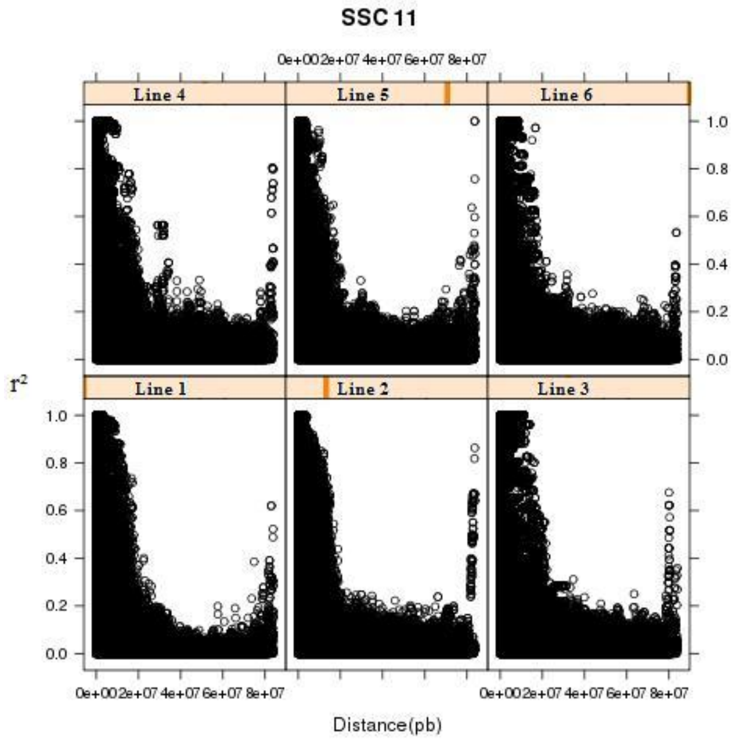

Figure 11
Linkage Disequilibrium between SNP pairs in relation to physical distance between loci in pig chromosome 11 for six commercial lines.

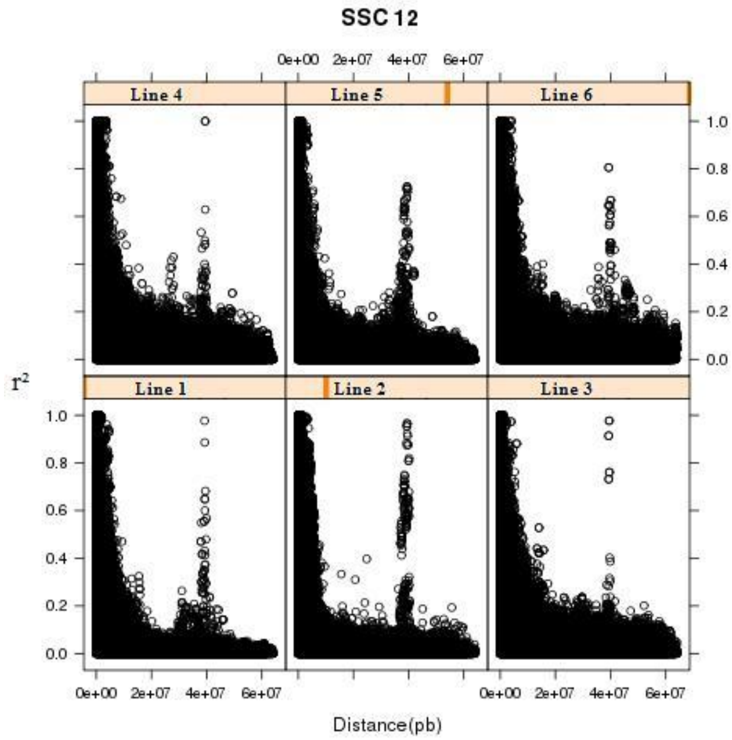

Figure 12
Linkage Disequilibrium between SNP pairs in relation to physical distance between loci in pig chromosome 12 for six commercial lines.

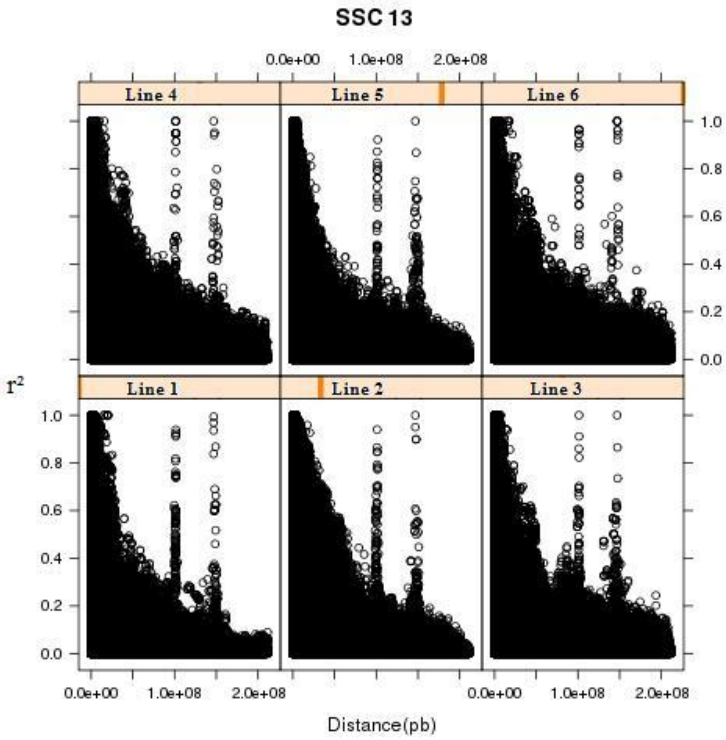

Figure 13
Linkage Disequilibrium between SNP pairs in relation to physical distance between loci in pig chromosome 13 for six commercial lines.

