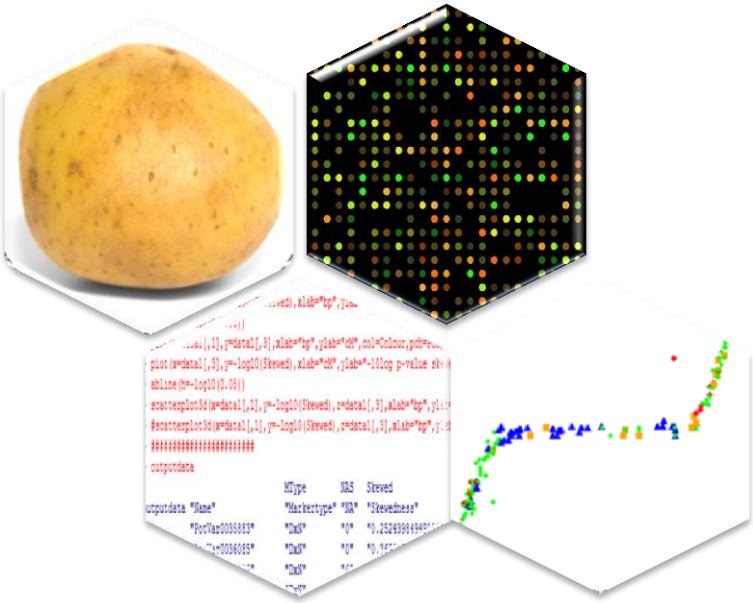
MSc Thesis

Methods for mapping and linkage map integration in tetraploid potato.



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“Let the sky rain potatoes” - Sir John Falstaff in Shakespeare – The Merry Wives of Windsor

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http://barringtonstageco.org/blog/pmp-blog-you-say-potato/

http://commons.wikimedia.org/wiki/File:DNA_microarray.svg

Abstract

Potato, *Solanum tuberosum ssp. tuberosum,* is an economically important crop. Cultivated potato is an autotetraploid with four homologs of every chromosome. Due to its polyploidy, genetic analysis of potato is more complicated than that of diploids. Linkage mapping is an important tool in genetic analysis, but due to the more complicated genetics, programmes or algorithms that can handle polyploid species are lacking or very basic. In this thesis, methods are presented to cover all the steps in linkage mapping process of autotetraploid crops. First, the recombination frequencies between simplex x nulliplex (SxN) markers are calculated and these markers are assigned to chromosomes on the basis of their pairwise LOD-scores. Thereafter, the markers are assigned to homologs based on a novel approach, namely a phase-tree, together with and duplex x nulliplex (DxN) linkages. The recombination frequencies and LOD-scores of these marker types, as well as those of others, were used in a linear regression approach for the ordering and position estimation of the markers on the homologs. As a final step, the homolog maps were integrated per chromosome using the graph theory approach of the R package LPmerge. This led to a high marker density integrated linkage map of potato which covered 1406.13 cM for 12 chromosomes with 5165 SNP markers. The integrated map has a high coverage and can be used for haplotyping, QTL analysis and as a reference linkage map.

Keywords: potato, autotetraploidy, linkage mapping, homologs, integration, LPmerge

Samenvatting

Aardappel, *Solanum tuberosum ssp. tuberosum,* is een economisch belangrijk gewas. De gecultiveerde aardappel is een autotetraploide plant met vier homologen van elk chromosoom. Door de polyploïdie-graad is genetische analyse van aardappel gecompliceerder dan dat van diploïde planten. Het maken van een genetische kaart is een belangrijk gereedschap in de genetische analyse, maar door de complexe genetica zijn programmas of algoritmes die dit aankunnen afwezig of simpel. In deze thesis worden methodes gepresenteerd die alle stappen in het maken van een genetische kaart dekken van autotetraploïde gewassen. Allereerst werden de recombinatie frequenties tussen simplex x nulliplex (SxN) merkers berekend en werden deze merkers toegewezen aan chromosomen op de basis hun paarsgewijze LOD-scores. Daarna werden deze merkers toegewezen aan homologen op basis van een nieuwe techniek, namelijk een fase-boom, samen met DxN koppeling. De recombinatie frequenties en LOD-scores van deze merkertypes, alswel als de recombinatie frequencies en LOD-scores van andere merkertypes, werden gebruikt in een lineare regressie aanpak voor het ordenen van merkers en positie bepaling van de merkers op de homologen. Als laatste stap werden de homoloog kaarten geintegreerd per chromosoom door middel van de R-package LPmerge, die werkt met een grafentheorie. Dit leidde tot een genetische kaart van aardappel met een hoge merkerdichtheid die 1406.13 cM spant voor 12 chromosomen met5165 SNP merkers. De geintegreerde kaart heeft een hoge dekking en kan gebruikt worden voor haplotypering, QTL analyse, en als referentie kaart.

Trefwoorden: aardappel, autotetraploïdie, genetische kaart, homologen, integratie, LPmerge

Table of Contents

Introduction

Potato and polyploidy

Potato, *Solanum tuberosum ssp. tuberosum*, is the 5th most produced crop globally, after sugar cane, maize, rice and wheat, with a production of 365 million mega tonnes in 2012 (FAOSTAT, 2012). The biggest producer of potato is China, but the origin of potato lies in the Andes of Chile (Hosaka & Hanneman, 1988). From there on it was spread to other regions in Southern America and in the 16th century was brought to Europe by the Spanish.

The origin and evolution of potato is intriguing, since the potato is an autotetraploid (Felcher *et al.*, 2012), which means that is has four copies of every chromosomes (these copies are called homologues chromosomes or homologs) due to whole genome duplication arisen from unreduced gametes. Because potato is an autopolyploid (2n=4x=48), and has polysomic inheritance (Wu *et al.*, 2002), no preferential pairing of the chromosomes occurs in contrast with allopolyploids, like wheat, in which preferential pairing does happen (Jauhar *et al.*, 1991). Autpolyploidy means that every homologous chromosome has an equal chance of pairing with any of the other homologs in meiosis. Potato has mainly bivalent pairing, although multivalent formation does occur sometimes (Gavrilenko *et al.*, 2007), which in turn can lead to double reduction (Wu *et al.*, 2002). Furthermore, potato is an outcrossing species suffering from inbreeding depression and has a high level of heterozygosity in its genome (The Potato Genome Sequencing Consortium, 2011).

SNP markers

When molecular markers are considered for tetraploids, it is good to notice that nowadays SNPs are often used during genetic analysis. SNPs are markers that are polymorphic at a single nucleotide site and therefore four different alleles (GACT) can occur (Mammadov *et al.*, 2012). SNPs are codominant and highly abundant in the genome, which makes them useful for all kinds of genome studies. Autopolyploidy means that during meiosis, the homologs form random pairs of bivalents or multivalents and for a highly heterozygous outbreeding species, like potato, this can result in a large number of allelic combinations. 36 genotypes could be found in the most extreme case if 8 different alleles segregate independently (Meyer *et al.*, 1998). However, in this thesis the focus is on SNPs which are biallelic, which makes scoring more reliable. The markers can be assigned to five different dosage classes in tetraploids, namely nulliplex (aaaa), simplex (Aaaa), duplex (AAaa), triplex(AAAa) and quadruplex (AAAA) (Rifkin *et al.*, 2012), while diploids have a maximum of three possible genotypes (aa, Aa and AA). It is good to keep in mind that every dosage can be converted by using symmetry argumentation, for example a triplex is a simplex for the other allele (Vukosavljev *et al.*, 2014). Furthermore, the classification of these five classes takes only one parent into account, while during genetic studies usually two parents are crossed. Therefore the dosages of both parents are considered in combination with the symmetry argumentation (Table 1). By doing so, 6 marker segregation types (of which 4 are used in this thesis) of SNP markers can be recognized: simplex x nulliplex (SxN), duplex x nulliplex (DxN), simplex x simplex (SxS), simplex x triplex (SxT), duplex x simplex (DxS) and duplex x duplex (DxD). These SNP markers can thus be used in genetic studies, such a linkage mapping.

The SNP markers are used in a pipeline for genetic analysis that spans from marker development to QTL (Quantative Trait Loci) analysis. A general pipeline that can be used for both diploid and polyploid species is briefly explained in Figure 1. An important step in this pipeline from marker development to QTL-analysis is the development of a linkage map, which is the focus of this thesis.

Linkage mapping

Linkage mapping is an important tool in breeding for potato, since it can be used for the study of inheritance (Ripol *et al.*, 1999), anchoring the genome (Sharma *et al.*, 2013), as a requisite for QTL analysis (Wu *et al.*, 2004a), which in itself is a step towards marker assisted breeding, or estimation of the physical chromosome size (Chakravarti *et al.*, 1991). An approach to linkage mapping in tetraploids is to use a related diploid species (Rifkin *et al.*, 2012) or to use a doubled monoploid developed from a tetraploid (The Potato Genome Sequencing Consortium, 2011). In both cases a diploid is mapped and this procedure is developed well over the past years. However a linkage map based on diploids, lacks important dosage information. The number of genotypes in a tetraploid is larger than in a diploid (Ripol *et al.*, 1999) and this may lead to dosage effects and allele interactions not present in diploids. Thus, it may well be that not all characteristics of a tetraploid can be mapped in a diploid background (Yu & Pauls, 1993). In addition to that, polyploidization during evolution is a dynamic process and therefore it may not be wise to use a diploid approximation for a tetraploid (Luo *et al.*, 2004). Thus, making inferences from the diploid level to the tetraploid level has its difficulties and is undesired, since scientists and breeders want to carry out their experiments or breeding efforts on crosses of tetraploid potatoes rather than on diploid potato populations. These reasons are all about the inference of the diploid to the tetraploid level, but there is also a more practical reason, namely by mapping tetraploid potato directly, precious time and laboratory labour can be saved (Hackett *et al.*, 1998) because doubled monoploids potatoes, created from tetraploids, are generally male-sterile (Mann *et al.*, 2011). A reason why linkage mapping is done at all, on both diploid and tetraploid level, is that with comparing the physical map with the linkage map, genotyping, or sequence alignment errors can be found which would otherwise go unnoticed.

Considering these arguments, it is useful to focus on mapping tetraploid potatoes. The steps of linkage mapping in tetraploids are 1) creating a mapping population, 2) genotyping the parents and the offspring, 3) calculating the recombination frequencies 4), grouping of the markers into linkage groups and homologs, 5) determining the order within the homolog and 6) integrating the homologs (Figure 1). Mapping cross-pollinated diploids and tetraploids, including potato, is often done by creating linkage maps for the parents separately and integrating those maps thereafter (Mann *et al.*, 2011). This strategy is called the pseudo-test cross strategy.

The most important step of the development of a linkage map is the ordering of the markers. For a linkage map with only a few markers, it will not be a problem to consider all the possible orders (n!/2 possible orders for every n markers to be ordered (Liu, 1997c), but for large datasets this is a huge computational problem, which bears similarity to the "travelling salesman problem" (Nelson, 2005). To cope with this problem, algorithms have been developed to find (near-)optimal orders while avoiding time consuming calculations, for example seriation (Nelson, 2005) which is a 'greedy' algorithm that grows outwards by adding one marker at a time to the order. Another algorithm, simulated annealing , uses 'temperature' to accept changes in the order that might be unfavourable and does this so avoid getting stuck in a local optimum (Nelson, 2005).

Other algorithms are stepwise search, branch and bound, genetic algorithms (Hackett *et al.*, 2003) or evolutionary strategy algorithms (Mester *et al*., 2003a). In this thesis, a linear regression approach is used to order the markers, because it is theoretically easy to understand and implement practically (Chapter 5 and 6).

All algorithms use criteria to find the optimum order given all the estimated recombination frequencies or the counts of recombination events. Examples of optimization criteria are minimum the sum of adjacent recombination frequencies (SARF) (Van Os *et al.*, 2005), the maximum likelihood, the maximum sum of adjacent LOD scores (SALOD), the minimum number of cross-overs, the minimum least square locus order, the minimization of the total number of expected recombinations (Hackett *et al.*, 2003), sum of adjacent distances (SAD) or the weighted least squares(WLS) (Stam, n.d.), which is used in this thesis. The algorithms are used together with the criteria, for example RECORD minimises the number of cross-overs by a branch and bound algorithm, while JoinMap can use a stepwise search to minimise the sum of adjacent recombination (Isidore *et al.*, 2003).

It is good to keep in mind that there are no 'good' or 'bad' algorithms and criteria, but the final ordering result is based on the genotype data, model and criteria used. Therefore there is a demand to simulate how the different algorithms handle data with, for example, missing data or genotype errors. Also, it should be noted that programmes or algorithms that can handle polyploid species are lacking, very basic (Dufresne *et al.*, 2014) or cannot handle large number of markers (Hackett & Luo, 2003), since polyploids have a more complex segregation pattern (Voorrips *et al.*, 2011) when compared to diploids. Fortunately, some options for mapping exist. A map can be estimated based on SxN markers in coupling phase because the segregation ratio and recombination frequencies are the same as with a diploid cross between a homozygous and heterozygous parent (Voorrips *et al.*, 2011). These maps based on SxN markers can serve as a backbone map for the other segregation type markers which can be added one by one. It is also possible to calculate the recombination frequencies beforehand and present them to programmes like JoinMap (Nelson, 2005).

Once the map order is there, the relative position between the markers is something that one would want to know. The distance between markers can be calculated by transforming the recombination frequencies into map distances. The two most widely used mapping functions are Haldane's and Kosambi's. Haldane's mapping function assumes that the crossovers follow a Poisson distribution and are independent regardless of their relative location, while Kosambi's mapping function takes positive interference into account (Vinod, 2011; Chapter 5). Kosambi's mapping function has been used to convert recombination frequencies into mapping distances of diploid potato (Sharma *et al.*, 2013), while Haldane's mapping function was used to map tetraploid potato (Hackett *et al.*, 2013). On the other hand, the differences between these mapping functions may be small when the marker density is high and adjacent distances are small (Van Eck, personal communication).

The ordering step in linkage mapping leads to 96 (2 parents x 4 homologs x 12 chromosome) homolog maps for tetraploid potato. Those individual maps still need to be integrated to be highly powerful for QTL-analysis. By combining the homolog information into one integrated map, the QTL analysis will be more powerful when compared to a QTL analysis on the homolog level. There are several strategies to integrate the homolog maps into a single consensus map, namely visual alignment, determination the consensus map directly from the recombination frequencies and LOD-scores, or a graph-theory approach (Yap *et al.*, 2003). In this thesis a graph-theory approach is used (Chapter 6).

Goal and strategy

The goal of this thesis is the development of methods for linkage mapping autotetraploids. The strategy used in in this thesis to estimate a genetic linkage map, with a linear regression approach, was to start with calculating the map based on the highly informative SxN markers. Another reason, apart from the informativeness, is that SxN markers in coupling phase can be analysed in the same way as if the markers came from a diploid population instead of a tetraploid one. Thereafter, homolog maps with the other marker segregation types were estimated by calculating the linkage between SxN markers and those other markers.

During this thesis potato was used as a model crop since it is considered to be a true autotetraploid, the abundant SNP data available and access to the physical locations of most markers. Every step of linkage mapping tetraploid potato is elaborated in the subsequent chapters. Every chapter starts first with a theoretical introduction of the (statistical) method used and thereafter the results from the analysis of tetraploid potato are shown and briefly discussed. In Chapter 1, the mode of inheritance of potato is investigated by calculating the recombination frequencies of SxN markers. In Chapter 2, the SxN markers are assigned to linkage groups. In Chapter 3, the SxN markers are assigned to homologs based on a so-called phase-tree and DxN linkage Furthermore DxN and SxS markers are assigned to chromosomes and homologs. In Chapter 4, the recombination frequencies of the other marker types are calculated. In addition, the SxT markers are assigned to chromosomes and homologs. In Chapter 5, the theory of ordering markers of a homolog with the linear regression method is explained. The results of the mapping procedure are presented in Chapter 6. In Chapter 7, the homolog maps are integrated into a consensus map. In order to simplify explanation and limit the number of results to be presented, all these topics are explained on the basis of a single chromosome, chromosome 11, while information of the other chromosomes can be found in the Appendices.

Apart from the development of an integrated linkage map of potato, methods are developed for linkage mapping for other autotetraploids. This is in done in R, since it is scriptable (R Core Team, 2012), in contrast to JoinMap. Furthermore, the methods are developed in R as an alternative to JoinMap since JoinMap was designed for diploids and although the integration procedure of JoinMap could be used, it will take a long time to run when the marker number exceeds 150 (Wu *et al.*, 2008). Time is a problem for many people, although others claim that a good solution is more important than a fast algorithm (Mester *et al*., 2004).

During this thesis the physical genome information is used to verify the results. However, one should be careful with the physical genome information as well, since it is in itself estimation and might require rearrangements in the initial years after sequencing (Cheema & Dicks, 2009; Felcher *et al.*, 2012). The use of genome information is limited, since for other species the genome sequence might not be available, and thus the sequence positions are primarily used as verification of the methodology in the case of potato. The steps carried out in this thesis are developed to be general so that they can be applied to marker data sets in mapping populations of other autotetraploid crops, even though their sequence is not available.

Table 1. Segregation ratios of an autotetraploid of different biallelic SNP marker types. Six marker types can be distinguished based on their segregation ratio. The segregation ratios are not considering double reduction and according to Mendelian laws.

	Type of parents	Dose of parents	Possible Gametes	Possible offspring	Segregation	
	Parent 1 x Parent 2	Parent 1 x Parent 2	P1 P2		Co-dominant	Dominant (Presence: Absence)
Simplex x Nulliplex	Simplex x Nulliplex	Aaaa x aaaa	Aa, aa aa	Aaaa, aaaa	1:1	1:1
	Triplex x Nulliplex	AAAa x aaaa	AA, Aa aa	AAaa, Aaaa	1:1	1:0
	Triplex x Quadriplex	AAAa x AAAA	AA, Aa AA	AAAA, AAAa	1:1	1:0
	Simplex x Quadriplex	Aaaa x AAAA	Aa, aa AA	AAAa, AAaa	1:1	1:0
Duplex x Nulliplex	Duplex x Nulliplex	AAaa x aaaa	AA, Aa, aa aa	AAaa, Aaaa, aaaa	1:4:1	5:1
	Duplex x Quadriplex	AAaa x AAAA	AA, Aa, aa AA	AAAA, AAAa, AAaa	1:4:1	1:0
Simplex x Simplex	Simplex x Simplex	Aaaa x Aaaa	Aa, aa Aa, aa	AAaa, Aaaa, aaaa	1:2:1	3:1
	Triplex x Triplex	AAAa x AAAa	AA, Aa AA, Aa	AAAA, AAAa , AAaa	1:2:1	1:0
Triplex x Simplex	Triplex x Simplex	AAAa x Aaaa	AA,Aa Aa,aa	AAAa,AAaa,Aaaa	1:2:1	1:0
Duplex x Simplex	Duplex x Simplex	AAaa x Aaaa	AA, Aa, aa Aa, aa	AAAa , AAaa, Aaaa, aaaa	1:5:5:1	11:1
	Duplex x Triplex	AAaa x AAAa	AA, Aa, aa AA, Aa	AAAA, AAAa , AAaa, Aaaa	1:5:5:1	1:0
Duplex x Duplex	Duplex x Duplex	AAaa x AAaa	AA, Aa, aa AA, Aa, aa	AAAA, AAAa, AAaa, Aaaa, aaaa	1:8:18:8:1	35:1

Marker development
When molecular markers are developed, the following criteria are considered: polymorphism, distribution throughout the genome, resolution of genetic differences, expenses, labour, time, amount of DNA-sample needed and linkage to phenotypes (Agarwal *et al*., 2008).