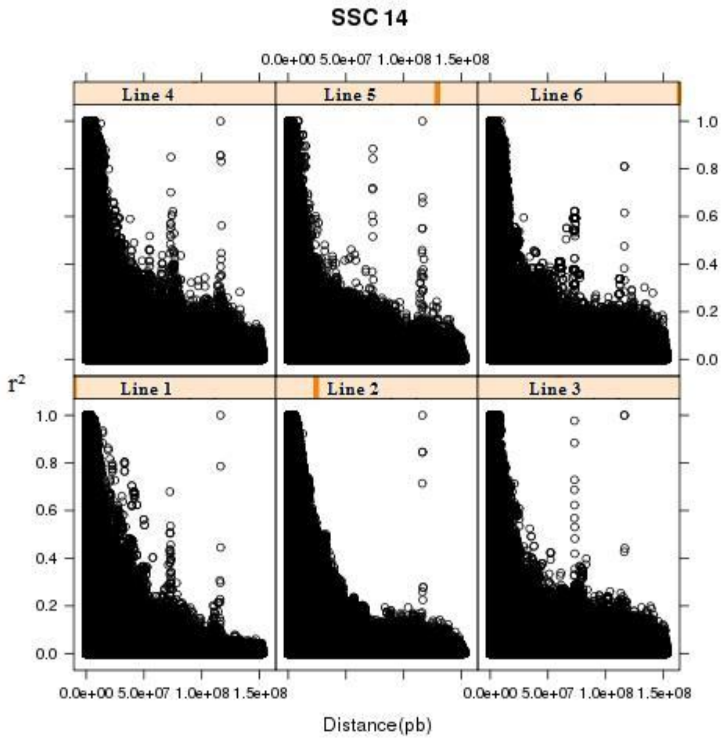

Figure 14
Linkage Disequilibrium between SNP pairs in relation to physical distance between loci in pig chromosome 14 for six commercial lines.

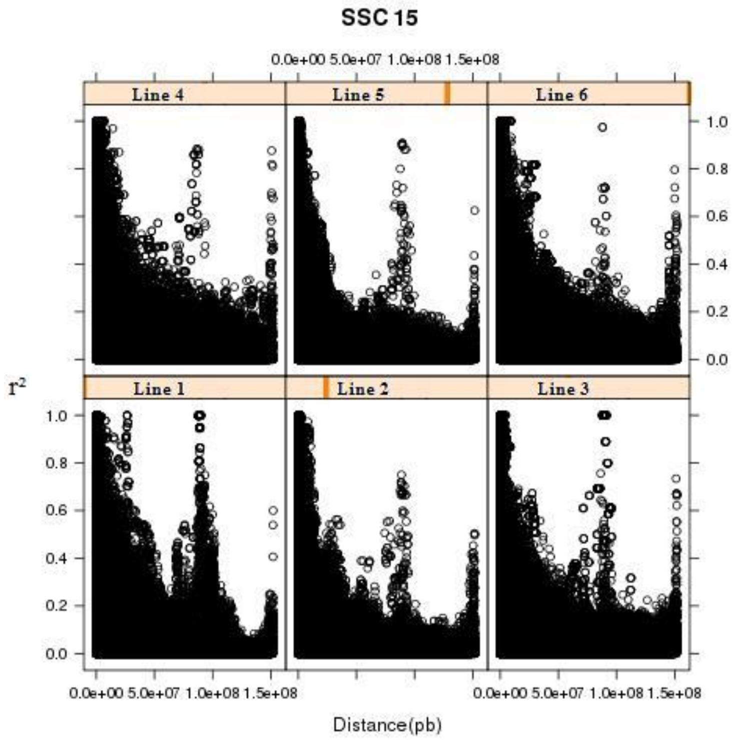

Figure 15
Linkage Disequilibrium between SNP pairs in relation to physical distance between loci in pig chromosome 15 for six commercial lines.

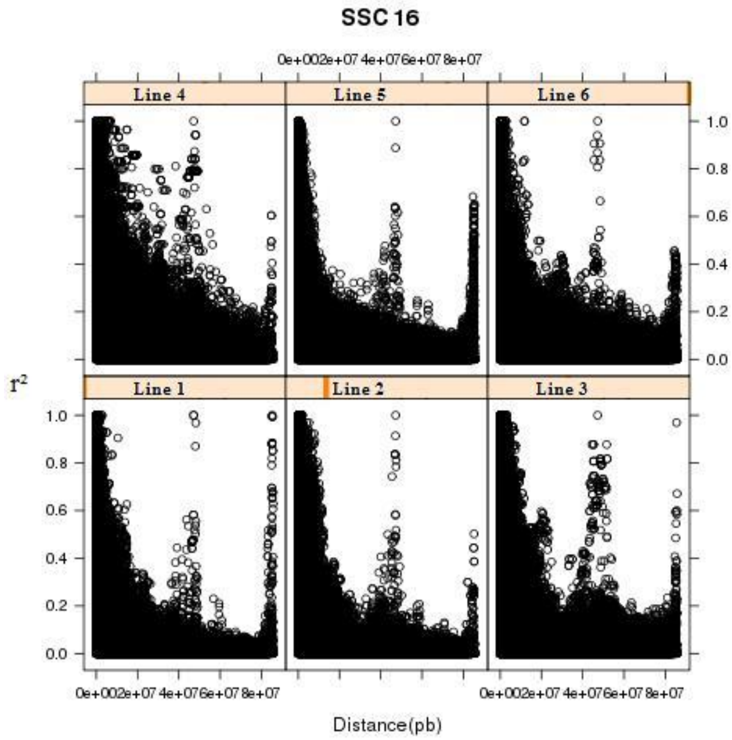

Figure 16
Linkage Disequilibrium between SNP pairs in relation to physical distance between loci in pig chromosome 16 for six commercial lines.