Population
Whenever two plants are crossed, the offspring forms a population which the can be used during the genetic analysis. Backcrosses, doubled haploids, recombinant inbred lines and F2-populations are examples of such crossing strategies (Schneider, 2005). The few people that are working on tetraploid potato create F1 populations (Douches & Coombs, 2012, Hackett *et al.*, 2013), since there is already segregation in the F1 because the parental lines are heterozygous. Another reason is that the possibility of using other population types, such as commonly used inbred lines, is limited by constrains like inbreeding depression.

Genotyping and dosages
In the distant past, linkage maps were based on morphological characteristics, however nowadays mostly molecular markers are used. There are several marker types ranging from RFLPs to SNPs, which all can be used in linkage mapping for both diploid and tetraploid populations (Nguyen & Wu, 2005), although currently mostly SNPs are used. Software such as fitTetra (Voorrips *et al*., 2011) can be used to translate the raw genotypes of tetraploids into useful dosages.

Linkage map
Linkage mapping is an important tool in breeding for potato, since it can be used for the study of inheritance (Ripol *et al.*, 1999), anchoring the genome (Sharma *et al.*, 2013) and QTL-analysis (Wu *et al.*, 2004), which in itself is a step in marker assisted breeding.

Haplotype propoabilites or phase reconstruction
The reconstruction of the linkage phase of the parents is the last step in linkage analysis (Luo *et al*., 2001). This means that the markers are mapped over the homologs within a parent and not across a parent. The markers are assigned to one of the parents in coupling or repulsion phase. This step is useful for further analysis such as QTL-analysis. Reconstructing a tetraploid is more difficult than constructing a diploid since a tetraploid has twice as many homologs.

QTL-analysis
QTLs, or Quantitative trait loci, are common in plants and are of interest due to commercial important traits. QTL mapping is a combination of linkage mapping and traditional quantative genetics (Liu, 1997e). During QTL analysis, an significant association between traits and markers is searched for. Significant association between traits and markers may be evidance that a QTL is located nearby. By using the marker of an integrated linkage map, one makes sure to combine all the marker as efficient as possible. This leads to greater power to find QTLs.

Calculation recombination frequencies and LOD-scores
The calculation of the recombination frequency between two markers is determined by the used model, which ,in turn, is determined by the population type and expected genotype frequencies. For some situations an analticaly estimator can be calculated, while for situatons the recombination frequency cannot be found analytically, but can still be found by an iterative maximum likelihood estimation (Luo *et al.*, 2001).

Marker assignment to linkage groups
The markers are grouped after the recombination frequencies and LOD scores are calculated. When markers in a tetraploid are grouped, the chromosomes are likely to be reconstructed by grouping the markers into linkage groups. Grouping, or clustering, can be done by making a dendogram with a nearest-neighbour analysis (Luo *et al.*, 2001), k-means clustering (Hackett *et al.*, 2013), or clustering based on the significance of the chi-square test for independent segregation (Hackett *et al.*, 2013) together with corrections for multiple-testing (Luo *et al.*, 2001).

Marker assignment to homologs
Apart from grouping the markers into 'chromosome'-groups, the markers are also clustered in homologous groups and this is unique to autopolyploids (Ripol *et al.*, 1999) and this is not done for diploids. Several cluster analyses may be run and combined manually as well (Hackett *et al.*, 2013).

Mapping homologs
Ordering the markers within each linkage group is the most important step of linkage mapping. The possible orders of markers increases exponentially with every marker added to the analysis (Van Os *et al.*, 2005). There are several algorithms which are used in ordering programmes. All algorithms use criteria to find the optimum order given all the estimated recombination frequencies or the counts of recombination events. Mapping functions are used that can convert recombination frequencies into genetic distances.

Integration
Integration of the homolog map is desired for QTL-analysis. There are several strategies to integrate the homolog maps into a single consensus map, namely visual alignment, determine the consensus map directly from the recombination frequencies and LOD-scores, or a graph-theory approach (Yap *et al.*, 2003).

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Figure 1, previous page. Summary of the pipeline from genotype to QTL-analysis for diploid and tetraploids and a pipeline for linkage mapping in tetraploids. The pipeline covers all the essential steps from genotyping to QTL analysis with a focus on linkage mapping in tetraploids

Programmes, Data and Assumptions

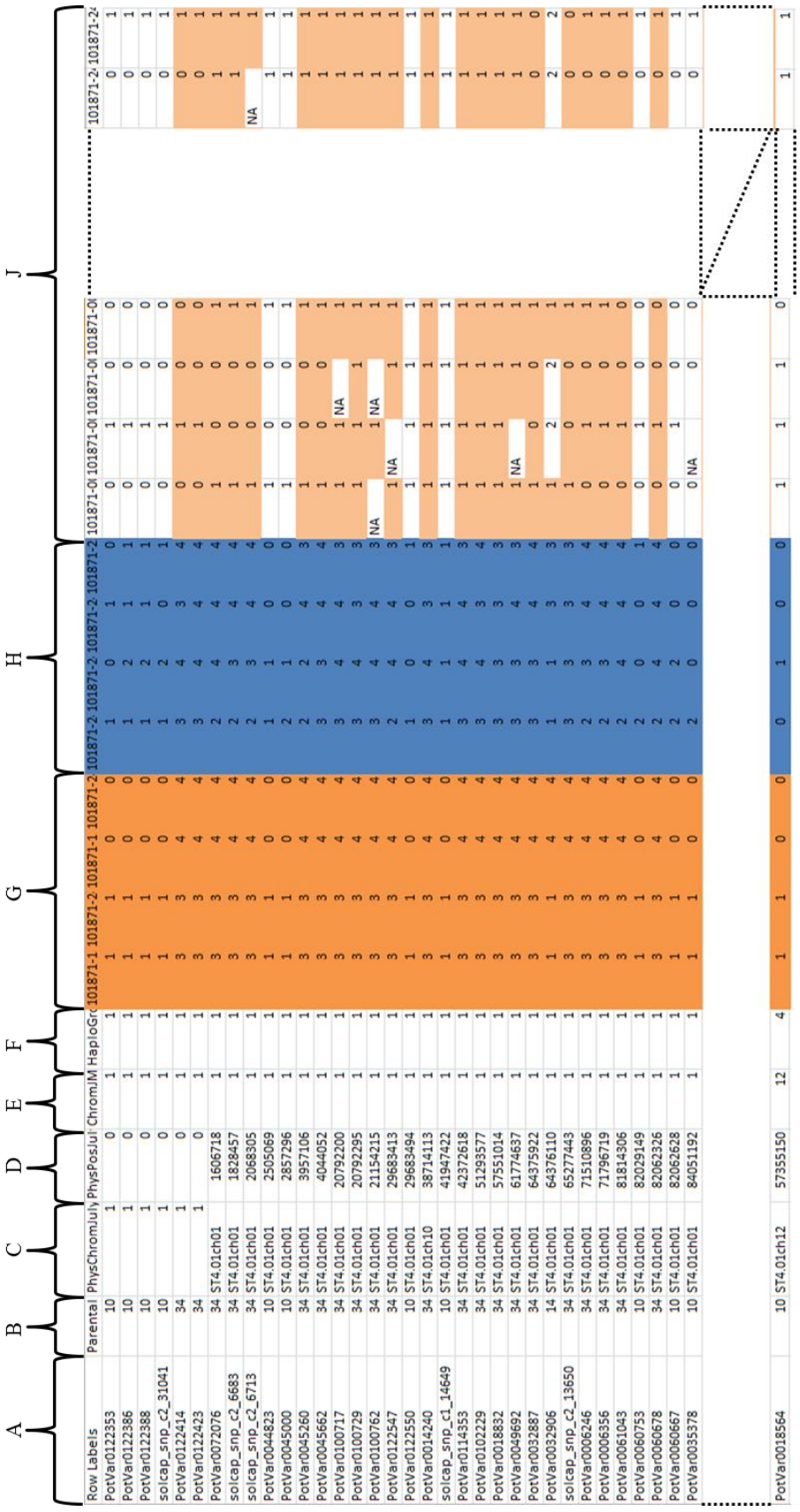
The programmes, data and assumptions are the starting point for linkage mapping in this thesis. Therefore the data, assumptions and programmes are explained here.

Data

Linkage mapping is basically a data analysis and it is therefore wise to take a look at the data first. In the beginning two tetraploid potato accessions (A x C) were crossed. The population consists of 237 individuals, and such population size would be enough to identify the homologs (Hackett *et al.*, 1998). Thereafter, the DNA was extracted of 237 F1 offspring, the parents, 3 grandparents and 1 great-grandparent (Maliepaard *et al.*, n.d.). The DNA was then applied to the recently developed 20K SolSTW array. This array contains 17987 useful SNPs (Vos *et al.*, 2014). The SNPs on the array are biallelic, which makes scoring easier when compared to SNPs with four different alleles. When the extracted DNA was applied on the array, two fluorescent probes were added which bind to one of the two alleles. Thereafter, the fluorescence signal was measured.

The raw SNP data needed to be converted to useful dosages, the number of copies of a SNP allele. By using fitTetra software, markers were scored for dosages ranging from 0 to 4 copies (Voorrips *et al.*, 2011). The markers were selected based on consistency of parental scores across the replicates and expected segregation ratios. Thereafter, the markers were divided according to the (Mendelian) segregation ratio (Table 1) in the progeny.

Diving the markers according to their segregation ratio resulted in four datasets: a SxN dataset for both P1 and P2 (with an expected segregation ratio of 1:1), a DxN dataset (1:4:1) and a SxS and SxT dataset (1:2:1; SxS and SxT are in one dataset). The SxN dataset contains 1547 SNPs for P1 and 1733 SNPs for P2, the DxN dataset contains 471 SNPs for P1 and 424 for P2 (Maliepaard *et al.*, n.d.) and the SxS dataset contains 956 SxS SNPs and 445 SxT SNPs. To give a quick impression of what these datasets contain, an example of the SxN dataset of P1 is given in Figure 2 and the dataset is briefly explained below.



Row Labels	Parental	PhysChrom	JulyChrom	PhysPos	JulyChrom	ChromJM	HaploGro	101871-1	101871-2	101871-1	101871-2	101871-2	101871-2	101871-0	101871-0	101871-0	101871-0	101871-2	101871-2
PotVar0122353	10		1		0	1	1	1	1	0	0	1	0	0	1	0	0	0	1
PotVar0122386	10		1		0	1	1	1	1	0	0	1	2	0	1	0	0	0	1
PotVar0122388	10		1		0	1	1	1	1	0	0	1	2	1	1	0	0	0	1
solcap_snp_c2_31041	10		1		0	1	1	1	1	0	0	1	2	0	1	0	0	0	1
PotVar0122414	34		1		0	1	1	3	3	4	4	3	4	3	4	0	0	0	1
PotVar0122423	34		1		0	1	1	3	3	4	4	3	4	4	4	1	0	0	1
PotVar0072076	34	ST4.01ch01		1606718		1	1	3	3	4	4	2	4	4	4	1	0	1	1
solcap_snp_c2_6683	34	ST4.01ch01		1828457		1	1	3	3	4	4	2	3	4	4	1	0	1	1
solcap_snp_c2_6713	34	ST4.01ch01		2068305		1	1	3	3	4	4	2	3	4	4	1	0	1	1
PotVar0044823	10	ST4.01ch01		2505069		1	1	1	1	0	0	1	1	0	0	1	0	NA	1
PotVar0045000	10	ST4.01ch01		2857296		1	1	1	1	0	0	2	1	0	0	1	0	1	1
PotVar0045260	34	ST4.01ch01		3957106		1	1	3	3	4	4	2	2	4	4	3	0	1	1
PotVar0045662	34	ST4.01ch01		4044052		1	1	3	3	4	4	3	3	4	4	3	0	1	1
PotVar0100717	34	ST4.01ch01		20792200		1	1	3	3	4	4	3	4	4	4	3	0	1	1
PotVar0100729	34	ST4.01ch01		20792295		1	1	3	3	4	4	3	4	3	4	3	0	1	1
PotVar0100762	34	ST4.01ch01		21154215		1	1	3	3	4	4	3	4	4	4	3	0	1	1
PotVar0122547	34	ST4.01ch01		29683413		1	1	3	3	4	4	2	4	4	4	3	0	1	1
PotVar0122550	10	ST4.01ch01		29683494		1	1	1	1	0	0	1	0	0	1	0	0	1	1
PotVar0014240	34	ST4.01ch10		38714113		1	1	3	3	4	4	3	4	3	3	1	0	1	1
solcap_snp_c1_14649	10	ST4.01ch01		41947422		1	1	1	1	0	0	1	1	1	1	1	0	1	1
PotVar0114353	34	ST4.01ch01		42372618		1	1	3	3	4	4	3	4	4	4	1	0	1	1
PotVar0102229	34	ST4.01ch01		51293577		1	1	3	3	4	4	3	4	3	4	1	0	1	1
PotVar0018832	34	ST4.01ch01		57551014		1	1	3	3	4	4	3	3	3	3	1	0	1	1
PotVar0049692	34	ST4.01ch01		61774637		1	1	3	3	4	4	3	3	4	3	1	0	1	1
PotVar0032887	34	ST4.01ch01		64375922		1	1	3	3	4	4	3	3	4	4	1	0	0	0
PotVar0032906	14	ST4.01ch01		64376110		1	1	1	1	4	4	1	1	3	3	1	0	2	1
solcap_snp_c2_13650	34	ST4.01ch01		65277443		1	1	3	3	4	4	3	3	3	3	1	0	2	2
PotVar0006246	34	ST4.01ch01		71510896		1	1	3	3	4	4	2	3	4	4	0	0	0	0
PotVar0006356	34	ST4.01ch01		71796719		1	1	3	3	4	4	2	3	4	4	0	0	0	1
PotVar0061043	34	ST4.01ch01		81814306		1	1	3	3	4	4	2	4	4	4	0	0	0	1
PotVar0060753	10	ST4.01ch01		82029149		1	1	1	1	0	0	2	0	0	1	0	0	0	1
PotVar0060678	34	ST4.01ch01		82062326		1	1	3	3	4	4	2	4	4	4	0	0	0	1
PotVar0060667	10	ST4.01ch01		82062628		1	1	1	1	0	0	2	2	0	0	0	0	0	1
PotVar0035378	10	ST4.01ch01		84051192		1	1	1	1	0	0	2	0	0	0	0	0	0	1
PotVar0018564	10	ST4.01ch12		57355150		12	4	1	1	0	0	0	1	0	0	1	1	0	1

Figure 2. Part of the SxN dataset of P1. This dataset contains the marker names, the dosages and other information.

In Figure 2, the different symbols represent different types of information:

A) represents the names of the SNP markers (Vos *et al.*, 2014).

B) stands for the parental dosages. This can be simplex x nulliplex (10), triplex x quadruplex (34), triplex x nulliplex (30) or simplex x quadruplex (14), which all have the same segregation ratios. Obviously, the segregating allele is segregating in P1.

C) represents the physical chromosome on which the SNP markers are supposed to be located. The ST4 format is used for information about physical chromosomes based on the sequence, while to others format types come from different information sources.

D) gives information of the physical position of the marker based on the genome assembly in base pairs. When a 0 is given, it means that this marker has not been given a position on the physical sequence map yet.

E) stands for the chromosome to which the markers are assigned to by JoinMap. Although JoinMap is designed for linkage mapping in diploids, it can handle coupling SxN data. Although, the repulsion estimate for the recombination frequency of SxN marker is wrong, the assignment still works.

F) represents the homolog to which a certain marker belongs. This is based on several types on information, of which JoinMap is the main information source. As mentioned above, JoinMap can handle coupling SxN markers and will give chromosome assignment. JoinMap will map the markers along this chromosome. From the position of this linkage map, the homologs can be deduced (Hackett *et al.*, 2013; Maliepaard, personal communication). However, in some cases JoinMap will not give four homologs, but more than that. In those cases other information, like the physical position and DxN data was used to assign the markers to the homologs.

G) gives the assigned dosages for the two replicates of each of the parents by fitTetra.

H) gives the assigned dosages for the three grandparents and the single great-grandparent by fitTetra.

J) gives the assigned dosages of the 237 offspring plants by fitTetra.

The four datasets have a slightly different format, and the differences compared to the SxN dataset of P1 is briefly explained here:

The SxN dataset for P2 has does not contain information about the chromosomes and homologs assigned by JoinMap (E & J). Also it does not contain the parental dosages (B) but this can be deduced from the dosages of the two replicates for each parent (G). Furthermore, the missing values in this dataset are split into two categories, namely the missing values caused by double reduction (see Assumptions) and the missing values caused by an incorrect dosage assignment or no dosage assignment by fitTetra. In addition to this, it has a summary about these missing values for each SNP marker. The DxN dataset for P1 and P2 look similar to the SxN dataset of P2.

The SxS dataset has information about the parental dosages (B) as well as the information of the assignment of each marker to a certain chromosome JoinMap (E), but not the assignment of the homologs (F). Furthermore, the missing values are categorized into two groups mentioned above, but are not summarized.

However, in the SxS dataset the SxT and TxS markers were transformed incorrectly. Therefore, another dataset, with the raw-dosages, was created. This dataset contains all the markers with their names (A), and the correctly transformed dosages (J). The raw dosages dataset is therefore mainly used for TxS markers.

Halfway during the thesis, another dataset became available, namely a dataset which contains an updated version of the physical positions (Figure 3). From Chapter 6 onwards, this dataset is used. In Figure 3, the different symbols represent different types of information:

A) represents the names of the SNP markers (Vos *et al.*, 2014).

B & D) represent the physical chromosome on which the SNP markers are supposed to be located (sites about genome ref). ST4.01 is the chromosome assignment of version 1 of July 2012, ST4.03 is version 3 of September 2012.

C & E) gives information of the physical position of the marker based on the genome assembly (July 2012 and September 2012) in base pairs. When a #N/B is given, it means that this marker has not been given a position of the physical genome yet.

The 5 datasets were slightly edited before the usage in this thesis for practical reasons (Appendix 1).