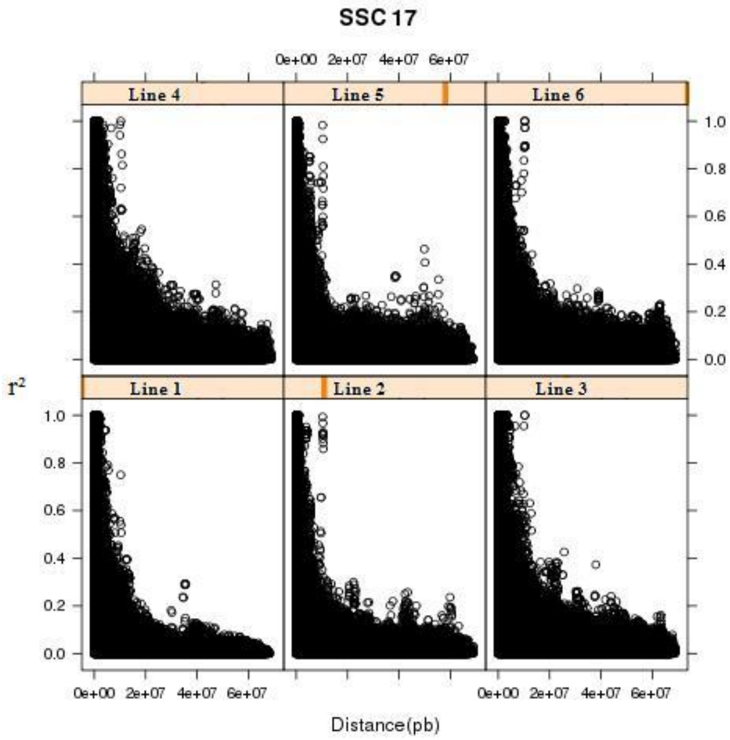

Figure 17
Linkage Disequilibrium between SNP pairs in relation to physical distance between loci in pig chromosome 17 for six commercial lines.

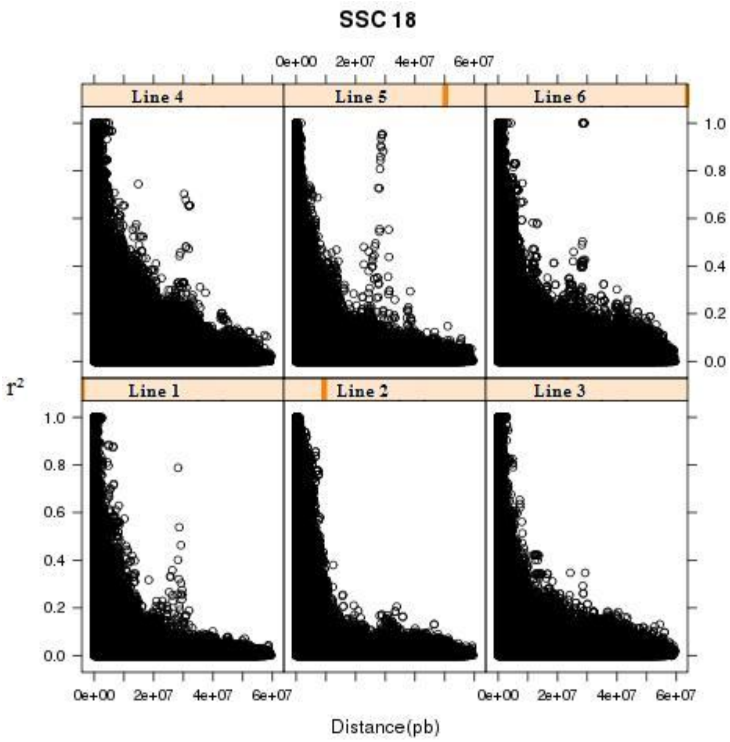

Figure 18
Linkage Disequilibrium between SNP pairs in relation to physical distance between loci in pig chromosome 18 for six commercial lines.

Table 2. Number of blocks, total number of SNPs in the blocks, average number SNP / block, standard deviation number of SNP / block, average block size (Kb), standard deviation block size (Kb), maximum block size (Kb) and minimum block size (Kb).

SSC1								
Line	Number of blocks	Total number of SNPs in the blocks	Average number of SNP/ block	SD number of SNP/ block	Average block size (Kb)	SD block size (Kb)	Maximum Block size (Kb)	Minimum block size (Kb)
1	415	3,018	7.272	7.513	407.711	649.653	0.028	5658.450
2	410	3,049	7.437	6.539	398.807	533.019	0.028	3810.670
3	382	2,939	7.694	8.150	454.669	892.514	0.358	9889.490
4	391	2,850	7.289	6.611	393.074	531.058	0.025	3973.860
5	420	2,956	7.038	6.447	360.708	520.886	0.025	4484.410
6	416	3,187	7.661	7.116	410.359	589.244	0.025	5303.950
SSC2								
Line	Number of blocks	Total number of SNPs in the blocks	Average number of SNP/ block	SD number of SNP/ block	Average block size (Kb)	SD block size (Kb)	Maximum Block size (Kb)	Minimum block size (Kb)
1	273	1,484	5.436	4.310	257.003	404.701	0.120	3176.680
2	243	1,398	5.753	5.182	309.329	637.668	0.153	6314.630
3	271	1,328	4.900	3.797	236.270	433.180	0.153	4878.920
4	221	1,451	6.566	7.264	384.586	707.005	0.153	4790.340
5	293	1,353	4.618	3.755	201.700	398.609	0.153	4069.410
6	248	1,402	5.653	4.978	254.514	409.605	0.153	3352.020

Cont. Table 2. Number of blocks, total number of SNPs in the blocks, average number SNP / block, standard deviation number of SNP / block, average block size (Kb), standard deviation block size (Kb), maximum block size (Kb) and minimum block size (Kb).

SSC3								
Line	Number of blocks	Total number of SNPs in the blocks	Average number of SNP/ block	SD number of SNP/ block	Average block size (Kb)	SD block size (Kb)	Maximum Block size (Kb)	Minimum block size (Kb)
1	224	1,024	4.571	3.555	222.899	348.721	0.165	2309.850
2	199	1,066	5.357	4.303	280.085	436.220	0.078	3633.280
3	216	1,084	5.019	3.967	257.602	406.892	0.078	3673.590
4	227	1,070	4.714	3.673	212.348	303.108	0.761	1741.430
5	243	987	4.062	2.840	152.532	227.254	0.165	1416.070
6	206	992	4.816	3.986	216.364	330.359	0.078	1891.680
SSC4								
Line	Number of blocks	Total number of SNPs in the blocks	Average number of SNP/ block	SD number of SNP/ block	Average block size (Kb)	SD block size (Kb)	Maximum Block size (Kb)	Minimum block size (Kb)
1	310	1,554	5.013	4.991	196.349	435.027	0.180	6656.220
2	236	1,297	5.496	5.630	235.413	474.297	0.651	5255.580
3	240	1,415	5.896	6.720	248.801	457.508	0.651	5431.330
4	243	1,463	6.021	6.156	274.070	510.712	1.310	6211.920
5	247	1,338	5.417	5.850	208.934	443.406	0.651	5341.820
6	216	1,306	6.046	5.901	276.028	552.217	2.217	5659.440

Cont. Table 2. Number of blocks, total number of SNPs in the blocks, average number SNP / block, standard deviation number of SNP / block, average block size (Kb), standard deviation block size (Kb), maximum block size (Kb) and minimum block size (Kb).