A B C D E

markername	Scaffold	Position_On_Scaffold	Chromosom	Pseudomolec	Genome_Position	Chromosoomjuly	Positie op	chromosoom_july201	Positie op	chromosoom_Sept2012
I_locus_(Stan2)_d_LG10	NA	37	chr10	NA	1	chr10	#N/B	#N/B	#N/B	chr10	#N/B
I_locus_(Stan2)_e_LG10	NA	38	chr10	NA	1	chr10	#N/B	#N/B	#N/B	chr10	#N/B
Plocus_F35H_a1_LG11	NA	40	chr11	NA	1	chr11	#N/B	#N/B	#N/B	chr11	#N/B
Plocus_F35H_a2_LG11	NA	44	chr11	NA	1	chr11	#N/B	#N/B	#N/B	chr11	#N/B
Plocus_F35H_b1_LG11	NA	41	chr11	NA	1	chr11	#N/B	#N/B	#N/B	chr11	#N/B
Plocus_F35H_b2_LG11	NA	45	chr11	NA	1	chr11	#N/B	#N/B	#N/B	chr11	#N/B
Plocus_F35H_c1_LG11	NA	42	chr11	NA	1	chr11	#N/B	#N/B	#N/B	chr11	#N/B
Plocus_F35H_c2_LG11	NA	46	chr11	NA	1	chr11	#N/B	#N/B	#N/B	chr11	#N/B
Plocus_F35H_d_LG11	NA	43	chr11	NA	1	chr11	#N/B	#N/B	#N/B	chr11	#N/B
PotVar0000005	PGSC0003DME	1052941	chr01	18	13783937	ST4.01ch01	32843910	1052941	PGSC0003	ST4.03ch01	32843910
PotVar0000007	PGSC0003DME	1053010	chr01	18	13784006	ST4.01ch01	32843979	1053010	PGSC0003	ST4.03ch01	32843979
PotVar0000025	PGSC0003DME	1162026	chr01	18	13893022	ST4.01ch01	32952995	1162026	PGSC0003	ST4.03ch01	32952995
PotVar0000040	PGSC0003DME	1162576	chr01	18	13893572	ST4.01ch01	32953545	1162576	PGSC0003	ST4.03ch01	32953545
PotVar0000042	PGSC0003DME	1162694	chr01	18	13893690	ST4.01ch01	32953663	1162694	PGSC0003	ST4.03ch01	32953663
PotVar0000060	PGSC0003DME	1162953	chr01	18	13893949	ST4.01ch01	32953922	1162953	PGSC0003	ST4.03ch01	32953922
PotVar0000061	PGSC0003DME	1162982	chr01	18	13893978	ST4.01ch01	32953951	1162982	PGSC0003	ST4.03ch01	32953951
PotVar0000062	PGSC0003DME	1162993	chr01	18	13893989	ST4.01ch01	32953962	1162993	PGSC0003	ST4.03ch01	32953962
PotVar0000066	PGSC0003DME	1163049	chr01	18	13894045	ST4.01ch01	32954018	1163049	PGSC0003	ST4.03ch01	32954018
PotVar0000067	PGSC0003DME	3226779	chr01	18	15957775	ST4.01ch01	35017748	3226779	PGSC0003	ST4.03ch01	35017748
PotVar0000071	PGSC0003DME	3226870	chr01	18	15957866	ST4.01ch01	35017839	3226870	PGSC0003	ST4.03ch01	35017839
PotVar0000073	PGSC0003DME	3226882	chr01	18	15957878	ST4.01ch01	35017851	3226882	PGSC0003	ST4.03ch01	35017851
PotVar0000077	PGSC0003DME	3226928	chr01	18	15957924	ST4.01ch01	35017897	3226928	PGSC0003	ST4.03ch01	35017897
solcap_TUBER_SHAPE_c2	PGSC0003DME	31	chr10	778	1	chr10	#N/B	#N/B	#N/B	#N/B	#N/B
solcap_TUBER_SHAPE_c2	PGSC0003DME	32	chr10	778	1	chr10	#N/B	#N/B	#N/B	#N/B	#N/B

Figure 3. Dataset containing the physical position. This dataset contains two versions of the physical positions of the markers.

Now that origin of the data has been explained, it is time to take a look at it. The first thing to do is to look at how the different segregation type markers are distributed over the chromosomes (Figure 4). It should be taken into account that these markers need to cover 96 homologs (2 parents x 12 chromosomes x 4 homologs). On a first glance it seems that the marker density is good enough for mapping and integration but when a closer look is taken at the density of the markers, it can be noted that, for example, the coverage of duplex x nulliplex markers of P1 on chromosome 2 is not high. This can have implications for clustering and ordering the markers. Furthermore, it is good to point out that the resolution of the map does not depend on the amount of markers but it depends on the amount of recombination events, which in turn depends on the amount of offspring. In addition to population size, the spacing of the markers is also important.

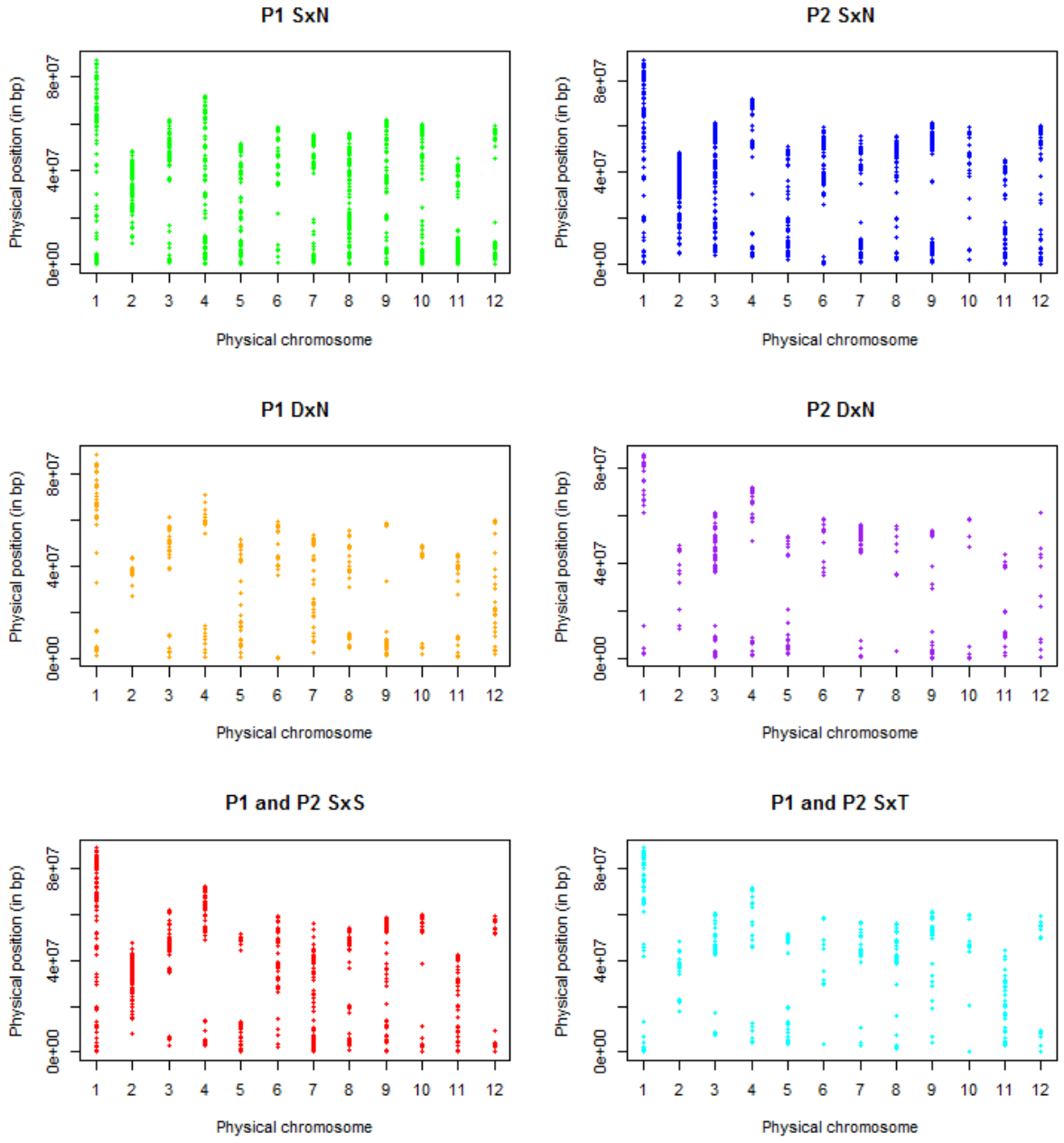


Figure 4. Distribution of the marker types over the physical chromosomes. The different marker types are plotted against their physical position on the chromosomes. This gives some indication of coverage.

Assumptions

Linkage mapping is a form of genetic modelling. During a modelling procedure, assumptions are made and it is good to keep these assumptions in mind while doing the linkage mapping and test, whenever possible, if the assumptions are violated. Ripol *et al.* (1999) summarized the following assumptions for linkage mapping in tetraploids:

- Assumption 1: "homologous chromosomes segregate from each other at meiosis".
- Assumption 2: "non-homologous chromosomes segregate independently".
- Assumption 3: "no segregation distortion".
- Assumption 4: "no cross-over position interference".
- Assumption 5: "no chromatid interference".
- Assumption 6: "each locus can belong to only one homologous group".
- Assumption 7: "homologous chromosomes form random pairs at meiosis".
- Assumption 8: "no double reduction — each chromosome will segregate from its pair at meiosis into a different gamete".

As a consequence of assumption 1, all the gametes should have one of every kind of chromosome. Also aneuploidy should not be possible. Assumptions 2 and 3 lead to equal probability for every homolog to be transmitted to the gametes and absence of selection at gamete or zygote level. Assumption 4 means that recombination events are randomly distributed over the genome and Assumption 5 means that all sister chromatids are equally likely to be involved in a recombination event (Zhao *et al*., 1995). In reality, hot-spots and cold-spots are observed where recombination happens more often or more rarely (Petes, 2001). In turn, this can lead to non-linearity when the genetic maps are compared to the physical maps. Assumption 6 is related to the SNPs used. These SNPs should only be present on one location in the genome. This assumption can therefore be violated when a certain SNP is duplicated and can thus be found on multiple locations across the genome. Assumption 7 states that the potatoes act like an autopolyploid since all the homologs have an equal chance to pair with the other homologs (and thus no preferential pairing occurs). This also means that during meiosis mainly bivalents are formed in contrast to multivalents (Gavrilenko *et al.*, 2007). According to literature potatoes are considered to be autopolyploid (Bradshaw, 1994) and therefore this is a safe assumption. As a consequence of Assumption 7, Assumption 8 states that no double reduction occurs throughout the genome. Bourke *et al.* (2015) and Haynes & Douches (1993) observed that double reduction occurs in potato.

In the addition to the assumption Ripol *et al.* (1999) made, there are a few more assumptions in this thesis with regards to mapping and map integration of a tetraploid species:

- Assumption 9: the pairwise recombination estimates are accurate.
- Assumption 10: the residuals of the pairwise recombination estimates are independent of each other.
- Assumption 11: the recombination rate is equal in both parents.
- Assumption 12: mapping functions designed for diploids are applicable to tetraploids.
- Assumption 13: there is a single correct order of markers for the cross as a whole.

During this thesis, pairwise recombination frequencies were calculated, while some studies suggest that the multipoint recombination fractions could correspond more closely to the physical distance between markers (Liu, 1997a), although in general there is no fixed relationship between the physical distance and recombination frequency of markers, since the commonly used mapping function do not take the physical location or the genome region into account (Liu, 1997d). Furthermore, the residuals of the recombination frequencies are treated as independent of each other for the linear regression approach used in Chapter 5. For the calculation of recombination frequency of SxS and SxT markers (that are across both parents), it is assumed that the recombination frequencies in both parents are equal. This is also a common assumption in linkage mapping of diploids. It is known for other plant species that this might not always be true (Plomion & O'Malley, 1996), however, if unequal recombination frequency in the parents is also a phenomenon in potato is currently not known, although very unlikely. In this thesis, the Haldane mapping function is used. This mapping function, like all other mapping functions, was designed for diploids and one could argue whether it can also be applied to tetraploids (Van Ooijen, personal communication). Furthermore, for integration, there is the assumption that there is an single correct order for the cross and that the homolog maps are all different samples of the single correct order (Yap *et al.*, 2003).

Programmes

R

R is a language designed for statistical analysis and graphics (R Core Team, 2012). R is based on the S language, but has since then become more dominant. R is an interactive language and allows the users to write their own scripts and functions for powerful analysis of the data. R and its source code are freely available and this is one of the key factors of its success. RStudio has a more user friendly interface when compared to R (Verzani, 2011). For this thesis both R version i386 3.1.2 and RStudio version 0.98.1102 are used.

R has a highly active community. This community is not only active on help-forums, but also in the creation of packages for R. Packages include specialized functions and corresponding documentation. Currently there are over 6,000 packages on the Comprehensive R Archive Network (CRAN), on which R packages are stored (Wickham, 2015). The variety of R packages is tremendous and this is one of the reasons why R is popular. During this thesis several packages are used, namely abind (Plate & Heiberger, 2011), MASS (Venables & Ripley, 2002), R/qtl (Broman *et al.*, 2003), Combinat (Chasalow, 2005), RVAideMemoire (Hervé, 2014), NMF (Gaujoux & Seoighe, 2010), flexclust (Leisch, 2005). Furthermore the package fitTetra was used to acquire the dosages (Voorrips & Gort, 2011), which are explained in the Data chapter. LPmerge (Endelman & Plomion, 2014) is used for the integration of homologs and will be further explained in Chapter 7.

JoinMap

The recombination frequencies between SxN markers in coupling phase can be calculated as if the markers came from a diploid backcross instead of a tetraploid. JoinMap, one of the most popular linkage mapping programmes (Cheema & Dicks, 2009), is designed for the calculation of diploid linkage maps, can thus be used for coupling phase SxN markers of tetraploids. In the past this has been done for several tetraploids crops like medicago (Julier *et al.*, 2003), rose (Vukosavljev *et al.*, 2014), and potato (Meyer *et al.*, 1998). JoinMap is developed by Kyazma B.V. and Biometris of the Wageningen University (Van Ooijen, 2006).

The user-friendly interface of JoinMap allows users to inspect errors by colouring the marker genotypes. This allows users to quickly check for labelling errors. Furthermore, the genotype frequencies and segregation ratios (Table 1) of every SNP can be inspected.

The second thing the programme does is grouping the markers in linkage groups. There are four criteria JoinMap can use (Van Ooijen, 2006).The first criterion is the pairwise recombination frequency. The second criterion is the LOD-score of the estimated pairwise recombination frequency compared with a recombination frequency of 0.5, corresponding to 'no linkage'. This is called the LOD for linkage. The third criterion is the G^2-statistic. The last criterion JoinMap can use is the independence LOD-score, which is a LOD score based on the G^2-test statistic and which is not affected by distorted marker segregation ratios as the LOD for linkage is. The users can choose which criterion JoinMap will use to group the markers into linkage groups. JoinMap allows different thresholds for grouping the SNP markers and in this way ideally the number of linkage groups should be equal to the number of chromosomes. In the case of potato, there are 12 linkage groups which represent the 12 chromosomes when the LOD-threshold for grouping between 4 and 6 is used (Maliepaard *et al.*, n.d.). If the physical position of the markers is available, a careful user should check whether the assigned linkage group of an individual marker in genetic mapping corresponds to the same linkage group on the physical chromosome.

Previous analysis showed that occasional differences were observed between the assignment of SxN markers to linkage groups and physical chromosomes (Maliepaard *et al.*, n.d.).

Once the linkage groups are determined, the linkage map can be calculated for each group. The user can choose between two algorithms by which the grouped markers are mapped, namely by linear regression or by maximum likelihood. Both methods should "lead to more-or-less the same map orders" (Van Ooijen, 2006). After mapping, the user can evaluate the mapping by several quality parameters.

As mentioned above, JoinMap is not designed for the analysis of tetraploids. However, when the recombination frequencies and LOD-scores of marker pairs are calculated beforehand and thereafter supplied to JoinMap, JoinMap is able to produce a map based on those recombination estimates. Furthermore, in the same fashion, JoinMap can integrate map of different population by the use of its linear regression algorithm, hence the name JoinMap (see Chapter 7).

JoinMap has no option to assign markers to homologs. Still JoinMap can be used for the assignment of markers to homologs. The approach is to assign markers to linkage groups, order the markers within this linkage group, then deduce the homologs and do the ordering again for a single homolog (Hackett *et al.*, 2013; Maliepaard, personal communication).

One of the advantages of JoinMap is, is that it presents maps based on MapChart (Voorrips, 2002). The visualisation of JoinMap by MapChart allows easy comparison of maps by visualisation.

MapChart

MapChart is a computer programme that displays linkage maps (Voorrips, 2002). The linkage maps are projected as vertical bars. Furthermore it allows for inclusion of QTL-projection. Mapchart is incorporated in JoinMap. In this thesis MapChart version 2.2 is used

PedigreeSim

PedigreeSim is a computer package that allows the simulation of offspring of crosses of multiple polyploidy levels (Voorrips & Maliepaard, 2012). These kinds of simulations prove to be very useful to check if genetic models and its assumptions are correct. PedigreeSim is used in this thesis to check the maximum likelihood estimators for the recombination frequencies and the corresponding likelihood functions as well.

Chapter 1: Mode of inheritance

Summary Chapter 1:

Potato is assumed to be an autotetraploid, which means that there is tetrasomic inheritance. The recombination frequencies between SxN markers are calculated under disomic and tetrasomic inheritance. The recombination frequency between SxN markers in coupling phase is the same under both models, but is different for SxN markers in repulsion. By performing a Binomial test, together with a Bonferroni correction to account for multiple testing, the mode of inheritance was investigated. Only a few repulsion marker pairs were found to be significant for disomic inheritance, meaning that the assumption of tetrasomic inheritance is not falsified. After this, the recombination frequencies allowing only for the tetrasomic inheritance were calculated.

Counting the offspring

In the Programmes, Data and Assumptions, the assumptions of this research are mentioned. One of the assumptions is that potato is an autotetraploid, which means that there is tetrasomic inheritance. This assumption is tested in this chapter by calculating the recombination frequencies and LOD-scores between SxN markers. This follows one of the approaches to study inheritance as indicated in an inheritance investigation of garden rose (Vukosavljev *et al.*, 2014).

The first obvious step in calculating the recombination frequencies between two markers is counting the number of offspring with a specific dosage. The number of offspring with a certain dosage combination of two markers are indicated as n_{xy}, with x being the dosage of marker A and y being the dosage of marker B. This notation deviates from previous literature, which mainly works with letters (a to d for example), however the notation here has the advantage that it can be applied to every pair of markers, regardless of its marker segregation type.

Preferential pairing and multiple testing

Based on the number of offspring with a certain dosage, linkage between markers can be estimated. Mather (1951) found that systematic association between two markers, and thus linkage, can be estimated by using a χ^2-test (Equation 1). Due to the large number of χ^2-tests, a multiple-testing correction is necessary. A common way to account for multiple testing is to adjust the α, commonly 0.05 or 0.01, to a stricter threshold by using the Bonferroni correction, which needs an α and the number of independent tests. A Bonferroni correction is used in genetic studies to gain an experiment-wide threshold (Cheverud, 2001; Lander & Botstein, 1989). In this thesis, the number of independent test is considered to be the number of chromosomes, and so the Bonferroni correction was calculated (Equation 2) to adjust α, the threshold for significance. In this case, significance means that the two markers tested are significantly linked.

Equation 1 $\chi^2 = {(n00 + n11 - n01 - n10)^2}/{n_{tot}} \sim \chi_1^2$

Equation 2 $\alpha' = {\alpha}/{k} = {0.01}/{12} = 0.0083$

* χ^2 is the Chi-square test statistic following, under the null hypothesis, a χ^2-distribution with 1 degree of freedom, n01 is the number of markers that have genotype aaaa and Bbbb, n10 is the number of markers that have genotype Aaaa and bbbb, n00 is the number of markers that have genotype aaaa and bbbb, n11 is the number of markers that have genotype Aaaa and Bbbb, ntot is the sum of n10, n01, n00 and n11, the A's (for example Aaaa) and B's (for example Bbbb) are not position dependent, α is the a significance threshold of 0.01, α' is the adjusted α and k is the number of independent test, in this case 12, since there are 12 chromosomes.

Recombination frequency and LOD-score between SxN Markers

If two markers are found to be significant linked according to Mathers test, the procedure is continued by calculating the logarithm of odds (LOD-score). The remarkable thing about the LOD-score of a pair of SxN markers is that the equation is the same regardless of the phase or mode of inheritance (Equation 3; Box 1).

In cases of complete linkage either n00+n11 or n10+n01 is equal to 0, since recombinants do not occur. A log of 0 is infinite and likewise calculations will return non-realistic values. Therefore Equation 3 (Box 1) is modified to cope with this situation. Although a log of 0 is infinite, this infinite value is multiplied by the amount of recombinants, which is 0 and thus the product of the two will also be 0. Therefore the recombinants are neglected in the new formula. This leaves the parental types, which are then equal to the total number of offspring. By doing so, Equation 4 (Box 1) arises and this formula is used when the recombination frequency is zero.

After calculating the LOD-score of a marker pair, the recombination frequencies for repulsion and coupling phase under disomic and tetrasomic inheritance are calculated. The recombination frequency in repulsion phase is different for the repulsion phase for tetrasomic inheritance (equation 6 in Box 1) and disomic inheritance (Equation 7 in box 1), while the recombination frequency for coupling phase is the same under both models (Equation 5 in Box 1).

All three estimates for the recombination frequency are calculated. If the estimate of r1 is the minimum of the three estimates, the two markers are considered to be in coupling phase with each other. If r1 is not the minimum of the three, then either r2 or r3 is chosen to be the correct estimate and the two markers are considered to be repulsion phase. Under the tetrasomic model, the expected proportion of recombinants (n00+n11) is 1/3 for completely linked markers (Qu & Hancock, 2001), while under the disomic model with complete preferential pairing there are no recombinants expected (r3=0). To determine whether r2 or r3 is the correct estimate, a Binomial test was carried out for the repulsion marker pair. In this test, the recombinants (n00+n11) are compared to 1/3. Again due to the many marker pairs tested, a multiple testing correction is needed. Within one chromosome (one linkage group) there are 36 linkages (8+7+6+5+4+3+2+1) possible between two markers, when a chromosome arm is taken as the entity of independent tests. Of all these linkages, 8 are in coupling within the same chromosome arm, 4 are in coupling linkages on different chromosome arms (but still on the same homolog), while the majority of the linkages (24) is across the different homologs (Figure 5). Only the repulsion linkages are of interest to test for preferential pairing with a Binomial test. The amount of possible repulsion linkages is used in the Bonferroni correction (Equation 8).

Equation 3 $\alpha' = {}^{\alpha}/_{k} = {}^{0.01}/_{24} = 0.00417$

*α is the significance threshold of 0.01, α' is the adjusted α and k is the number of independent test, in this case 24, since there are 24 repulsion linkages within one chromosome (Figure 5).

If the observed frequency of recombinants is significantly lower than 1/3, the two markers are evidence for preferential pairing, while on the other hand, when the test is not significant, the two markers are in repulsion under the tetrasomic model or in repulsion in disomic inheritance at a large distance.

If the null-hypothesis is accepted (tetrasomic inheritance), r2 is estimated to be the correct recombination frequency. When r2 is below zero, r2 is set to 0, following the approach by Hackett *et al.* (1998), to get an allowed estimate between 0 and 0.5. This is done since an under estimation of the recombination frequency is better than an over estimation (Hackett *et al.*, 1998). Negative estimates for r2 can happen and when this happens often, this could indicate a violation of the assumptions (Wu *et al.*, 1992). Hackett *et al.* (1998) suggest that setting the recombination frequency at 0 when there is a negative estimate of the recombination frequency might shorten the integrated linkage map when integration is done with a regression method, or sometimes otherwise called, a statistical pooled approach (Jackson *et al.*, 2005; Chapter 7). However, it was mentioned that "smaller true recombination fractions may give smaller negative estimates, and therefore that using zero as an estimate, regardless of the size of the negative estimator, is losing some information."

The procedure, as described above, was carried out for all SxN marker pairs for both parental types.

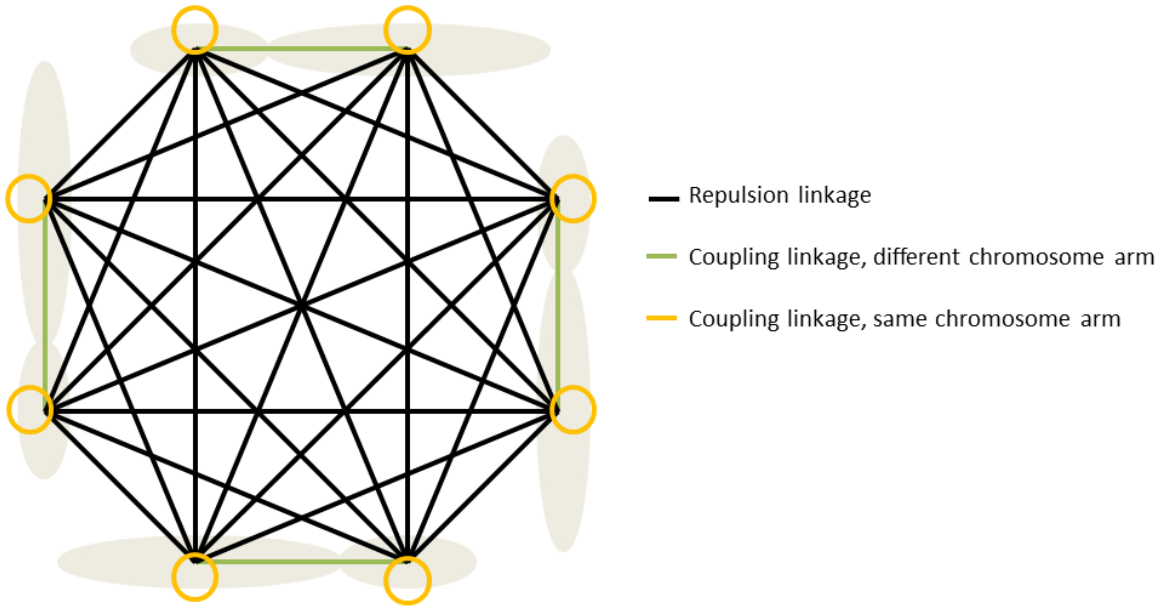


Figure 5. Possible linkages within one chromosome (or linkage group) of one parent. Considering, two chromosome arms per homolog, there are 36 linkages possible, of which 8 are in coupling phase on the same chromosome arm, 4 in coupling phase on different chromosome arms of the same chromosomes and 24 repulsion linkages

Box 1. Recombination frequency and LOD calculations between two SxN markers. In this box the calculations for the LOD-score between two SxN markers are shown for the different-phase situations are shown.

Simplex x nulliplex
Simplex x nulliplex

Equation 4 $LOD = \text{ntot} * \log10(^{2}/_{\text{ntot}}) + (\text{n00} + \text{n11}) * \log 10(\text{n00} + \text{n11}) + (\text{n10} + \text{n01}) * \log10(\text{n10} + \text{n01})$

Equation 5 $LOD_{r=0} = ntot * \log 10(^{2}/_{ntot}) + ntot * \log 10(ntot) = ntot * \log 10(^{2}/_{ntot} * ntot) = ntot * \log10(2)$

Coupling
Aaaa x aaaa
Bbbb x bbbb

Equation 6 $r1 = \frac{\text{n01+n10}}{\text{ntot}}$

Repulsion
Aaaa x aaaa
bBbb x bbbb

Equation 7 $r2 = \frac{2*(\text{n00+n11})-(\text{n10+n01})}{\text{ntot}}$

Equation 8 $r3 = \frac{\text{n11+n00}}{\text{ntot}}$

* LOD is the logarithm of odds ratio, r1 is the estimate of the recombination frequency of two SxN markers in coupling phase, r2 is the estimate of the recombination frequency of two SxN markers in repulsion phase under tetrasomic inheritance, r3 is the estimate of the recombination frequency of two SxN markers in repulsion phase under disomic inheritance (or preferential pairing), n01 is the number of markers that have genotype aaaa and Bbbb, n10 is the number of markers that have genotype Aaaa and bbbb, n00 is the number of markers that have genotype aaaa and bbbb, n11 is the number of markers that have genotype Aaaa and Bbbb, ntot is the sum of n10, n01, n00 and n11, the A's (for example Aaaa) and B's (for example Bbbb) are not position dependent.

Results

The majority of the repulsion pairs are in repulsion under tetrasomic inheritance while only a few marker pairs show signs of preferential pairing under disomic inheritance (Appendix 2). From this, it can be concluded that there is indeed no preferential pairing as was assumed and the tetrasomic model is the best model, which corresponds to literature (Bradshaw, 1994). Thus, the recombination frequencies and LOD-scores were calculated again by only considering the tetrasomic estimators (r1 and r2).

Conclusion Chapter 1:

In this chapter, the mode of inheritance was investigated by calculating the recombination frequencies of SxN markers under the tetrasomic and disomic model. Only a few repulsion marker pairs were found to be significant for disomic inheritance, meaning that the assumption of tetrasomic inheritance is good. After this, the recombination frequencies under the tetrasomic model only were calculated.

Chapter 2: Clustering of SxN markers along chromosomes

Summary Chapter 2:

The SxN markers are assigned to linkage groups based on the LOD-scores, the measurement of linkage. The approach used here follows the approach of JoinMap. The SxN markers of P1 were clustered at a LOD-threshold of 5, while the SxN markers of P2 were clustered at a LOD-threshold of 5.15. In both cases this resulted in 12 linkage groups, corresponding to the number of chromosomes. The results of the clustering method were compared with JoinMap and the physical positions. The clustering and the clustering of JoinMap gave identical results, while there were some deviations between the clustering and the physical chromosomes. In total 1545 SxN markers for P1 and 1727 SxN markers for P2 were clustered into linkage groups.

Algorithm for clustering SxN markers into linkage groups

In the previous chapter, the recombination frequencies of SxN markers were calculated. The next step in the mapping process is assigning each SxN marker to a linkage group. This is necessary since markers that are not from the same linkage map inherit independently and therefore a linear map between those markers is not possible or meaningful (Van Ooijen & Jansen, 2013a). Ideally, the clusters (or linkage groups) are the same number as the number of chromosomes.

One of the cluster criteria to group markers is based on the LOD-score of linkage, the measurement for the likelihood of linkage. JoinMap presents a foldable tree by which the user can check the robustness of the clustering. Van Ooijen & Jansen (2013a) describe the easy procedure how this is done by the software:

- *Step 1a*: start with the first pair of markers.
- *Step 1b*: assess the next pair of markers.
- *Step 2*: if the marker pair is unlinked, continue with *step 1b*.
- *Step 3*: if the marker pair is linked, there are four situations possible:
    - *Step 3a*: if one of the markers has already been assigned to a linkage group. → assign the other marker to this linkage group as well.
    - *Step 3b*: if both markers have been assigned to different linkage group. → combine the linkage groups as one linkage group.
    - *Step 3c*: if both markers have been assigned to the same linkage group. → do nothing
    - *Step 3d*: if both markers have not been assigned to a linkage group yet.→ create a new linkage group and assign both markers to it.
- *Step 4*: Continue with *step 1b* until all marker pairs are accounted for.

Clustering thresholds

By following this procedure every marker pair is only considered once for each given linkage-threshold which increases the computational efficiency of the procedure. Different kinds of linkage measurements, like the test-statistic of Mather used in Chapter 1, are possible depending on the preference of the user. Here the LOD-score of linkage, as was calculated in Chapter 1, is used as a linkage-threshold to determine the amount of linkage groups as this is also one of the clustering criteria of JoinMap. Therefore, this will make comparison between the clustering method of JoinMap and the clustering method described above meaningful. The LOD-thresholds considered here are 3, 4, 5, 6, 7, 8 for P1 and 3, 4, 5, 5.1, 5.15, 5.2, 5.3, 5.4, 5.5, 6, 7, 8 for P2. The reason why these LOD-thresholds were chosen is described below. The result of each clustering threshold was compared to the physical positions and, for P1, also with the clustering of JoinMap (since the clustering by JoinMap was only available for P1 at the time (see Data)).

To quantify the comparison between the clusters, the Rand Index is used. The Rand Index is a measurement for the similarity between two clustering methods, which, in this case, relates to the accuracy (Rand, 1971). The value for the Rand Index ranges between 0 and 1 with 1 indicating that the two clustering methods are identical while a 0 indicates that there is no agreement between the two clustering methods (Equation 9).

Equation 9 $$R = \frac{a+b}{a+b+c+d}$$

* Two clustering methods are compared with the Rand Index, a is the number of pairs that ended up in the same cluster by both clustering methods, b is the number of pairs that ended up in different clusters by both clustering methods, c is the number of pairs that are in the same clusters by the first clustering method but are in different clusters by the second clustering method, d is the number of pairs that are in different clusters by the first clustering method but are in the same clusters by the second clustering method.

Clustering results

The Rand Index of the comparison between the clustering method used here and the physical chromosomes was 0.978 for P1 at a LOD-score of 5 and 0.982 for P2 at a LOD-score of 5.15 (Figure 6), meaning that the clustering method is very similar to the grouping according to the physical chromosomes. In both cases, the Rand Index was the maximum of all LOD-thresholds considered. The Rand Index of the clustering at a LOD of 5 was not optimal for P2 and did not contain 12 linkage groups, therefore, a LOD-threshold slightly higher than a LOD of 5.15 was chosen (Figure 6). With the optimal LOD-thresholds chosen, the number of clusters (or linkage groups) is equal to the number of chromosomes and this fact is of great importance (which could otherwise be used as criterion for the selection of the LOD-threshold). An explanation for the fact that the Rand Index was not 1 could be that the marker assignment to physical chromosomes was not correct for some markers (Appendix 3).

Furthermore, the clustering method of JoinMap for P1 was compared with the clustering method used here. The Rand Index was 1 at a LOD-threshold of 5. This means that the clustering method used by JoinMap and the method used here gave identical clusters.

In total 1545 SxN markers of P1 and 1727 SxN markers of P2 were assigned to the respective linkage groups (Table 2). Two SxN markers, PotVar0055484 and PotVar0077706, were not assigned to linkage groups in P2 and two SxN markers, PotVar0079248 and PotVar0059901 were not assigned to linkage groups n P1. This means that those four markers were not significantly linked with any other marker.

Table 2. Total number of SxN markers assigned to a certain linkage group or chromosome. The SxN markers are assigned on the basis of a LOD-threshold of 5 for P1 and 5.15 for P2.

	P1		P2	
Chromosome	**Cluster**	**Markers**	**Cluster**	**Markers**
1	2	159	5	183
2	3	155	1	235
3	4	109	2	225
4	5	144	8	134
5	6	192	10	195
6	7	76	7	152
7	8	105	3	134
8	1	186	4	104
9	9	117	11	107
10	10	83	12	43
11	11	137	9	129
12	12	82	6	86
Total		1545		1727

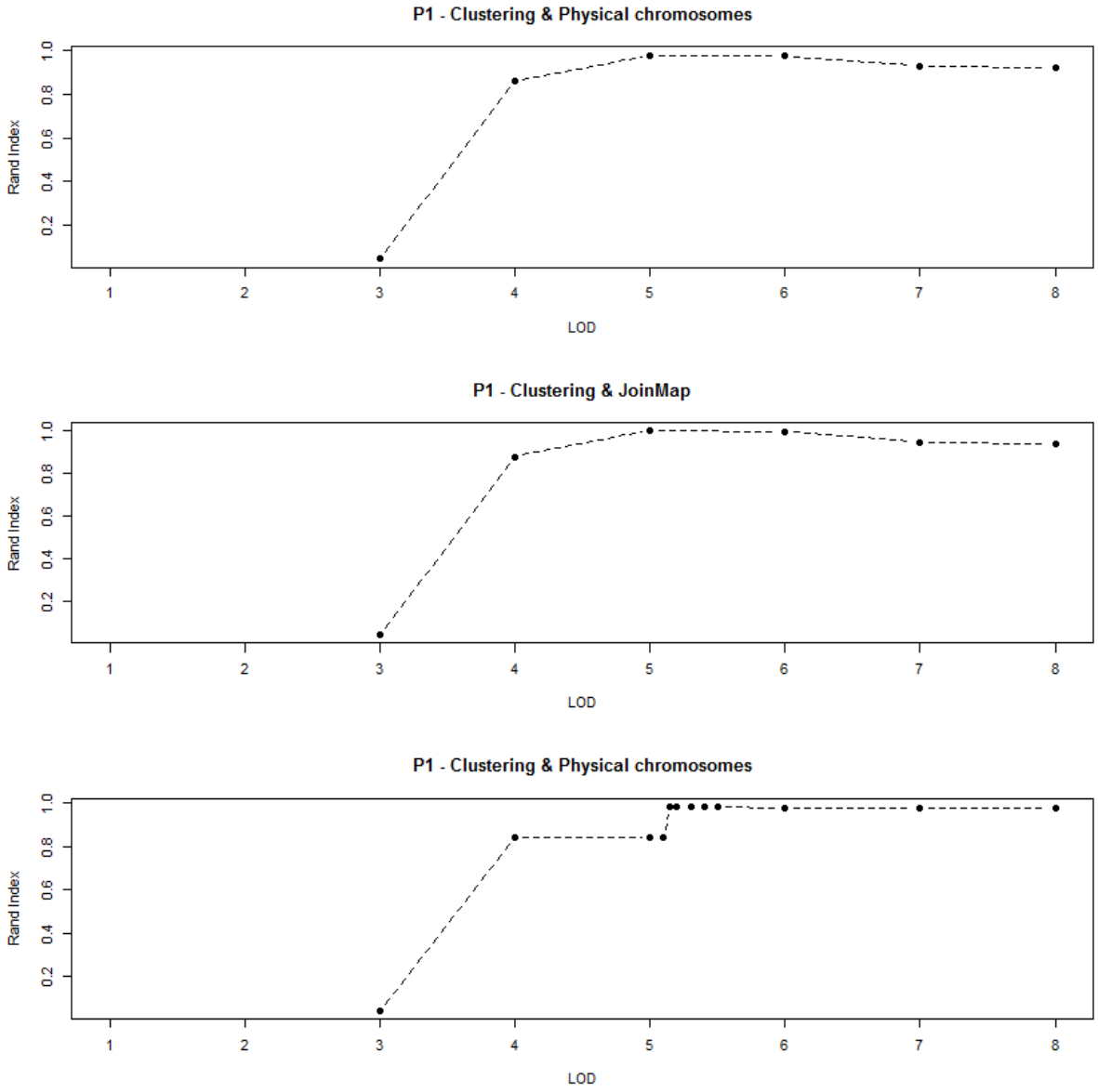


Figure 6. Rand Index of the clustering method used in this thesis compared with the physical positions and JoinMap. P1 is compared with both the physical chromosomes and JoinMap, while P2 is only compared with the physical chromosomes. The maximum of the Rand Index was at LOD 5 for P1 for both comparisons, while the maximum Rand Index for P2 was at 5.15 for the comparison with the physical chromosomes.