SSC5								
Line	Number of blocks	Total number of SNPs in the blocks	Average number of SNP/ block	SD number of SNP/ block	Average block size (Kb)	SD block size (Kb)	Maximum Block size (Kb)	Minimum block size (Kb)
1	166	851	5.127	4.036	240.734	386.136	3.246	2835.580
2	171	904	5.287	4.728	256.248	467.214	1.076	4447.230
3	159	763	4.799	3.598	226.575	294.402	0.017	1745.980
4	162	918	5.667	4.772	332.321	498.366	0.017	4028.970
5	177	780	4.407	3.121	198.564	313.192	0.186	1945.660
6	152	820	5.395	4.288	263.464	370.645	0.017	1825.990
SSC6								
Line	Number of blocks	Total number of SNPs in the blocks	Average number of SNP/ block	SD number of SNP/ block	Average block size (Kb)	SD block size (Kb)	Maximum Block size (Kb)	Minimum block size (Kb)
1	256	1,423	5.559	5.803	303.521	657.056	0.161	6075.710
2	238	1,251	5.256	4.854	272.235	543.398	0.164	5482.680
3	246	1,367	5.557	5.459	299.627	579.075	0.061	5647.650
4	221	1,299	5.878	5.242	335.502	569.661	0.164	5098.040
5	228	1,198	5.254	4.899	265.950	497.240	0.061	3601.010
6	212	1,252	5.906	6.481	304.916	704.741	0.061	8178.190

Cont. Table 2. Number of blocks, total number of SNPs in the blocks, average number SNP / block, standard deviation number of SNP / block, average block size (Kb), standard deviation block size (Kb), maximum block size (Kb) and minimum block size (Kb).

SSC7								
Line	Number of blocks	Total number of SNPs in the blocks	Average number of SNP/ block	SD number of SNP/ block	Average block size (Kb)	SD block size (Kb)	Maximum Block size (Kb)	Minimum block size (Kb)
1	206	1,196	5.806	4.857	266.944	380.293	0.189	2594.350
2	214	1,303	6.089	6.417	269.331	446.712	2.003	3889.550
3	193	1,087	5.632	5.740	225.973	371.153	2.798	2536.370
4	204	1,167	5.721	5.385	276.376	442.455	2.003	2860.270
5	216	1,227	5.681	5.530	241.824	385.482	2.003	3676.670
6	196	1,226	6.255	6.774	270.695	451.560	2.003	4286.290
SSC8								
Line	Number of blocks	Total number of SNPs in the blocks	Average number of SNP/ block	SD number of SNP/ block	Average block size (Kb)	SD block size (Kb)	Maximum Block size (Kb)	Minimum block size (Kb)
1	211	1,163	5.512	5.891	342.879	633.601	0.317	4885.830
2	182	1,060	5.824	6.035	371.049	903.434	0.250	9654.750
3	217	1,009	4.650	3.402	249.708	444.328	0.301	3255.010
4	158	1,024	6.481	7.104	490.930	1439.820	0.314	16589.580
5	168	800	4.762	4.397	292.754	454.570	0.250	2463.200
6	189	1,017	5.381	5.068	319.040	866.073	0.158	10845.340

Cont. Table 2. Number of blocks, total number of SNPs in the blocks, average number SNP / block, standard deviation number of SNP / block, average block size (Kb), standard deviation block size (Kb), maximum block size (Kb) and minimum block size (Kb).

SSC9

Line	Number of blocks	Total number of SNPs in the blocks	Average number of SNP/ block	SD number of SNP/ block	Average block size (Kb)	SD block size (Kb)	Maximum Block size (Kb)	Minimum block size (Kb)
1	277	1,302	4.700	4.016	239.480	413.730	0.069	3480.660
2	251	1,352	5.386	4.499	257.768	370.103	0.360	2272.700
3	265	1,266	4.777	4.361	207.247	333.159	0.030	2552.340
4	246	1,386	5.634	5.070	282.608	417.853	0.069	2378.920
5	265	1,164	4.392	4.097	178.290	308.094	0.153	2016.850
6	225	1,295	5.756	4.946	310.849	449.450	0.153	2376.340

SSC10

Line	Number of blocks	Total number of SNPs in the blocks	Average number of SNP/ block	Sd number of SNP/ block	Average block size (Kb)	Sd block size (Kb)	Maximum Block size (Kb)	Minimum block size (Kb)
1	126	500	3.968	3.392	155.350	292.867	0.035	1988.280
2	113	452	4.000	2.712	147.799	229.374	2.083	1424.600
3	109	487	4.468	2.911	183.127	259.740	0.077	1375.860
4	113	610	5.398	4.918	280.150	469.651	0.077	3567.660
5	115	460	4.000	2.421	134.943	211.903	1.159	1491.330
6	115	525	4.565	4.044	189.444	305.406	0.964	1913.480

Cont. Table 2. Number of blocks, total number of SNPs in the blocks, average number SNP / block, standard deviation number of SNP / block, average block size (Kb), standard deviation block size (Kb), maximum block size (Kb) and minimum block size (Kb).

SSC11								
Line	Number of blocks	Total number of SNPs in the blocks	Average number of SNP/ block	SD number of SNP/ block	Average block size (Kb)	SD block size (Kb)	Maximum Block size (Kb)	Minimum block size (Kb)
1	153	704	4.601	3.767	192.548	299.038	0.170	2063.090
2	130	636	4.892	5.257	232.806	529.103	0.170	4411.690
3	131	672	5.130	7.344	250.897	633.445	0.170	6382.570
4	133	677	5.090	7.817	254.693	664.822	1.666	6691.500
5	148	643	4.345	4.191	177.213	387.809	0.170	3189.320
6	114	659	5.781	8.315	275.943	688.055	0.170	6745.410

SSC12								
Line	Number of blocks	Total number of SNPs in the blocks	Average number of SNP/ block	Sd number of SNP/ block	Average block size (Kb)	Sd block size (Kb)	Maximum Block size (Kb)	Minimum block size (Kb)
1	148	567	3.831	3.157	121.874	229.591	0.029	1968.790
2	130	532	4.092	3.214	147.389	230.071	0.029	1110.500
3	145	534	3.683	2.715	109.896	187.949	0.029	1110.010
4	137	594	4.336	3.088	153.116	240.316	0.029	1574.380
5	145	567	3.910	3.356	123.964	227.085	0.029	1574.380
6	114	562	4.930	5.507	197.114	319.405	0.029	1575.370

Cont. Table 2. Number of blocks, total number of SNPS in the blocks, average number SNP / block, standard deviation number of SNP / block, average block size (Kb), standard deviation block size (Kb), maximum block size (Kb) and minimum block size (Kb).

SSC13								
Line	Number of blocks	Total number of SNPs in the blocks	Average number of SNP/ block	SD number of SNP/ block	Average block size (Kb)	SD block size (Kb)	Maximum Block size (Kb)	Minimum block size (Kb)
1	269	1,637	6.086	5.254	414.672	751.277	1.412	6663.270
2	231	1,606	6.952	8.179	442.527	827.449	0.362	7971.370
3	234	1,540	6.581	8.014	437.107	838.698	0.362	7452.140
4	215	1,559	7.251	9.560	512.289	931.154	0.385	7197.040
5	280	1,594	5.693	4.964	359.720	582.458	0.162	5046.620
6	200	1,682	8.410	9.624	575.979	959.058	0.385	5919.680

SSC14								
Line	Number of blocks	Total number of SNPs in the blocks	Average number of SNP/ block	Sd number of SNP/ block	Average block size (Kb)	Sd block size (Kb)	Maximum Block size (Kb)	Minimum block size (Kb)
1	249	1,815	7.289	9.957	316.472	581.274	2.595	5368.550
2	234	1,818	7.769	11.629	356.867	712.262	0.048	8219.920
3	250	1,863	7.452	8.237	313.220	443.208	0.126	2625.770
4	197	1,855	9.416	15.588	441.016	950.879	2.181	9188.500
5	240	1,641	6.838	7.813	285.322	423.005	2.181	3060.990
6	209	1,638	7.837	9.234	353.823	534.613	0.048	4893.980

Cont. Table 2. Number of blocks, total number of SNPs in the blocks, average number SNP / block, standard deviation number of SNP / block, average block size (Kb), standard deviation block size (Kb), maximum block size (Kb) and minimum block size (Kb).

SSC15								
Line	Number of blocks	Total number of SNPs in the blocks	Average number of SNP/ block	SD number of SNP/ block	Average block size (Kb)	SD block size (Kb)	Maximum Block size (Kb)	Minimum block size (Kb)
1	217	1,214	5.594	5.315	300.350	469.996	0.237	2297.550
2	188	1,072	5.702	6.187	372.998	710.677	0.666	6475.920
3	177	963	5.441	6.004	332.160	574.888	0.237	4411.780
4	169	1,030	6.095	5.293	420.142	789.106	0.659	6802.560
5	189	953	5.042	5.128	286.366	503.109	0.237	3811.530
6	193	1,121	5.808	4.326	338.384	479.171	0.237	4107.330
SSC16								
Line	Number of blocks	Total number of SNPs in the blocks	Average number of SNP/ block	SD number of SNP/ block	Average block size (Kb)	SD block size (Kb)	Maximum Block size (Kb)	Minimum block size (Kb)
1	158	725	4.589	2.893	193.721	254.519	1.105	1593.400
2	137	652	4.759	3.904	217.677	341.809	0.021	2467.150
3	112	732	6.536	8.837	357.952	679.476	0.021	4916.010
4	112	752	6.714	7.697	364.007	652.205	0.021	4958.950
5	138	569	4.123	2.891	161.337	235.792	0.021	1309.500
6	132	601	4.553	2.880	192.386	273.063	0.138	1614.610

Cont. Table 2. Number of blocks, total number of SNPs in the blocks, average number SNP / block, standard deviation number of SNP / block, average block size (Kb), standard deviation block size (Kb), maximum block size (Kb) and minimum block size (Kb).

SSC17								
Line	Number of blocks	Total number of SNPs in the blocks	Average number of SNP/ block	SD number of SNP/ block	Average block size (Kb)	SD block size (Kb)	Maximum Block size (Kb)	Minimum block size (Kb)
1	125	582	4.656	4.080	175.077	266.206	0.101	2397.810
2	111	526	4.739	3.521	180.561	213.345	0.180	1062.780
3	121	667	5.512	3.841	210.320	258.798	1.046	2141.670
4	112	655	5.848	4.485	255.349	310.623	1.453	1831.970
5	120	540	4.500	2.948	153.917	173.673	1.453	770.013
6	104	607	5.837	5.299	247.715	374.064	1.470	2413.900

SSC18								
Line	Number of blocks	Total number of SNPs in the blocks	Average number of SNP/ block	Sd number of SNP/ block	Average block size (Kb)	Sd block size (Kb)	Maximum Block size (Kb)	Minimum block size (Kb)
1	134	539	4.022	2.716	153.993	201.731	1.557	1109.560
2	97	446	4.598	3.249	209.104	285.731	0.885	1596.960
3	114	480	4.211	3.107	139.869	193.024	0.424	876.766
4	109	530	4.862	3.614	197.633	244.487	0.424	1271.230
5	94	386	4.106	2.321	182.581	249.660	0.412	1089.180
6		472	4.627	3.063	199.626	272.014	0.412	1569.850

Table 3. Adjusted average block size by line and autossome.