Conclusion Chapter 2:

The SxN markers were clustered in 12 linkage groups, corresponding to the number of chromosomes. The clustering method used in this thesis and the clustering method of JoinMap gave identical results, while there were some deviations between the clustering method and the physical chromosomes. This means that the clustering method is a good method of clustering SxN markers along linkage groups. In total 1545 SxN markers for P1 and 1727 SxN markers for P2 were clustered into linkage groups.

Chapter 3: Clustering of SxN markers along homologs

Summary Chapter 3:

In this chapter, the SxN markers are assigned to homologs. This is done by constructing a so-called phase-tree, which is based on the phase information of a SxN marker pair (coupling or repulsion). For most chromosomes, the phase-tree method led to four distinctive homologs to which the SxN markers were assigned. However, in some cases five or six sub clusters (or artificial homologs) were found. In those situations, the sub clusters were put together into homologs based on linkages between DxN and SxN markers that closed the gap between the artificial homologs. In two occasions other information sources had to be used to end up with four distinctive homologs. In addition, by using this methodology the DxN and SxS markers were assigned to chromosomes and homologs.

Clustering of SxN markers into homologs with a phase-tree

In the previous chapter the SxN markers were clustered into the linkage groups (corresponding to chromosomes). The next step is to assign the markers to homologs and this step is unique for polyploids.

A previous approach to assign SxN markers to homologs was to use JoinMap to estimate the homologs. When JoinMap assigned the SxN markers to linkage groups and the SxN markers within this linkage group were ordered, the homologs can be deduced from the map positions (Hackett *et al.,* 2013; Maliepaard, personal communication). However, this approach was laborious. Therefore, there is a desire to have software that can assign markers to homologs within the R pipeline. A new approach to estimate the homologs is given in this chapter.

In Chapter 1 information about the phase of marker pairs (coupling or repulsion) has been gathered. The phase information provides much information about the homologs, since markers on the same homolog should ideally be in coupling phase with each other while being in repulsion with markers on other homologs. Markers close together on the same homolog have a similar phase-pattern, meaning that linked markers are in coupling or repulsion with regards to other markers. To make use of this pattern, a phase matrix was constructed based on the phase-information. The marker pairs in coupling phase were given the value of 1 while the marker pairs in repulsion phase were given the value of 0.1. Although the actual values given are not of great importance, the fact that those values are dissimilar is important.

After this phase matrix was constructed, the Euclidean distances were calculated between the markers in the matrix. This resulted in a distance matrix, which was used to construct a hierarchical tree, or a phase-tree. The hierarchical tree produced from SxN markers within one linkage group gave usually four distinct sub-clusters (or homologs; Table 3), as can be seen, for example, in the hierarchical clustering of chromosome 11 of P2 (Figure 7). By careful visual inspection of the trees of every chromosome, the trees were cut into four, five or six sub clusters (or homologs) (Appendix 4).

For some chromosomes the numbers of SxN markers are more or less distributed over the homologs while on other chromosomes some homologs are over- or underrepresented (Table 3).

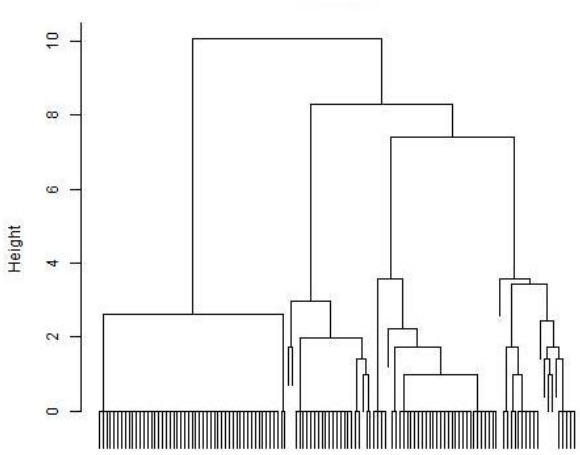


Figure 7. The phase-tree of chromosome 11 of P2. The phase-tree of chromosome 11 of P2 clearly splits into 4 distinctive homologs (or sub clusters). The phase-trees of the other chromosomes can be found in Appendix 4.

Table 3. Number of SxN markers divided over chromosomes and homologs based of the clustering method based on the LOD-threshold and based on the phase-tree. Some chromosomes have more than 4 homologs, which are therefore called sub clusters and are in those situations not biologically meaningful.

	P1							**P2**					
Chromosome	**Cluster**	**Sub cluster**						**Cluster**	**Sub cluster**				
		1	*2*	*3*	*4*	*5*	*6*		*1*	*2*	*3*	*4*	*5*
1	*2*	44	55	34	26			*5*	61	60	25	24	13
2	*3*	46	44	34	31			*1*	55	75	89	8	8
3	*4*	6	11	23	12	57		*2*	42	110	47	26	
4	*5*	21	98	5	20			*8*	46	38	32	18	
5	*6*	50	101	32	9			*10*	76	69	34	10	6
6	*7*	12	35	15	14			*7*	50	28	51	23	
7	*8*	21	36	13	35			*3*	46	48	28	12	
8	*1*	99	24	40	20	3		*4*	24	37	31	12	
9	*9*	61	8	24	8	15	1	*11*	15	41	39	12	
10	*10*	22	14	13	30	4		*12*	23	11	5	4	
11	*11*	37	34	22	44			*9*	34	51	23	21	
12	*12*	20	27	15	20			*6*	14	20	19	25	8

Clustering of SxN markers into homologs by means of DxN linkage

Four chromosomes for each parent have more than four homologs (8 chromosomes in total). This is of course not desired and artificial. These artificial homologs have to be merged together into biologically meaningful homologs. One method of doing this is by looking at DxN markers that could bridge the gaps within a homolog (Figure 8). When a DxN marker shows significant linkage to three sub clusters instead of two, then this is an indication that two of the three sub clusters are actually the same homolog. Concluding that two sub clusters are actually the same homolog based on just a single DxN marker alone is not considered to be reliable (but could theoretically be enough in some situations). Therefore, recombination frequencies are calculated between all pairs of DxN and SxN markers and are considered for a chromosome in cases where there were 5 or more homologs.

The number of individuals in each of the dosage classes of DxN markers and SxN markers are counted and the recombination frequencies for coupling and repulsion phase are estimated from these (Equation 12 and 14 in Box 2). The minimum recombination frequency (of the repulsion and coupling estimate) is estimated to be the most likely estimate. Thereafter, the LOD-score corresponding to the minimum recombination frequency is calculated (Equation 13 and 15 in Box 2). The DxN markers are assigned to homologs based on the majority of linkages with a SxN marker with a LOD-score equal or higher than 3. The DxN markers are assigned to the two homologs based on the majority of coupling-linkages within the same chromosome if the total number of coupling linkages were more than 1. Whenever a chromosome had more than 4 homologs, the DxN marker was assigned 3 sub clusters (in case of 5 sub clusters within the chromosome, when there were coupling linkages with 3 sub clusters) or 4 (in case of 6 sub clusters, when there were coupling linkages with 4 sub clusters).

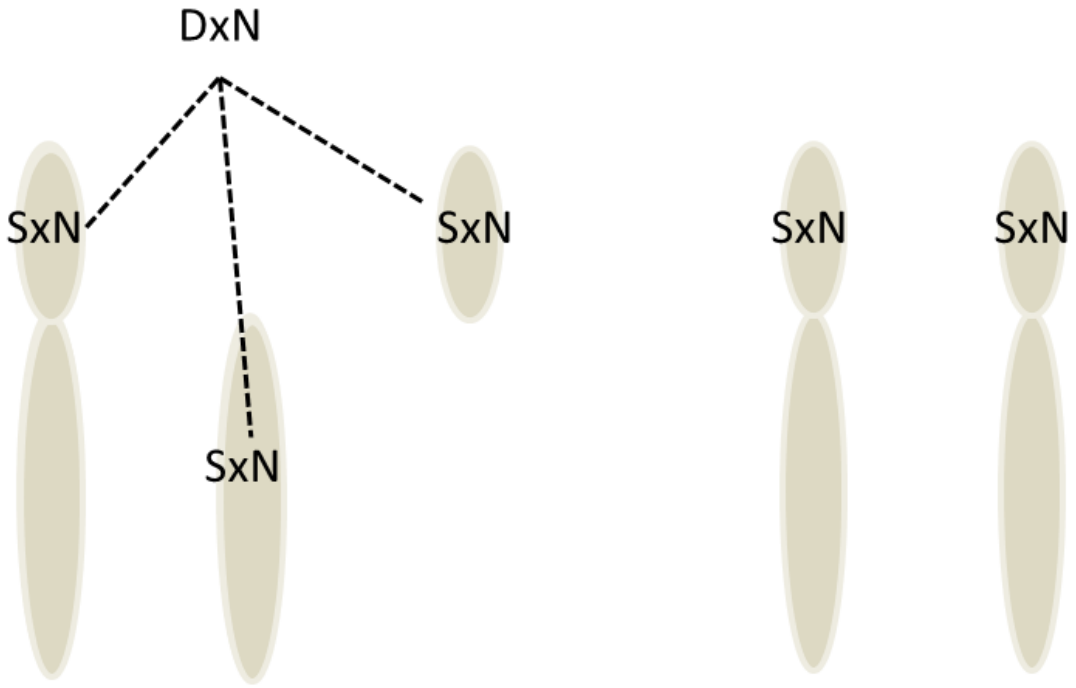


Figure 8 DxN and SxN linkage that can bridge the gaps between sub clusters of the same homolog. The DxN marker that has yet to be assigned to a homolog has coupling linkages with 3 (out of the 5) homologs. This indicates that 2 of the 3 homologs should be merged into a single biologically meaningful homolog.

Box 2. Recombination frequency and LOD calculations between a SxN marker and a DxN marker. In this box the calculations for the LOD-score between a SxN marker and a DxN marker are shown. Furthermore, the different recombination frequency estimates for the different-phase situations are shown.

Duplex x nulliplex
Simplex x nulliplex

Coupling r1
AAaa x aaaa
Bbbb x bbbb

Equation 12 $r1 = \frac{n20+n01}{n00+n21+n20+n01}$

Equation 13 $LOD = (n00 + n21 + n20 + n01) * log10(2) + (n00 + n21) * log10(1 - r) + (n20 + n01) * log10(r)$

Repulsion r2
AAaa x aaaa
bbBb x bbbb

Equation 14 $r2 = \frac{n00+n21}{n00+n21+n20+n01}$

Equation 15 $LOD = (n00 + n21 + n20 + n01) * log10(2) + (n00 + n21) * log10(r) + (n20 + n01) * log10(1 - r)$

* LOD is the logarithm of odds ratio, r1 is the estimate of the recombination frequency of a DxN marker and a SxN marker in coupling phase, r2 is the estimate of the recombination frequency of DxN marker and a SxN marker in repulsion phase, n01 is the number of markers that have genotype aaaa and Bbbb, n20 is the number of markers that have genotype AAaa and bbbb, n00 is the number of markers that have genotype aaaa and bbbb, n21 is the number of markers that have genotype AAaa and Bbbb, the A's (for example Aaaa) and B's (for example Bbbb) are not position dependent.

After the DxN markers have been assigned to sub clusters (or homologs), the number of DxN markers are counted for each sub cluster, in cases when a chromosome had more than 4 sub clusters or artificial homologs. For example, chromosome 8 of P1 has 5 sub clusters. 19 DxN markers have been assigned to sub cluster 1, of which 4 are also assigned to sub cluster 2, 9 also assigned to sub cluster 3, 6 also assigned to sub cluster 4 and 4 also assigned to sub cluster 5 (Table 4). As was mentioned above, when DxN markers on two sub clusters inherited together, this is an indication that the two sub clusters are part of the same homolog. In other words, the DxN markers close the gap between the distantly linked SxN markers on the same homolog.

The counted number of DxN markers can also be presented as a percentage to make inspection, visualisation, and judgement more easy. The number of DxN markers assigned to a certain sub cluster as well as to another are divided by the total number of DxN markers assigned to this sub cluster (the diagonal). For example, the 4 DxN markers that were assigned to sub cluster 1 and sub cluster 2 make up 21% of the total DxN markers on sub cluster 1 and 19% on sub cluster 2 (Table 5). This can be done for every combination of sub clusters. For this chromosome, sub cluster 5 always (100%) inherits together with sub cluster 2, meaning that these are part of the same biological homolog. This was done similarly for all chromosomes with more than 4 sub clusters.

Table 4. The number of DxN markers assigned to sub clusters for chromosome 8 of P1. Every DxN marker has been assigned to three sub clusters.

	Sub cluster 1	Sub cluster 2	Sub cluster 3	Sub cluster 4	Sub cluster 5
Sub cluster 1	19	4	9	6	4
Sub cluster 2	4	21	9	8	6
Sub cluster 3	9	9	23	5	2
Sub cluster 4	6	8	5	19	0
Sub cluster 5	4	6	2	0	6

Table 5. The percentage of DxN markers assigned to a certain sub cluster over the total number of DxN markers assigned to that sub cluster for chromosome 8 of P1. The percentage of DxN markers is based on the number of DxN markers presented in Table 5. Due to rounding the percentages of the sub clusters might not add up to 100%.

	Sub cluster 1	Sub cluster 2	Sub cluster 3	Sub cluster 4	Sub cluster 5
Sub cluster 1	100%	19%	39%	31%	67%
Sub cluster 2	21%	100%	39%	42%	100%
Sub cluster 3	47%	43%	100%	26%	33%
Sub cluster 4	31%	39%	22%	100%	0%
Sub cluster 5	21%	29%	9%	0%	100%

For chromosome 3, sub cluster 1 inherits together with sub cluster 2 (100%). For chromosome 9 sub cluster 6 inherits always together with sub cluster 1 (100%) but in this case there is still one sub cluster too many. For chromosome 10, sub cluster 5 inherits together with sub cluster 2 and with sub cluster 4 (both 100%). The DxN markers of P2 that are assigned to the different sub clusters of chromosome 2 of show no clear inheritance of two homologs (with a maximum of 64%). For chromosome 1, sub cluster 5 always inherits together with sub cluster 4 (100%). For chromosome 5 the assigned DxN markers show no clear inheritance of two homologs (with a maximum of 57%). For chromosome 12, sub cluster 5 inherits always together with sub cluster 1 (100%).

As described above, the coupling information of the DxN markers with SxN information provided some information to combine sub clusters in cases where there are more than 4 sub clusters. However, the information is not conclusive in some other cases (meaning that sub clusters could not be merged based on coupling DxN information only). Therefore, also information about the repulsion phase of DxN with SxN is taken into account since the repulsion phase has the same information content.

However, the repulsion estimates did not provide a clear homolog inheritance either, and therefore this repulsion information was combined with the coupling information by adding the two percentages up (in this way a total of 200% can be reached).

For chromosome 1 of P2, the highest cumulative percentage was that of sub cluster 5 with sub cluster 4 with 152% while the second most likely candidate (sub cluster 5 with sub cluster 2) had only 132%, it can therefore be concluded that the most likely situation is that sub cluster 4 and 5 are part of the same homolog. For chromosome 5 of P2, the highest cumulative percentage was that of sub cluster 5 with sub cluster 4 with 132% while the second most likely candidate (sub cluster 2 with sub cluster 1) had only 115.8%, it can therefore be concluded that the most likely situation is that sub cluster 4 and 5 are part of the same homolog. For chromosome 9 of P1, the three pairs of sub clusters had a high cumulative percentage (sub cluster 6 with sub cluster 2 173%, sub cluster 4 with sub cluster 3 173% and sub cluster 2 with sub cluster 1 175%) and thus it cannot be concluded which sub clusters are actually one homolog. For chromosome 10 of P1, both sub cluster 5 with sub cluster 2 and sub cluster 5 with sub cluster 4 inherited together 200% of the time, and therefore it can also not be concluded if either sub cluster 4 or sub cluster 2 is a real homolog together with sub cluster 5.

Clustering of SxN markers into homologs by means of other types of information

To get four homologs in the last two cases, chromosome 10 and chromosome 9 of P1, the physical positions are considered. By plotting the physical positions of the SxN markers against the sub clusters, sub clusters could potentially be inferred (Figure 9). For chromosome 9 of P1, the physical positions of the SxN markers indicate that sub cluster 5 and sub cluster 4 could be part of the same real homolog. For chromosome 10 of P1, such a thing could not be said, since sub cluster 5 could be linked to sub cluster 4 and sub cluster 2 as also the DxN information indicated. Therefore, the sub clusters are linked together based on the work of Bourke *et al.*(2015), which means that sub clusters 5 and 2 are joined together as one real homolog.

The assignment of SxN markers by the two methods, by hierarchical clustering and DxN information, leads to the same homolog clustering as with JoinMap. As can be seen from Table 6 and 7, the SxN markers are not equally distributed over the chromosomes and the homologs, for example 110 SxN markers were assigned to homolog 2 of chromosome of P2, while only 4 markers were assigned to homolog 4 of chromosome 10 of P2.

The correct homolog assignment can be checked with other marker types. Therefore, the recombination frequencies and LOD-scores between SxS markers and SxN markers are calculated, since this is also an informative marker type. First, the usual counting of the dosages happens. Secondly the different estimates for the recombination frequency are calculated (Equations 16 and 18 in Box 3). When r1 is the smallest, the markers are estimated to be in coupling of each other. When r2 is smaller than r1 and is positive, the phase is estimate to be repulsion. When r2 is negative, but r1 is below 0.5, the phase is also coupling. When r2 is negative but r1 is above 0.5, then r2 is set at 0 (as was previously done with negative recombination frequencies between two SxN markers). After the estimation of the recombination frequency, the corresponding LOD-score is calculated (Equations 17 and 19 in Box 3).

The SxS markers are assigned to homologs based on the majority of linkages with a SxN marker with a LOD-score equal or higher than 3. The SxS markers are assigned to a homolog based on the majority of coupling-linkages within the same chromosome if there was more than one coupling linkage.

Visual inspection of the assignment of SxS markers to homologs confirmed the homolog estimation and sub cluster merging based on the SxN phase tree, DxN markers, physical positions and prior information of Bourke *et al.*(2015). The advantage of checking the homologs with other marker types is that those other marker types are now already assigned to the chromosomes and homologs (Table 6 and 7).

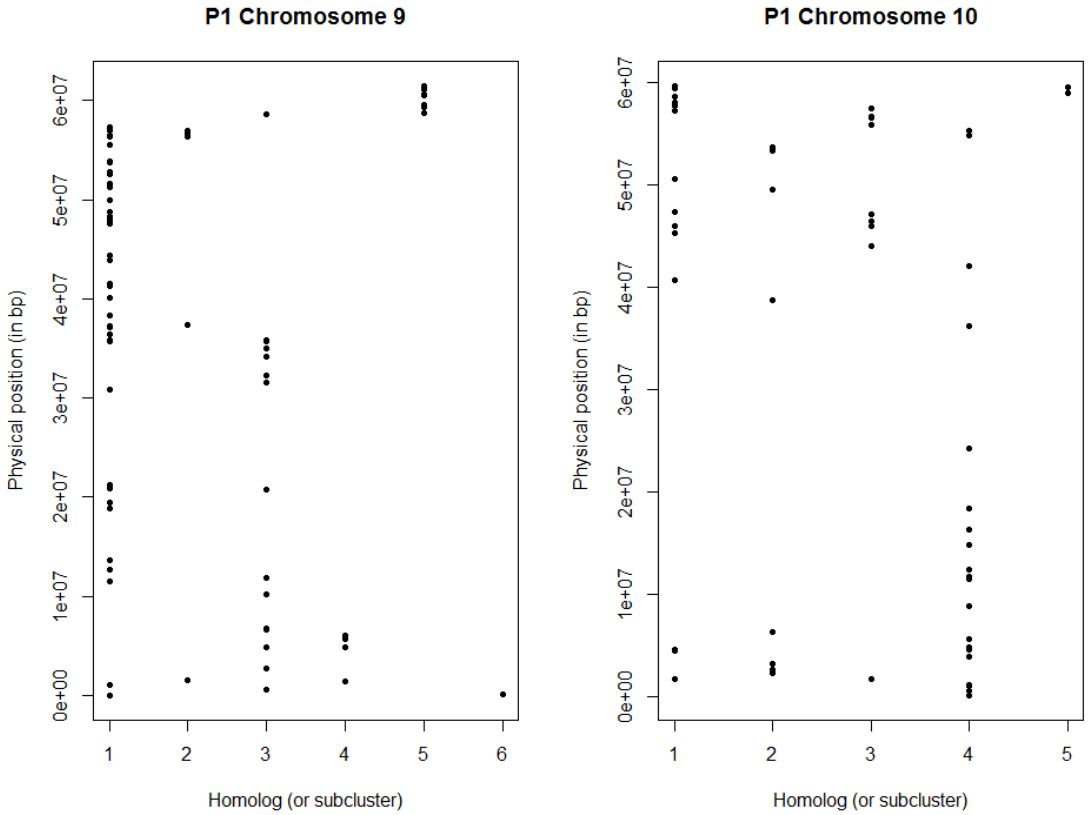


Figure 9. SxN markers on chromosome 9 and chromosome 10 of P1. The SxN markers are divided over the sub clusters. The sub clusters of chromosome 9 can be merged together based on DxN information and physical information. The sub clusters of chromosome 10 cannot be joined together in such a way and therefore prior knowledge (Bourke *et al.*, 2015) is used to merge those sub clusters together.

Box 3. Recombination frequency and LOD calculations between a SxN marker and a SxS marker. In this box the calculations for the LOD-score between a SxN marker and a SxS marker are shown. Furthermore, the different recombination frequency estimates for the different-phase situations are shown.

Simplex x simplex
Simplex x nulliplex

Coupling r1
Aaaa x Aaaa
Bbbb x bbbb

Equation 16 $r1 = \frac{\mathrm{n01+n20}}{\mathrm{n00+n21+n20+n01}}$

Equation 17 $LOD = (\mathrm{n21 + n00 + n01 + n20}) * \log10(2/(\mathrm{n21 + n00 + n01 + n20})) + (\mathrm{n01 + n20}) * \log10(\mathrm{n01 + n20}) + (\mathrm{n01 + n20}) * \log10(\mathrm{n21 + n00})$

Repulsion r2
Aaaa x Aaaa
bBbb x bbbb

Equation 18 $r2 = \frac{2(\mathrm{n00+n21})-(\mathrm{n01+n20})}{\mathrm{n00+n21+n20+n01}}$

Equation 19 $LOD = (\mathrm{n01 + n20 + n00 + n21}) * \log10(2/(\mathrm{n01 + n20 + n00 + n21})) + (\mathrm{n01 + n20}) * \log10(\mathrm{n01 + n20}) + (\mathrm{n00 + n21}) * \log10(\mathrm{n00 + n21})$

* LOD is the logarithm of odds ratio, r1 is the estimate of the recombination frequency of a SxS marker and a SxN marker in coupling phase, r2 is the estimate of the recombination frequency of SxS marker and a SxN marker in repulsion phase, n01 is the number of markers that have genotype aaaa and Bbbb, n20 is the number of markers that have genotype AAaa and bbbb, n00 is the number of markers that have genotype aaaa and bbbb, n21 is the number of markers that have genotype AAaa and Bbbb, the A's (for example Aaaa) and B's (for example Bbbb) are not position dependent.

Table 6. Number of markers per chromosome and homolog of P1. The number of markers of three marker types, SxN, DxN and the total number of markers on each chromosome and homolog is shown.

Chromosome	Cluster	SxN				DxN				SxS				Total			
		1	*2*	*3*	*4*	*1*	*2*	*3*	*4*	*1*	*2*	*3*	*4*	*1*	*2*	*3*	*4*
1	*2*	44	55	34	26	30	37	24	39	20	24	61	29	94	116	119	94
2	*3*	46	44	34	31	8	8	9	7	20	52	31	17	74	104	74	55
3	*4*	17	23	12	57	24	20	18	19	9	10	31	17	50	53	61	93
4	*5*	21	98	5	20	15	17	7	21	25	41	26	11	61	156	38	52
5	*6*	50	101	32	9	34	25	19	20	13	18	7	17	97	144	58	46
6	*7*	12	35	15	14	11	15	12	18	38	21	15	4	61	71	42	36
7	*8*	21	36	13	35	20	30	16	36	16	13	28	46	57	79	57	117
8	*1*	99	27	40	20	19	27	23	19	24	14	10	20	142	68	73	59
9	*9*	62	8	24	23	32	18	22	24	12	12	29	19	106	38	75	66
10	*10*	22	18	13	30	17	28	17	16	9	9	13	7	48	55	43	53
11	*11*	37	34	22	44	15	13	10	16	11	8	28	19	63	55	60	79
12	*12*	20	27	15	20	21	24	24	21	8	6	2	23	49	57	41	64

Table 7. Number of markers per chromosome and homolog of P2. The number of markers of three marker types, SxN, DxN and the total number of markers on each chromosome and homolog is shown.

Chromosome	Cluster	SxN				DxN				SxS				Total			
		1	*2*	*3*	*4*	*1*	*2*	*3*	*4*	*1*	*2*	*3*	*4*	*1*	*2*	*3*	*4*
1	5	61	60	25	37	17	16	17	35	33	19	27	52	111	95	69	124
2	1	55	75	89	16	22	13	20	14	24	22	45	29	101	110	154	59
3	2	42	110	47	26	42	45	29	27	19	29	6	13	103	184	82	66
4	8	46	38	32	18	26	26	27	25	32	22	8	37	104	86	67	80
5	10	76	69	34	16	23	20	25	31	25	9	9	12	124	98	68	59
6	7	50	28	51	23	3	12	15	6	12	33	26	7	65	73	92	36
7	3	46	48	28	12	26	27	34	27	46	16	30	11	118	91	92	50
8	4	24	37	31	12	8	4	2	4	19	10	20	29	51	51	53	45
9	11	15	41	39	12	12	22	19	17	16	23	26	7	43	86	84	36
10	12	23	11	5	4	7	10	4	7	6	7	15	12	36	28	24	23
11	9	34	51	23	21	17	19	15	15	10	32	16	8	61	102	54	44
12	6	39	20	19	8	12	9	8	9	7	9	13	10	58	38	40	27

Conclusion Chapter 3:

The new methodology to assign the SxN markers to homologs is based on a so-called phase-tree and significant DxN linkages. The cutting of the phase-tree into homologs worked for most chromosomes. However, for some chromosomes SxN with DxN linkage was necessary to end up with four homologs instead of five or six sub clusters. For two chromosomes, other types of information were necessary to end up with four homologs. It can therefore be concluded that the methodology used here works decently, but is not perfect yet.

Chapter 4: Other segregation type markers

Summary Chapter 4:

The recombination frequencies that have not been calculated in the previous chapters are calculated between the different marker types. When an analytical estimator is available, this is used. However, in some cases the analytical estimator for the recombination frequency is not possible or complicated. In those situations Brent's algorithm is used to optimize the likelihood function and in this way the recombination frequency for the different phases is estimated. With the analytical estimator or optimization with Brent's algorithm, the recombination frequency, LOD-score and phase for every marker pair is estimated. Furthermore, the SxT markers are assigned to chromosomes and homologs.

Estimation of the recombination frequency without analytical estimator

In the previous chapters, the recombination frequencies between SxN markers (Chapter 1), SxN with DxN markers and SxS with SxN markers (Chapter 3) have been calculated. In this chapter, the recombination frequencies between the other marker types and the corresponding LOD-scores are calculated.

There are many possibilities when pairs of markers of different types and in different phases are considered (Hackett *et al.*, 2013). For every marker type and configuration the expected genotype frequencies in terms of dosages can be calculated. A maximum likelihood equation can be derived from the genotype frequencies. Bourke (personal communication) developed an algorithm to automatically derive the maximum likelihood equation from the genotype frequencies. Whenever an analytical estimator for the recombination frequency can be found, this estimator is given as well. However, in many situations there is no analytical estimator or the expression is rather complicated. In those cases the likelihood function is maximised numerically with Brent's algorithm (Brent, 1973). Brent's algorithm finds the optimum of a function without the use of derivatives within specified bounds (0 and 0.5 for recombination frequencies).The best estimate for the recombination frequency is the recombination frequency with the maximum likelihood.

Recombination frequencies between DxN markers

In Chapter 3, the recombination frequencies between DxN and SxN markers are calculated. The recombination frequency of DxN markers among themselves are calculated in this chapter. Two DxN markers can be either in coupling, repulsion or a mixed phase (coupling for one pair of alleles and repulsion for the other pair). Each phase-situation has its own likelihood function (Equations 20, 21 and 22 in Box 4). The three likelihood functions are optimized with Brent's algorithm to find the maximum likelihood estimator of the recombination frequency. The maximum corresponds to the recombination frequency for the three situations. The minimum of the three recombination frequency estimates of the different phase-situations is estimated to be the most likely estimate and the corresponding phase is estimated as the most likely phase. The mixed situation is not very informative and has a high standard error (Meyer *et al.*, 1998) and has a smaller LOD-score. The coupling and repulsion situations are equally informative and these are more informative than to the mixed phase situation.

Box 4. Recombination frequency calculations between two DxN markers. In this box the calculations for the likelihood between two DxN markers are shown. This likelihood equation can be solved with an iterative approach

Duplex x nulliplex
Duplex x nulliplex

Coupling r1
AAaa x aaaa
BBbb x bbbb

Equation 20 $L(r)_{coupling} = (1/3 + 1/3 * (1 - \mathrm{r})^2 * 1/3\mathrm{r}^2)^{\mathrm{n11}} * (1/6 * (1 - \mathrm{r})^2)^{n22+\mathrm{n00}} * (1/6 * \mathrm{r}^2)^{\mathrm{n20+n02}} * (1/3 * \mathrm{r} * (1 - \mathrm{r}))^{\mathrm{n01+n10+n21+n12}}$

Repulsion r2
AAaa x Aaaa
bbBB x bbbb

Equation 21 $L(r)_{repulsion} = (1/3 + 1/3 * (1 - \mathrm{r})^2 * 1/3 * \mathrm{r}^2)^{\mathrm{n11}} * (1/6 * (1 - \mathrm{r})^2)^{\mathrm{n20+n02}} * (1/6 * \mathrm{r}^2)^{n22+\mathrm{n00}} * (1/3 * \mathrm{r} * (1 - \mathrm{r}))^{\mathrm{n01+n10+n21+n12}}$

Mixed (coupling-repulsion) r3
AAaa x aaaa
BbBb x bbbb

Equation 22 $L(r)_{mixed} = (1/3 + 1/3 * (1 - \mathrm{r}) * \mathrm{r})^{\mathrm{n11}} * (1/12 * \mathrm{r} * (1 - \mathrm{r}))^{\mathrm{n20+n20+n00+n22}} * (1/12 + 1/12 * (1 - \mathrm{r})^2 + 1/12 * \mathrm{r}^2)_{\mathrm{n01+n10+n21+n12}}$

* L(r) is the likelihood of r, r1 is the estimate of the recombination frequency of two DxN markers in coupling phase, r2 is the estimate of the recombination frequency of two DxN markers in repulsion phase, r3 is the estimate of the recombination frequency of two DxN markers in mixed phase, n01 is the number of markers that have genotype aaaa and Bbbb, n10 is the number of markers that have genotype Aaaa and bbbb, n00 is the number of markers that have genotype aaaa and bbbb, n11 is the number of markers that have genotype Aaaa and Bbbb, the A's (for example Aaaa) and B's (for example Bbbb) are not position dependent.

:

Recombination frequencies between SxS markers and other marker types

Another marker type that was also introduced in Chapter 3 is the SxS marker. The recombination frequency between SxS and SxN markers were already calculated in Chapter 3, but the recombination frequencies between SxS and DxN markers are calculated here. The likelihood function between DxN and SxS markers can be calculated (Equations 23 and 24 in Box 5). The minimum of the two recombination frequency estimates (coupling or repulsion) of the marker pair is estimated to be the most likely estimate and the corresponding phase is estimated as the most likely phase

Furthermore, the recombination frequencies among SxS markers themselves can be estimated by optimization of the likelihood function (Equations 25, 26 and 27 in Box 6). The minimum of the three recombination frequency estimates of the different phase-situations is estimated to be the most likely estimate and the corresponding phase is estimated as the most likely phase. SxS markers in coupling phase both parents are highly informative and have the highest LOD-scores of all possible marker type and phase combinations (Hackett *et al.*, 2013). The mixed and repulsion phase are likewise less informative and have a lower LOD-score.

Box 5. Recombination frequency calculations between a DxN marker and a SxS marker. In this box the calculations for the likelihood between a DxN and SxS marker are shown. This likelihood equation can be solved with an iterative and an analytical approach.

Duplex x nulliplex
Simplex x simplex

Coupling r1
AAaa x aaaa
Bbbb x Bbbb

Equation 23 $L(r)_{coupling} = 1/12^{n00+n01+n10+n21+n20+n12+n02+n22} * 2^{n10+n12} * (1-r)^{n00+n22} * r^{n20+n02} * 1/3^{n11}$

Repulsion r2
AAaa x Aaaa
bbBb x bbbb

Equation 24 $L(r)_{repulsion} = 1/12^{n00+n01+n10+n21+n20+n12+n02+n22} * 2^{n10+n12} * (1-r)^{n20+n02} * r^{n00+n22} * 1/3^{n11}$

* L(r) is the likelihood of r, r1 is the estimate of the recombination frequency of a SxS marker and a DxN marker in coupling phase, r2 is the estimate of the recombination frequency of SxS marker and a DxN marker in repulsion phase, n01 is the number of markers that have genotype aaaa and Bbbb, n20 is the number of markers that have genotype AAaa and bbbb, n00 is the number of markers that have genotype aaaa and bbbb, n21 is the number of markers that have genotype AAaa and Bbbb, n10 is the number of markers that have genotype Aaaa and bbbb, n02 is the number of markers that have genotype aaaa and BBbb, n22 is the number of markers that have genotype AAaa and BBbb, n12 is the number of markers that have genotype Aaaa and BBbb, the A's (for example Aaaa) and B's (for example Bbbb) are not position dependent.

Please note that an analytical estimator is possible as well.

Box 6. Recombination frequency calculations between two SxS marker. In this box the calculations for the likelihood between two SxS markers are shown. This likelihood equation can be solved with an iterative approach.

Simplex x simplex
Simplex x simplex

_____

Coupling r1
Aaaa x Aaaa
Bbbb x Bbbb

Equation 25 $L(r)_{coupling} = 1/2^{n11+n01+n10+n21+n12} * 1/4^{n00+n20+n22+n02} * (r^2)^{n02+n20} * ((1-r)^2)^{n00+n22} * (r*(1-r))^{n01+n10+n21+n12} * (r^2+(1-r)^2)^{n11}$

_____

Repulsion r2
Aaaa x Aaaa
bBbb x bBbb

Equation 26 $L(r)_{mixed} = 1/12^{n00+n01+n02+n10+n12+n10+n22} * (1-r^2)^{n00+n22} * (2*r^2-2r+2)^{n01+n10+n21+n12} * \left(r*(2-r)\right)^{n01+n20} * (4*r-4*r^2+2)^{n11}$

_____

Mixed (coupling-repulsion) r3
Aaaa x Aaaa
Bbbb x bBbb

Equation 27 $L(r)_{repulsion} = (5/18 - 1/6*r + 1/9*r^2)^{n11} * (1/36 + 1/18*r + 1/36*r^2)^{n00+n22} *$

$(1/9 + 1/18*r - 1/18*r^2)^{n01+n10+n21+n12} * (1/9 - 1/9*r + 1/36*r^2)^{n20+n02}$

* L(r) is the likelihood of r, r1 is the estimate of the recombination frequency between two SxS markers in coupling phase, r2 is the estimate of the recombination frequency between two SxS markers in coupling phase , r3 is the estimate of the recombination frequency between two SxS markers in mixed phase, n01 is the number of markers that have genotype aaaa and Bbbb, n20 is the number of markers that have genotype AAaa and bbbb, n00 is the number of markers that have genotype aaaa and bbbb, n21 is the number of markers that have genotype AAaa and Bbbb, n10 is the number of markers that have genotype Aaaaa and bbbb, n02 is the number of markers that have genotype aaaa and BBbb, n22 is the number of markers that have genotype AAaa and BBbb,, n12 is the number of markers that have genotype Aaaa and BBbb, n11 is the number of markers that have genotype Aaaa and Bbbb, the A's (for example Aaaa) and B's (for example Bbbb) are not position dependent.

Assignment of SxT markers to chromosomes and homologs

The last marker type that has not been considered so far is SxT. Hackett *et al.* (2013) call this marker type XSS, probably because the segregation ratio of a SxS marker and SxT marker is the same. However in this thesis this marker type is called SxT, since in one parent the marker has a simplex allele and in the other parent a triplex allele. In a normal SxS marker, both the segregating simplex alleles are informative, but in a SxT marker, the one simplex allele is informative in one parent whereas the segregating non-triplex allele is informative in the other. When one tries to transform SxT markers (to SxS), he or she will notice that this is not possible without wrongfully transforming one parent. The recombination frequencies and LOD-scores between a SxT marker and a SxN can be estimated analytically (Equations 28 until 34 in Box 7).