Line	Adjusted average block size (Kb)*	Standard error
	SSC1	
1	416.725	17.371
2	395.735	17.477
3	432.681	18.108
4	400.858	17.896
5	386.950	17.271
6	390.773	17.352
	SSC2	
1	256.798	20.608
2	285.172	21.850
3	276.505	20.705
4	299.072	22.991
5	263.276	19.944
6	237.898	21.625
	SSC3	
1	234.488	14.546
2	235.102	15.463
3	236.986	14.817
4	213.693	14.447
5	200.838	14.005
6	210.370	15.166
	SSC4	
1	238.578	13.593
2	243.602	15.563
3	228.787	15.435
4	245.262	15.343
5	222.676	15.213
6	245.407	16.273
	SSC5	
1	238.835	17.604
2	241.778	17.348
3	250.421	17.995
4	287.993	17.847
5	253.199	17.092
6	240.496	18.404

*The average was adjusted by the number of SNPs in the block

Cont. Table 3. Adjusted average block size by line and autossome.

Line	Adjusted average block size (Kb)	Standard error
	SSC6	
1	303.685	17.864
2	301.237	18.532
3	299.952	18.224
4	305.212	19.232
5	295.135	18.934
6	271.971	19.637
	SSC7	
1	270.375	15.783
2	255.870	15.487
3	239.774	16.308
4	284.896	15.861
5	252.734	15.415
6	247.305	16.187
	SSC8	
1	328.656	33.750
2	317.733	36.357
3	343.390	33.341
4	355.400	39.112
5	372.400	37.862
6	321.202	35.659
	SSC9	
1	265.944	13.194
2	236.214	13.857
3	228.322	13.486
4	243.718	14.009
5	226.304	13.508
6	263.462	14.654
	SSC10	
1	185.333	15.983
2	175.529	16.872
3	177.651	17.162
4	208.650	16.969
5	162.673	16.725
6	177.062	16.711

*The average was adjusted by the number of SNPs in the block

Cont. Table 3. Adjusted average block size by line and autossome.

Line	Adjusted average block size (Kb)	Standard error
	SSC11	
1	219.823	14.342
2	236.170	15.555
3	234.750	15.496
4	241.795	15.379
5	225.582	14.590
6	206.310	16.632
	SSC12	
1	136.859	10.887
2	147.691	11.610
3	133.219	11.007
4	139.734	11.314
5	134.494	10.996
6	150.340	12.446
	SSC13	
1	474.155	24.723
2	422.075	26.663
3	450.881	26.490
4	464.286	27.645
5	455.408	24.260
6	421.120	28.750
	SSC14	
1	340.068	11.613
2	353.449	11.978
3	327.652	11.589
4	344.918	13.079
5	334.333	11.834
6	346.573	12.674
	SSC15	
1	301.371	27.629
2	365.409	29.684
3	345.481	30.594
4	381.161	31.326
5	331.544	29.632
6	322.306	29.300

*The average was adjusted by the number of SNPs in the block

Cont. Table 3. Adjusted average block size by line and autossome.

Line	Adjusted average block size (Kb)	Standard error
	SSC16	
1	231.898	15.499
2	243.344	16.634
3	253.284	18.490
4	246.239	18.517
5	233.658	16.620
6	233.173	16.956
	SSC17	
1	204.661	11.679
2	205.304	12.387
3	189.796	11.862
4	215.176	12.350
5	192.628	11.931
6	208.225	12.813
	SSC18	
1	177.337	12.354
2	195.822	14.504
3	151.242	13.378
4	167.523	13.705
5	200.581	14.737
6	184.466	14.145

*The average was adjusted by the number of SNPs in the block

Table 4. Contrast between lines, standard error and P-value by autossome.

Contrast	Contrast Estimate	Standard Error	P-value
	SSC1		
1 vs 2	20.991	24.642	0.394
1 vs 3	-15.956	25.095	0.525
1 vs 4	15.867	24.940	0.525
1 vs 5	29.775	24.494	0.224
1 vs 6	25.952	24.555	0.291
2 vs 3	-36.946	25.166	0.142
2 vs 4	-5.123	25.014	0.838
2 vs 5	8.784	24.571	0.721
2 vs 6	4.961	24.627	0.840
3 vs 4	31.823	25.461	0.211
3 vs 5	45.731	25.028	0.068
3 vs 6	41.908	25.077	0.095
4 vs 5	13.908	24.870	0.576
4 vs 6	10.085	24.929	0.686
5 vs 6	-3.823	24.486	0.876
Boar x Sow	-24.903	43.073	0.563
	SSC2		
1 vs 2	-28.373	30.035	0.345
1 vs 3	-19.706	29.213	0.500
1 vs 4	-42.274	30.875	0.171
1 vs 5	-6.478	28.679	0.821
1 vs 6	18.900	29.872	0.527
2 vs 3	8.667	30.120	0.774
2 vs 4	-13.900	31.683	0.661
2 vs 5	21.895	29.611	0.460
2 vs 6	47.274	30.735	0.124
3 vs 4	-22.567	31.001	0.467
3 vs 5	13.228	28.701	0.645
3 vs 6	38.607	29.951	0.198
4 vs 5	35.796	30.530	0.241
4 vs 6	61.174	31.539	0.053
5 vs 6	25.378	29.437	0.389
Boar x Sow	-8.228	52.180	0.875

Cont. Table 4. Contrast between lines, standard error and P-value by autossome.

Contrast	Contrast Estimate	Standard Error	P-value
SSC3			
1 vs 2	-0.614	21.242	0.977
1 vs 3	-2.497	20.770	0.904
1 vs 4	20.796	20.501	0.311
1 vs 5	33.650	20.178	0.096
1 vs 6	24.119	21.016	0.251
2 vs 3	-1.883	21.395	0.930
2 vs 4	21.409	21.163	0.312
2 vs 5	34.264	20.915	0.102
2 vs 6	24.733	21.653	0.254
3 vs 4	23.293	20.695	0.261
3 vs 5	36.148	20.413	0.077
3 vs 6	26.616	21.200	0.210
4 vs 5	12.855	20.120	0.523
4 vs 6	3.323	20.946	0.874
5 vs 6	-9.532	20.651	0.644
Boar x Sow	9.381	36.103	0.795
SSC4			
1 vs 2	-5.024	20.660	0.808
1 vs 3	9.791	20.577	0.634
1 vs 4	-6.684	20.511	0.745
1 vs 5	15.903	20.395	0.436
1 vs 6	-6.828	21.217	0.748
2 vs 3	14.815	21.921	0.499
2 vs 4	-1.660	21.856	0.939
2 vs 5	20.926	21.762	0.336
2 vs 6	-1.805	22.520	0.936
3 vs 4	-16.475	21.757	0.449
3 vs 5	6.111	21.675	0.778
3 vs 6	-16.620	22.423	0.459
4 vs 5	22.586	21.611	0.296
4 vs 6	-0.145	22.357	0.995
5 vs 6	-22.731	22.281	0.308
Boar x Sow	-14.600	37.424	0.697

Cont. Table 4. Contrast between lines, standard error and P-value by autossome.