The SxT markers are assigned to chromosomes based on the majority of linkages with a LOD-score equal or higher than 3. For P1 the SxT markers are assigned to homologs based on the majority of coupling linkage (meaning that the simplex alleles of both markers are in coupling; Box 7). For P2 the SxT markers are assigned to homologs based on repulsion linkage, since the segregating allele of the P2 is the non-triplex allele (Box 7). The SxT markers are not equally distributed over the chromosomes and homologs (Table 8). Some chromosomes contain a fair amount of SxT markers while other chromosomes contain very few or none.

Table 8. Number of SxT **markers divided over chromosomes and homologs.** The SxT markers of P1 are assigned to chromosomes and homologs based on coupling linkage with SxN markers while the SxT marker of P2 are assigned to chromosomes and homologs based on repulsion linkage with SxN markers.

	P1				**P2**			
Chromosome	***1***	***2***	***3***	***4***	***1***	***2***	***3***	***4***
1	4	17	12	31	32	2	23	7
2	3	9	5	6	7	4	11	4
3	9	4	1	26	7	1	27	5
4	13	4	2	20	17	10	5	8
5	5	27	5	7	10	27	0	7
6	6	2	4	0	3	3	6	0
7	7	20	5	6	12	9	14	3
8	10	4	22	2	2	7	23	6
9	6	10	4	9	4	3	12	10
10	5	1	11	0	5	1	1	3
11	4	35	2	4	3	1	4	37
12	11	4	0	5	0	3	0	14

Box 7. Recombination frequency and LOD calculations between a SxN marker and a SxT marker. In this box the calculations for the LOD-score and recombination frequencies between a SxN marker and a SxT marker are shown for the different-phase situations are shown. For P1 the calculations of SxT with SxN are used and for P2 the calculations of TxS with SxN are used.

Simplex x triplex
Simplex x nulliplex

Coupling r1
Aaaa x AAAa
Bbbb x bbbb

Equation 28 $r = \frac{n30+n11}{n30+n11+n31+n10}$

Equation 29 $LOD = log10(\frac{1/4*(n20+n11+n21+n10+n31+n30)*(1-r)*(n11+n30)*r*(n10+n31)}{1/4*(n20+n11+n21+n10+n31+n30)*(1-1/2)*(n11+n30)*1/2*(n10+n31)})$

Repulsion r2
Aaaa x AAAa
bBbb x bbbb

Equation 30 $r = \frac{2*(n10+n31)-(n11+n30)}{(n11+n30+n10+n31)}$

Equation 31 $LOD = log10(\frac{1/4*(n21+n20)*(1/12+1/12*r)*(n10+n31)*(1/6-1/12*r)*(n11+n30)}{1/4*(n21+n20)*(1/12+1/12*1/2)*(n10+n31)*(1/6-1/12*1/2)*(n11+n30})$

Triplex x simplex
Simplex x nulliplex

Coupling r1
AAAa x Aaaa
Bbbb x bbbb

Equation 32 $r = \frac{2*(n11+n30)-(n10+n31)}{(n11+n30+n10+n31)}$

Equation 32 $LOD = log10(\frac{1/12*(n21+n10+n20+n11+n31+n30)*(2-r)*(n31+n10)*(1+r)*(n11+n30)}{1/12*(n21+n10+n20+n11+n31+n30)*(2-1/2)*(n31+n10)*(1+1/2)*(n11+n30)})$

Repulsion r2
AAAa x Aaaa
bbbB x bbbb

Equation 33 $r = \frac{n31+n10}{n30+n11+n31+n10}$

Equation 34 $LOD = log10(\frac{1/4*(n20+n11+n21+n10+n31+n30)*(1-r)*(n11+n30)*r*(n10+n31)}{1/4*(n20+n11+n21+n10+n31+n30)*(1-1/2)*(n11+n30)*1/2*(n10+n31)})$

* LOD is the logarithm of odds ratio, r1 is the estimate of the recombination frequency of a SxT marker and a SxN marker in coupling phase, r2 is the estimate of the recombination frequency of SxT marker and a SxN marker in repulsion phase, n11 is the number of markers that have genotype Aaaa and Bbbb, n30 is the number of markers that have genotype AAAa and bbbb, n10 is the number of markers that have genotype Aaaa and bbbb, n31 is the number of markers that have genotype AAAa and Bbbb, the A's (for example Aaaa) and B's (for example Bbbb) are not position dependent.

Recombination frequencies between SxT markers and other marker types

Furthermore, the linkages between the SxT markers and the other marker types can be calculated as well (Box 8, 9 and 10). Since an SxS and a SxT marker have the same segregation ratio, the informativeness and standard errors of SxT markers are similar to those of SxS markers. In addition, it should be noted that mixed and repulsion phases between SxS and SxT markers are very uninformative (Appendix 7). This can lead to a relative flat likelihood function and hence the optimization of the likelihood function may give wrong estimates for the recombination frequency. Experience showed that sometimes the estimated recombination frequency can be 0 for very distantly linked markers in the highly uninformative phases. Therefore extra care should be taken when considering estimated recombination frequencies of SxT with SxS markers in mixed and repulsion phase.

Box 8. Recombination frequency calculations between a SxT marker and a DxN marker. In this box the calculations for the likelihood between a SxT and DxN marker are shown. This likelihood equation can be solved with an iterative and an analytical approach.

Simplex x triplex
Duplex x nulliplex

Coupling r1
Aaaa x AAAa
BBbb x bbbb

Equation 35 $L(r) = (1/12 * \mathrm{r})^{\mathrm{n30+n12}} * 1/6^{\mathrm{n31+n22+n20+n11}} * (1/12 - 1/12 * \mathrm{r})^{\mathrm{n32+n10}} * 1/3^{\mathrm{n21}}$

Repulsion r2
Aaaa x AAAa
bBBb x bbbb

Equation 36 $L(r) = (1/12 - 1/12 * \mathrm{r})^{\mathrm{n30+n12}} * 1/6^{\mathrm{n31+n22+n20+n11}} * (1/12 * \mathrm{r})^{\mathrm{n32+n10}} * 1/3^{\mathrm{n21}}$

* L(r) is the likelihood of r, r1 is the estimate of the recombination frequency of a SxT marker and a DxN marker in coupling phase, r2 is the estimate of the recombination frequency of SxT marker and a DxN marker in repulsion phase, n32 is the number of markers that have genotype AAAa and BBbb, n20 is the number of markers that have genotype AAaa and bbbb, n30 is the number of markers that have genotype AAAa and bbbb, n21 is the number of markers that have genotype AAaa and Bbbb, n10 is the number of markers that have genotype Aaaa and bbbb, n22 is the number of markers that have genotype AAaa and BBbb, n01 is the number of markers that have genotype aaaa and Bbbb, n12 is the number of markers that have genotype Aaaa and BBbb, n31 is the number of markers that have genotype AAAa and Bbbb, n11 is the number of markers that have genotype Aaaa and Bbbb, the A's (for example Aaaa) and B's (for example Bbbb) are not position dependent.

Please note that an analytical estimator is possible as well.

Box 9. Recombination frequency calculations between a SxT marker and a SxS marker. In this box the calculations for the likelihood between a SxT and SxS marker are shown. This likelihood equation can be solved with an iterative approach.

Simplex x triplex
Simplex x simplex

Coupling r1
Aaaa x AAAa
Bbbb x Bbbb

Equation 37 $L(r) = (1/12 * \mathrm{r} + 1/12 * \mathrm{r}^2)^{\mathrm{n30+n12}} * (1/12 + 1/6 * \mathrm{r} - 1/6 * \mathrm{r}^2)^{\mathrm{n31+n22+n20+n11}} * (1/6 - 1/4 * \mathrm{r} + 1/12 * \mathrm{r}^2)^{\mathrm{n32+n10}} * (1/3 - 1/3 * \mathrm{r} + 1/3 * \mathrm{r}^2)^{\mathrm{n21}}$

Repulsion r2
Aaaa x AAAa
bBbb x bbbB

Equation 38 $L(r) = (1/6 - 1/4 * r + 1/12 * \mathrm{r}^2)^{n30+n12} * (1/12 + 1/6 * r - 1/6 * \mathrm{r}^2)^{n31+n22+n20+n11} * (1/12 * r + 1/12 * \mathrm{r}^2)^{n32+n10} * (1/3 - 1/3 * r + 1/3 * \mathrm{r}^2)^{n21}$

Mixed1 (repulsion-coupling) r3
Aaaa x AAAa
bBbb x Bbbb

Equation 39
$L(r) = (1/18 + 1/36 * \mathrm{r} - 1/36 * \mathrm{r}^2)^{\mathrm{n30+n12}} * (5/36 - 1/18 * \mathrm{r} + 1/18 * \mathrm{r}^2)^{\mathrm{n31+n22+n20+n11}} * (1/18 + 1/36 * \mathrm{r} - 1/36 * \mathrm{r}^2)^{\mathrm{n32+n10}} * (2/9 + 1/9 * \mathrm{r} - 1/9 * \mathrm{r}^2)^{\mathrm{n21}}$

Mixed2 (coupling- repulsion) r4
Aaaa x AAAa
Bbbb x bbbB

Equation 40 $L(r) = (1/4 * \mathrm{r} - 1/4 * \mathrm{r}^2)^{\mathrm{n30+n12}} * (1/4 - 1/2 * \mathrm{r} + 1/2 * \mathrm{r}^2)^{\mathrm{n31+n22+n20+n11}} * (1/4 * \mathrm{r} - 1/4 * \mathrm{r}^2)^{\mathrm{n32+n10}} * (\mathrm{r} - \mathrm{r}^2)^{\mathrm{n21}}$

* L(r) is the likelihood of r, r1 is the estimate of the recombination frequency of a SxS marker and a SxT marker in coupling phase, r2 is the estimate of the recombination frequency of SxS marker and a SxT marker in repulsion phase, r3 is the estimate of the recombination frequency of SxS marker and a SxT marker in mixed-1 phase, r4 is the estimate of the recombination frequency of SxS marker and a SxT marker in mixed-2 phase, n32 is the number of markers that have genotype AAAa and BBbb, n20 is the number of markers that have genotype AAaa and bbbb, n30 is the number of markers that have genotype AAAa and bbbb, n21 is the number of markers that have genotype AAaa and Bbbb, n10 is the number of markers that have genotype Aaaa and bbbb, n22 is the number of markers that have genotype AAaa and BBbb, n01 is the number of markers that have genotype aaaa and Bbbb, n12 is the number of markers that have genotype Aaaa and BBbb, n31 is the number of markers that have genotype AAAa and Bbbb, n11 is the number of markers that have genotype Aaaa and Bbbb, the A's (for example Aaaa) and B's (for example Bbbb) are not position dependent.

Box 10. Recombination frequency calculations between two SxT markers. In this box the calculations for the likelihood between two SxT markers are shown. This likelihood equation can be solved with an iterative approach.

Simplex x triplex
Simplex x triplex

Coupling r1
Aaaa x AAAa
Bbbb x BBBb

Equation 41 $L(r) = (1/4 * r^2)^{n13+n31} * (1/2 * r - 1/2 * r^2)^{n23+n32+n12+n21} * (1/4 - 1/2 * r + 1/4 * r^2)^{n33+n11} * (1/2 - r + r^2)^{n22}$

Repulsion r2
Aaaa x AAAa
bBbb x BBbB

Equation 42 $L(r) = (1/9 - 1/9 * r + 1/36 * r^2)^{n13+n31} * (1/9 + 1/18 * r - 1/18 * r^2)^{n23+n32+n12+n21} * (1/36 + 1/18 * r + 1/36 * r^2)^{n33+n11} * (5/18 - 1/9 * r + 1/9 * r^2)^{n22}$

Mixed1 (repulsion-coupling) r3
Aaaa x AAAa
bBbb x BBBb

Equation 43 $L(r) = (1/6 * r - 1/12 * r^2)^{n13+n31} * (1/6 - 1/6 * r + 1/6 * r^2)^{n23+n32+n12+n21} * (1/12 - 1/12 * r^2)^{n33+n11} * (1/6 + 1/3 * r - 1/3 * r^2)^{n22}$

Mixed2 (coupling- repulsion) r4
Aaaa x AAAa
Bbbb x BBbB

Equation 44 $L(r) = (1/6 * r - 1/12 * r^2)^{n13+n31} * (1/6 - 1/6 * r + 1/6 * r^2)^{n23+n32+n12+n21} * (1/12 - 1/12 * r^2)^{n33+n11} * (1/6 + 1/3 * r - 1/3 * r^2)^{n22}$

* L(r) is the likelihood of r, r1 is the estimate of the recombination frequency of between two SxT markers in coupling phase, r2 is the estimate of the recombination frequency between two SxT markers in repulsion phase, r3 is the estimate of the recombination frequency between two SxT markers in mixed-1 phase, r4 is the estimate of the recombination frequency between two SxT markers in mixed-2 phase, n32 is the number of markers that have genotype AAAa and BBbb, n23 is the number of markers that have genotype AAaa and BBBb, n33 is the number of markers that have genotype AAAa and BBBb, n21 is the number of markers that have genotype AAaa and Bbbb, n10 is the number of markers that have genotype Aaaaa and bbbb, n22 is the number of markers that have genotype AAaa and BBbb, n01 is the number of markers that have genotype aaaa and Bbbb, n13 is the number of markers that have genotype Aaaa and BBBb, n12 is the number of markers that have genotype Aaaa and BBbb, n31 is the number of markers that have genotype AAAa and Bbbb, n11 is the number of markers that have genotype Aaaa and Bbbb, the A's (for example Aaaa) and B's (for example Bbbb) are not position dependent.

Validation of the likelihood equation by means of simulation

Simulations with PedigreeSim showed that Brent's algorithm was able to give correct estimates of the simulated recombination frequencies by optimizing the likelihood function for the population size as used in this thesis (results not shown). However, for future estimations of the recombination frequency in this and other populations, the log-likelihood function would be recommended (Van Ooijen & Jansen, 2013).

Conclusion Chapter 4:

In this chapter the recombination frequencies, LOD-score and phase is estimated between all the marker pairs that were not considered in the previous chapters. This was done by using the analytical estimator or optimizing the likelihood function with Brent's algorithm, which worked well for the informative phases. Furthermore, the SxT markers were assigned to chromosomes and homologs in a similar matter as the other marker segregation types.

Chapter 5: Ordering with linear regression - Theory

Summary Chapter 5:

The recombination frequencies, calculated in the previous chapters, are transformed to distances with the Haldane's mapping function. The distances were used in a linear regression approach to estimate a linkage map. The linear regression approach is straightforward and deterministic. It uses the observed distances, the transformed recombination frequencies, to estimate the expected distances, the map distances, by minimising the sum of squares in a linear model. By doing so, the optimal map is found. Markers are added one by one based on the LOD-score. Markers can be rejected based on the Chi-square test-statistic, negative distances and a jump-test. The time to map markers with the linear regression approach is exponential with the number of markers.

Converting the recombination frequencies into distances.

Numerous methods to estimate linkage maps have been developed by scientist over the past century. One of the methods to estimate a linkage map is a linear regression approach and this method was used in this thesis to estimate the linkage maps of the homologs. Linear regression is a so-called greedy or nearest-neighbour algorithm (Van Ooijen & Jansen, 2013d). It is relatively straightforward and deterministic. The algorithm adds the closest marker to the marker order and builds the order step-by-step. How the linear regression works in practice is explained below.

Jensen and Jorgenson (1975) used the linear regression method for the first time to estimate a map of barley. They first converted the calculated recombination frequencies into map distances by a mapping function. The reason why recombination frequencies are converted to map distances first is that recombination frequencies are not additive (since they do not count even numbers of recombination events as recombinants). Therefore, mapping functions are used that can convert recombination frequencies into genetic distances that are additive. The two most widely used mapping functions are Haldane's and Kosambi's (Equation 46 and 47). Haldane's mapping function assumes that the crossovers follow a Poisson distribution and are independent of one another regardless of their relative location, while Kosambi's mapping function takes positive interference into account (Vinod, 2011). Before transforming the recombination frequencies into distances, the recombination frequencies of 0.5 are set at 0.499 (Hackett & Broadfoot, 2003). The difference between Haldane's and Kosambi's mapping functions is very small for small recombination frequencies (Figure 10).

Equation 45 $d_{Morgan} = r * 100$

Equation 46 $d_{Haldane} = -\frac{1}{2} * \ln(1 - 2 * r) * 100$

Equation 47 $d_{Kosambi} = \frac{1}{4} * \ln\left(\frac{1+2*r}{1-2*r}\right) * 100$

*d is the distance, r is the recombination frequency

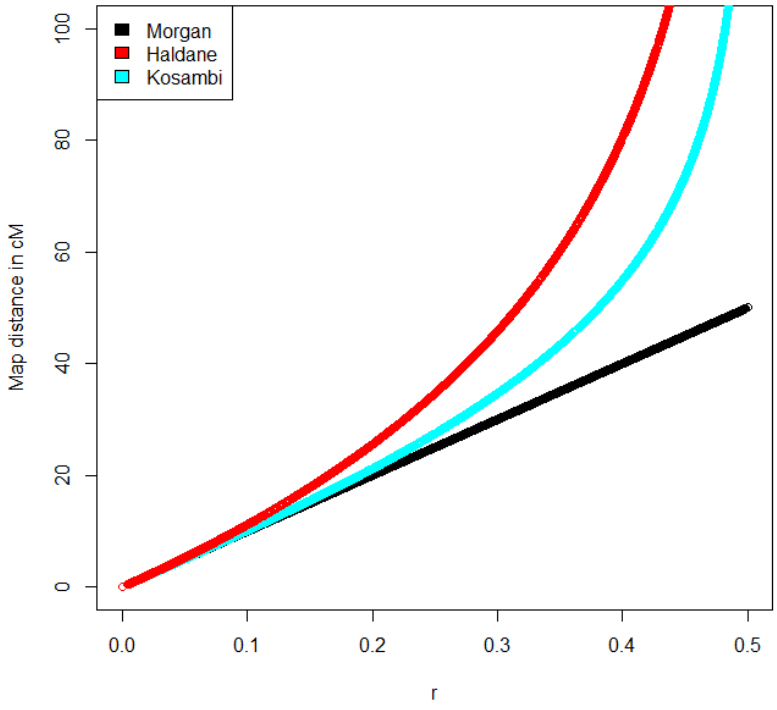


Figure 10. Distances by mapping functions plotted against the recombination frequencies. The recombination frequencies between SxN markers of P1 are used to create this plot. This plot corresponds to the plot described by Liu (1997d).

For the study of local map regions the used mapping function is not of high relevance, but for studying the total map length the choice of the mapping function is of importance. Both mapping functions are used so far for linkage mapping of potato. Kosambi's mapping function has been used to convert recombination frequencies into mapping distances of diploid potato (Sharma *et al.*, 2013), while Haldane's mapping function was used to map tetraploid potato (Hackett *et al.*, 2013; Hackett *et al.*, 1998). Haldane's mapping function was used in this thesis to be in correspondence with Hackett *et al.* (2013) and Hackett *et al.* (1998) and the assumption of no interference (Assumption 4 and 5). Furthermore, in this thesis it is assumed that Haldane's mapping function is applicable to tetraploids although it was developed for diploids (Assumption 12).