Contrast	Contrast Estimate	Standard Error	P-value
	SSC5		
1 vs 2	-2.944	24.715	0.905
1 vs 3	-11.587	25.175	0.645
1 vs 4	-49.159	25.067	0.050
1 vs 5	-14.364	24.538	0.558
1 vs 6	-1.661	25.467	0.948
2 vs 3	-8.643	25.002	0.730
2 vs 4	-46.215	24.876	0.063
2 vs 5	-11.420	24.369	0.639
2 vs 6	1.282	25.285	0.960
3 vs 4	-37.572	25.366	0.139
3 vs 5	-2.777	24.792	0.911
3 vs 6	9.926	25.750	0.700
4 vs 5	34.795	24.761	0.160
4 vs 6	47.498	25.617	0.064
5 vs 6	12.703	25.141	0.613
Boar x Sow	-45.099	43.408	0.299
	SSC6		
1 vs 2	2.448	25.740	0.924
1 vs 3	3.733	25.519	0.884
1 vs 4	-1.527	26.249	0.954
1 vs 5	8.550	26.031	0.743
1 vs 6	31.714	26.547	0.232
2 vs 3	1.286	25.991	0.961
2 vs 4	-3.974	26.715	0.882
2 vs 5	6.102	26.487	0.818
2 vs 6	29.267	27.008	0.279
3 vs 4	-5.260	26.495	0.843
3 vs 5	4.817	26.279	0.855
3 vs 6	27.981	26.790	0.296
4 vs 5	10.077	26.995	0.709
4 vs 6	33.241	27.478	0.227
5 vs 6	23.164	27.286	0.396
Boar x Sow	22.923	45.946	0.618

Cont. Table 4. Contrast between lines, standard error and P-value by autossome.

Contrast	Contrast Estimate	Standard Error	P-value
SSC7			
1 vs 2	14.505	22.113	0.512
1 vs 3	30.601	22.694	0.178
1 vs 4	-14.521	22.376	0.516
1 vs 5	17.641	22.061	0.424
1 vs 6	23.070	22.609	0.308
2 vs 3	16.097	22.493	0.474
2 vs 4	-29.025	22.170	0.191
2 vs 5	3.136	21.854	0.886
2 vs 6	8.565	22.398	0.702
3 vs 4	-45.122	22.748	0.048
3 vs 5	-12.960	22.438	0.564
3 vs 6	-7.531	22.982	0.743
4 vs 5	32.162	22.116	0.146
4 vs 6	37.591	22.666	0.097
5 vs 6	5.429	22.356	0.808
Boar x Sow	7.005	38.804	0.857
SSC8			
1 vs 2	10.923	49.600	0.826
1 vs 3	-14.734	47.455	0.756
1 vs 4	-26.743	51.643	0.605
1 vs 5	-43.743	50.731	0.389
1 vs 6	7.454	49.099	0.879
2 vs 3	-25.657	49.378	0.603
2 vs 4	-37.666	53.336	0.480
2 vs 5	-54.667	52.530	0.298
2 vs 6	-3.469	50.926	0.946
3 vs 4	-12.010	51.512	0.816
3 vs 5	-29.010	50.380	0.565
3 vs 6	22.188	48.816	0.650
4 vs 5	-17.000	54.530	0.755
4 vs 6	34.198	52.930	0.518
5 vs 6	51.198	52.009	0.325
Boar x Sow	-1.202	88.269	0.989

Cont. Table 4. Contrast between lines, standard error and P-value by autossome.

Contrast	Contrast Estimate	Standard Error	P-value
		SSC9	
1 vs 2	29.730	19.143	0.121
1 vs 3	37.622	18.857	0.046
1 vs 4	22.226	19.261	0.249
1 vs 5	39.640	18.861	0.036
1 vs 6	2.482	19.739	0.900
2 vs 3	7.891	19.343	0.683
2 vs 4	-7.504	19.690	0.703
2 vs 5	9.910	19.368	0.609
2 vs 6	-27.248	20.152	0.177
3 vs 4	-15.396	19.458	0.429
3 vs 5	2.019	19.070	0.916
3 vs 6	-35.140	19.931	0.078
4 vs 5	17.414	19.491	0.372
4 vs 6	-19.744	20.244	0.330
5 vs 6	-37.158	19.966	0.063
Boar x Sow	-7.041	33.814	0.835
		SSC10	
1 vs 2	9.804	23.213	0.673
1 vs 3	7.682	23.457	0.743
1 vs 4	-23.317	23.380	0.319
1 vs 5	22.660	23.107	0.327
1 vs 6	8.272	23.136	0.721
2 vs 3	-2.122	24.071	0.930
2 vs 4	-33.121	23.992	0.168
2 vs 5	12.856	23.732	0.588
2 vs 6	-1.533	23.758	0.949
3 vs 4	-30.999	24.122	0.199
3 vs 5	14.978	23.968	0.532
3 vs 6	0.590	23.952	0.980
4 vs 5	45.977	23.889	0.055
4 vs 6	31.588	23.788	0.185
5 vs 6	-14.389	23.654	0.543
Boar x Sow	-39.828	41.217	0.334

Cont. Table 4. Contrast between lines, standard error and P-value by autossome.

Contrast	Contrast Estimate	Standard Error	P-value
SSC11			
1 vs 2	-16.347	21.157	0.440
1 vs 3	-14.927	21.118	0.480
1 vs 4	-21.972	21.031	0.296
1 vs 5	-5.759	20.449	0.778
1 vs 6	13.512	21.975	0.539
2 vs 3	1.420	21.957	0.948
2 vs 4	-5.625	21.874	0.797
2 vs 5	10.588	21.325	0.620
2 vs 6	29.859	22.774	0.190
3 vs 4	-7.045	21.831	0.747
3 vs 5	9.168	21.290	0.667
3 vs 6	28.439	22.725	0.211
4 vs 5	16.213	21.203	0.445
4 vs 6	35.484	22.647	0.118
5 vs 6	19.271	22.147	0.384
Boar x Sow	-1.280	37.646	0.973
SSC12			
1 vs 2	-10.832	15.916	0.496
1 vs 3	3.641	15.469	0.814
1 vs 4	-2.874	15.709	0.855
1 vs 5	2.366	15.469	0.878
1 vs 6	-13.480	16.559	0.416
2 vs 3	14.473	15.998	0.366
2 vs 4	7.958	16.212	0.624
2 vs 5	13.198	15.991	0.409
2 vs 6	-2.648	17.021	0.876
3 vs 4	-6.515	15.796	0.680
3 vs 5	-1.275	15.550	0.935
3 vs 6	-17.121	16.651	0.304
4 vs 5	5.240	15.782	0.740
4 vs 6	-10.606	16.800	0.528
5 vs 6	-15.846	16.624	0.341
Boar x Sow	-4.248	27.905	0.879

Cont. Table 4. Contrast between lines, standard error and P-value by autossome.

Contrast	Contrast Estimate	Standard Error	P-value
SSC13			
1 vs 2	52.079	36.369	0.152
1 vs 3	23.273	36.229	0.521
1 vs 4	9.868	37.105	0.790
1 vs 5	18.746	34.599	0.588
1 vs 6	53.034	37.975	0.163
2 vs 3	-28.806	37.587	0.444
2 vs 4	-42.211	38.402	0.272
2 vs 5	-33.333	36.061	0.355
2 vs 6	0.955	39.192	0.981
3 vs 4	-13.405	38.292	0.726
3 vs 5	-4.527	35.912	0.900
3 vs 6	29.761	39.106	0.447
4 vs 5	8.878	36.810	0.809
4 vs 6	43.166	39.842	0.279
5 vs 6	34.288	37.710	0.363
Boar x Sow	15.350	64.950	0.813
SSC14			
1 vs 2	-13.381	16.684	0.423
1 vs 3	12.415	16.405	0.449
1 vs 4	-4.851	17.499	0.782
1 vs 5	5.734	16.576	0.729
1 vs 6	-6.505	17.191	0.705
2 vs 3	25.796	16.667	0.122
2 vs 4	8.530	17.733	0.631
2 vs 5	19.115	16.839	0.256
2 vs 6	6.876	17.438	0.693
3 vs 4	-17.266	17.480	0.323
3 vs 5	-6.681	16.560	0.687
3 vs 6	-18.921	17.174	0.271
4 vs 5	10.585	17.657	0.549
4 vs 6	-1.654	18.210	0.928
5 vs 6	-12.240	17.342	0.480
Boar x Sow	8.706	29.753	0.770

Cont. Table 4. Contrast between lines, standard error and P-value by autossome.

Contrast	Contrast Estimate	Standard Error	P-value
SSC15			
1 vs 2	-64.038	40.552	0.115
1 vs 3	-44.109	41.223	0.285
1 vs 4	-79.789	41.770	0.056
1 vs 5	-30.172	40.513	0.457
1 vs 6	-20.934	40.272	0.603
2 vs 3	19.929	42.630	0.640
2 vs 4	-15.751	43.151	0.715
2 vs 5	33.866	41.949	0.420
2 vs 6	43.104	41.706	0.302
3 vs 4	-35.680	43.797	0.415
3 vs 5	13.937	42.580	0.743
3 vs 6	23.175	42.365	0.584
4 vs 5	49.617	43.153	0.250
4 vs 6	58.855	42.882	0.170
5 vs 6	9.238	41.685	0.825
Boar x Sow	-50.623	72.803	0.487
SSC16			
1 vs 2	-11.446	22.721	0.615
1 vs 3	-21.386	24.182	0.377
1 vs 4	-14.341	24.210	0.554
1 vs 5	-1.760	22.684	0.938
1 vs 6	-1.275	22.949	0.956
2 vs 3	-9.940	24.907	0.690
2 vs 4	-2.894	24.932	0.908
2 vs 5	9.686	23.488	0.680
2 vs 6	10.171	23.738	0.668
3 vs 4	7.045	26.008	0.787
3 vs 5	19.626	24.964	0.432
3 vs 6	20.111	25.145	0.424
4 vs 5	12.581	24.997	0.615
4 vs 6	13.066	25.172	0.604
5 vs 6	0.485	23.701	0.984
Boar x Sow	-23.796	42.285	0.574

Cont. Table 4. Contrast between lines, standard error and P-value by autossome.

Contrast	Contrast Estimate	Standard Error	P-value
SSC17			
1 vs 2	-0.643	17.006	0.970
1 vs 3	14.865	16.662	0.373
1 vs 4	-10.515	17.028	0.537
1 vs 5	12.033	16.666	0.471
1 vs 6	-3.564	17.367	0.837
2 vs 3	15.508	17.164	0.367
2 vs 4	-9.872	17.517	0.573
2 vs 5	12.676	17.174	0.461
2 vs 6	-2.921	17.846	0.870
3 vs 4	-25.380	17.103	0.138
3 vs 5	-2.832	16.845	0.867
3 vs 6	-18.429	17.440	0.291
4 vs 5	22.548	17.211	0.191
4 vs 6	6.951	17.757	0.696
5 vs 6	-15.597	17.546	0.374
Boar x Sow	-10.604	30.051	0.724
SSC18			
1 vs 2	-18.485	19.066	0.333
1 vs 3	26.096	18.197	0.152
1 vs 4	9.814	18.484	0.596
1 vs 5	-23.243	19.212	0.227
1 vs 6	-7.129	18.797	0.705
2 vs 3	44.580	19.738	0.024
2 vs 4	28.299	19.938	0.156
2 vs 5	-4.759	20.687	0.818
2 vs 6	11.356	20.251	0.575
3 vs 4	-16.282	19.167	0.396
3 vs 5	-49.339	19.895	0.013
3 vs 6	-33.225	19.477	0.089
4 vs 5	-33.058	20.148	0.101
4 vs 6	-16.943	19.676	0.389
5 vs 6	16.114	20.439	0.431
Boar x Sow	70.509	33.887	0.038