The linear model

Now that the recombination frequencies are translated into additive distances, they can be used in a linear model. The parameters in the linear model (the linkage map) are the adjacent distances between markers, while all the pairwise distances are considered when estimating the model (Van Ooijen & Jansen., 2013b; Liu, 1997d). If a map with four markers in the order A-B-C-D, then the model can be defined as Set of equations 48.

Set of equations 48

$$
\begin{aligned}
dAB &= \delta AB + eAB \\
dBC &= \delta BC + eBC \\
dCD &= \delta CD + eCD \\
dAC &= \delta AB + \delta BC + eAC \\
dBD &= \delta BC + \delta CD + eBD \\
dAD &= \delta AB + \delta BC + \delta CD + eAD
\end{aligned}
$$

*With d_{xy} being the observed distance (based on recombination frequency) between marker x and marker y, δ_{xy} being the expected distance between marker x and y based on the model and e_{xy} the error corresponding to the distance between marker x and y

One can imagine that this set of equations becomes increasing more complicated when more markers are added to the given order. However, this is not the case, since the basic structure of the equations stays the same if the equations are put in matrix-format (Equation 49). The equation in matrix-format is a standard linear model with more known parameters than unknown parameters.

Equation 49
$$
\begin{pmatrix} dAB \\ dBC \\ dCD \\ dAC \\ dBD \\ dAD \end{pmatrix} = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \\ 1 & 1 & 0 \\ 0 & 1 & 1 \\ 1 & 1 & 1 \end{pmatrix} \begin{pmatrix} \delta AB \\ \delta BC \\ \delta CD \end{pmatrix} + \begin{pmatrix} eAB \\ eBC \\ eCD \\ eAC \\ eBD \\ eAD \end{pmatrix}
$$

*With d_{xy} being the observed distance (based on recombination frequency) between marker x and marker y, δ_{xy} being the expected distance between marker x and y based on the model and e_{xy} the error corresponding to the distance between marker x and y

One standard assumption of linear regression is that the standard errors have equal variances. However, this is not the case since small distances are more precisely estimated than large distances. To adjust for these unequal variances, a weighted least squares method is used (Van Ooijen & Jansen, 2013b). JoinMap (version 1) initially did this by using the LOD-score (Stam, 1993; Liu, 1997d), and in later versions the square of the LOD-score is used (Van Ooijen, 2006). In this thesis the LOD^2 was used as weight in correspondence with the current version of JoinMap (version 4.1). Another advantage of using the LOD-scores as weight is that the amount of individuals (or missing values) is automatically accounted for and non-informative pairings do not contribute very much to the map estimation.

Another assumption is that the residuals of the pairwise distances, or pairwise recombination frequencies, are independent of each other (Assumption 10). From computer simulations dependency of the residuals of distances did not appear to be a problem (Van Ooijen & Jansen, 2013b).

The parameters (δAB, δBC and δCD) in the linear model represent the final map distances. These parameters can be estimated by minimizing the SSE (Equation 50; Stam, 1993). This formula can be differentiated with respect to δAB, δBC and δCD and estimates for these parameters can be obtained. The estimated parameters (δAB, δBC and δCD) represent the final map distances. The matrix equation can easily be extended to contain more markers.

Equation 50 $SSE = {LOD_{AB}}^2 * (\delta AB - dAB)^2 + {LOD_{BC}}^2 * (\delta BC - dBC)^2 + {LOD_{CD}}^2 * (\delta CD - dCD)^2 + {LOD_{AC}}^2 * (\delta AC - dAB - dBC)^2 + {LOD_{BD}}^2 * (\delta BD - dBC - dCD)^2 + {LOD_{AD}}^2 * (\delta AD - dAB - dBC - dCD)^2$

*With d_{xy} being the observed distance (based on recombination frequency) between marker x and marker y, δ_{xy} being the expected distance between marker x and y based on the model and LOD_{xy} the LOD/score between marker x and y

Selecting the markers

A careful reader might have noted that the map can be estimated with the linear regression method for any given order, but that linear regression does not present a way to find the optimal order. The best order has to be chosen based on other criteria and during this thesis several possible criteria were used.

The first obvious step in regression mapping is finding the first pair. In the regression method of JoinMap, this is done by considering the marker pair that is most informative (Van Ooijen, 2006). Informativeness is reflected in the LOD-score and therefore the pair with the highest LOD-score was used as the starting pair in this thesis.

The next marker to be added is selected based on the sum of LOD-scores between this marker and the markers already in the order. Consider the following example in which the order consists of marker A-B-C and there are two markers, D and E, yet unmapped. The LOD-score of A-D is 8, B-D is 5, C-D is 6, A-E is 4, B-E is 4 and C-E is 7. The next marker to be added in the mapping procedure is then D, since the sum of LOD-scores is higher for this marker (8+5+6=19) than for marker E (4+4+7=15). LOD-scores between markers that are not yet in the order (in this example the LOD-score between marker D and E) are neglected in this procedure.

After the next marker is selected, the best fitting position is determined. The new marker is considered at every position of the marker order without changing the current map order (Stam, 1993). Consider again the order of marker A-B-C. The next marker, D, can fit at the following positions: D-A-B-C, A-D-B-C, A-B-D-C and A-B-C-D. The linear model, as described above, is applied to these different marker orders. From this, the residual sum of squares (SSE) is calculated automatically, since this is minimized by the least square method. The smaller the SSE is the better the model (the order of markers) fits the data. The marker order with the lowest SSE is the order with the best fit (Van Ooijen & Jansen, 2013c) and this new order contains the new marker.

After the next marker is fitted into the order, a reshuffling, or ripple, is performed. The ripple is considering all the possible orders within a moving window (of usually three markers) (Van Ooijen, 2006). Consider the previous example again with markers A-B-C-D being ordered. The ripple will look at all permutations within a moving window of three markers. Thus marker orders of A-B-C-D, A-C-B-D,C-A-B-D,C-B-A-D, B-C-A-D (for the first moving window) and A-B-C-D, A-B-D-C, A-D-B-C, A-D-C-B, A-C-D-B and A-C-B-D (for the second moving window). Based on all these orders, the most optimal order is determined again by the lowest SSE. As one can imagine from seeing the many possibilities of the ripple, the ripple is a time-consuming process (Stam, 1993; see below), but is needed to find the best global order instead of a local order

Evaluation of markers

To see if the optimal map order is actually any good, the map distances are transformed back to recombination frequencies with the reverse of the Haldane mapping function (Van Ooijen, 2006; Vinod, 2011; Equation 51).

Equation 51 $r = \frac{1}{2} * (1 - e^{-2d_{Haldane}})$

When there is a negative recombination frequency (either observed or expected) between 0 and -0.001 the recombination frequency is considered to be 0. This will lead to a poorer fit, since the observed and expected recombination frequency have a larger difference, but the marker order is still evaluated. When there is a negative recombination frequency below -0.001 it is considered to be a negative recombination frequency. Negative recombination frequencies (or distances) cannot happen in reality and therefore the order with the next marker is rejected.

After this step, the goodness-of-fit Chi-square is calculated (Set of equations 52; Van Ooijen (personal communication). The goodness-of-fit is a likelihood ratio test. The degrees of freedom of this test are roughly equal to the number of pairs with a direct estimate (the number of parameters in the model) minus the number of map distances (Van Ooijen, 2006). When the test statistic is not significant it means that the expected and observed recombination frequencies are not different and the linear model (the order) is considered to be good. On the other hand, when the Chi-square statistic is significant, the order is considered to have a poor fit and the new marker is rejected from the order.

Set of equations 52:

$$\chi 2 = \sum R * \ln(\frac{r_{obs}}{r_{exp}}) \sim \chi^2_{df}$$

$$with\ R = N * robs$$

$$with\ N = \frac{LOD}{s * log10(s) + r_{obs} * log10(r_{obs}) + log10(2)}$$

$$with\ s = 1 - r_{obs}$$

$$with\ df \approx number\ of\ pairs\ with\ a\ direct\ estimate - number\ of\ total\ map\ distances$$

*r_{obs} is the observed recombination frequency, r_{exp} is the recombination frequency from the model, χ^2 is the Chi-Square value, df is the degrees of freedom, R is the number of recombinants, N is the number of individuals, LOD is the logarithm of odds ratio.

The goodness-of-fit Chi-square indicates whether the added marker is at a likely position and doesn't create a conflicting order. However, this does not tell if the order with the added marker is better than the order without the added marker. To compare the order with and without the added marker, the goodness-of-fit Chi-square is also used. In the so called jump-test, two Chi-square values (one for the order without the new marker and one for the order with the new marker), are compared (Van Ooijen, personal communication). However, since the Chi-square values originated from different degrees of freedom, the Chi-square values need to be normalized first (Equation 53; Ooijen personal communication). When the jump test is larger than 3, the result is significant and the new marker is rejected (Van Ooijen, 2006). When the test is not significant, the new marker fits well and the search continues for a next marker and the procedure is repeated until all markers are considered. The idea behind this is that a poor marker will cause conflicts in the newly estimated order and thus cause a poorer fit (Van Ooijen & Jansen, 2013d)

Equation 53 $Jump = {(\chi^2_{after} - \chi^2_{before})} \Big/ {(2 * (df_{after} - df_{before})^2)} > 3$

* χ^2 is the Chi-Square value, df is the degrees of freedom,

The markers that are removed from the ordering, either by negative distances, significant Chi-square values or significant jump-tests, are considered again in a so-called second round (Van Ooijen, 2006). This may prove to be useful, since there are now more markers in the model and therefore it is still possible that a marker can be placed.

Time-efficiency and co-segregating markers

As mentioned above, the rippling function is a time-consuming process. A way to reduce the amount of time spend by rippling is to reduce the amount of markers to be mapped. This might sound conflicting since the goal is a marker dense map. However, there are many markers that can be mapped without actually using them in the mapping procedure. Those markers are co-segregating markers. For every marker pair with zero recombination, one of the two markers is taken out before the ordering and put back at end of the ordering procedure. For example, when the ordering time of SxN markers only, without taking out co-segregating markers is considered, the time it takes to order markers appears to be exponential (Figure 11). When co-segregating markers are taken out, the time-increase is tremendous. This proves that it is time can be gain by taking out co-segregating markers. It should be mentioned that the markers used in the actual ordering still follow an exponential function.

When different marker types are considered, it is wise to keep the marker types with the highest information content in the ordering procedure. Therefore the marker type is considered when taking out one of the two co-segregating markers in a pair. Whenever a SxN marker with any other marker type has a recombination frequency of 0, the SxN marker is kept in. When a SxN marker is co-segregating with another SxN marker, the marker with the smallest number of missing values is kept. When a SxS marker is co-segregating with DxN marker, the SxS marker is kept. When a SxS marker is co-segregating with SxT marker, both markers are kept since the co-segregation condition (r=0) might be caused by some situation in which the phase is highly uninformative. When a SxS marker is co-segregating with another SxS marker, which maker to be taken out is based on the number of missing values. Whenever a DxN marker is co-segregating with a SxT marker, the DxN marker is taken out. When a DxN marker is co-segregating with a marker of the same type, again the number of missing values is taken as a criterion to take the marker out. When a SxT marker is co-segregating with another SxT marker, the marker to be taken out is also determined by the amount of missing values. In this way, the most informative markers are used in the mapping procedure.

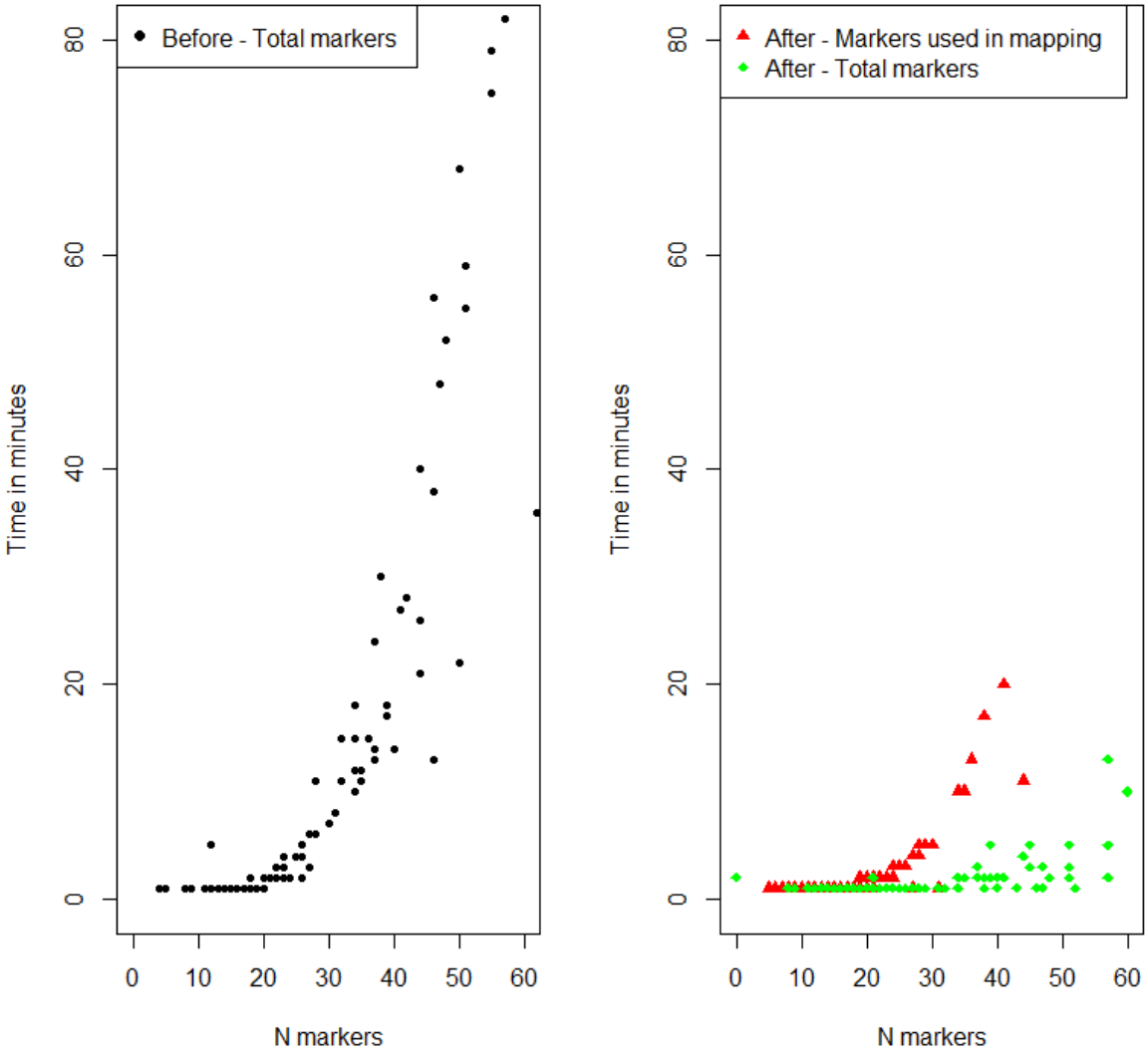


Figure 11. Time for ordering SxN markers with and without taking out co-segregating markers. The plot on the left shows the time in minutes the linear regression takes to calculate SxN homolog maps with co-segregating markers included. The plot on the right show the time in minutes linear regression takes to calculate SxN homolog maps when co-segregating markers are taken out based on missing values.

Conclusion Chapter 5:

The linear regression approach is a straightforward and deterministic method of linkage mapping. By converting the recombination frequencies into distances, practically any marker type can be ordered. However, the time to order markers is exponential with the number of markers. Therefore, co-segregating markers are taken out of the mapping procedure.

Chapter 6: Homolog maps

Summary Chapter 6:

In the previous chapter, ordering markers by means of the linear regression method is explained. In this chapter, homolog maps, based on SxN markers only, are compared with maps estimated by JoinMap's maximum likelihood method. Both methods were very comparable. Furthermore, the SxN maps, as well as DxN maps (based on SxN and DxN markers), SxS maps (based on SxN, DxN and SxS markers) and SxT maps (based on SxN, DxN, SxS and SxT markers), were compared with the physical positions. The physical positions and the map positions were comparable and the maps clearly showed the centromere and chromosome arms. In addition, two methods of map evaluation are provided, namely a heatmap-method based on the recombination frequencies and the LOD-scores, and a method of evaluating the observed versus the expected distances.

Types of maps

In the previous chapter, the theory behind ordering markers by means of linear regression was explained. In accordance with that procedure, the SNP markers were ordered for each homolog. First only SxN markers were ordered in a map (called the SxN map), next SxN and DxN markers (called the DxN map), followed by SxN, DxN and SxS markers (called the SxS map) and finally maps were created with these three marker types and SxT markers (called the SxT map). This was done to study the effect of the different marker types on the ordering. However, in practice, one would like to map all marker types in one go. In total 95 SxN maps were created (homolog 3 of chromosome 10 of P2 had 3 or less unique markers). 96 DxN maps and 96 SxS maps were created. 88 SxT maps were completed (because there was an unknown error in the ordering procedure of homolog 2 of chromosome 2 of P2, homolog 3 of chromosome 3 of P1, homolog 2 of chromosome 3 of P2, homolog 1 of chromosome 6 of P1, homolog 2 of chromosome 10 of P1, homolog 2 and 3 of chromosome 10 of P2 and homolog 2 of chromosome 11 of P2). Due to these errors, 14 SxT markers assigned to homologs were never considered in the ordering procedure.

SxN maps

Since the SxN markers can also be ordered by software that is developed for diploid organisms, it is wise to compare the linear regression method (described in Chapter 5) with methods developed for diploids. When homolog 1 of chromosome 11 of P2 is ordered with the linear regression method of this thesis and with the maximum likelihood and linear regression method (Round 2) of JoinMap, the ordering is similar (Figure 12). There are no internal map inversions. The distances are not equal, but distances of the linear regression method of this thesis are very similar to the maximum likelihood approach of JoinMap.

Another way of looking at the similarity between two mapping approach is by plotting the map positions of common markers against each other as was proposed to compare map positions of different maps of tomato (Sim *et al.*, 2012). If both mapping methods are similar, the map positions of both maps should follow a straight line when plotted against each other. Therefore, the SxN map of homolog 1 of chromosome 11 of P2 by the linear regression method is compared with SxN maps from Bourke e*t al.* (2015) by the maximum likelihood approach of JoinMap. Indeed we see a very straight line with a Pearson correlation of 0.9995 (Figure 13). Of course, such quantification is easy to generate for all the 95 SxN maps.

As can be seen from Figure 14, the vast majority of the SxN maps generated by the linear regression approach in this thesis (except 1 map) are significantly correlated with the maximum likelihood approach of JoinMap. This gives confidence that ordering with the linear regression approach described in this thesis works for SxN markers.

Comparing the results of linear regression in this thesis with other mapping methods is only part of the story, since there is another comparison to be made, namely with the physical position. When the physical positions are compared with order of SxN markers estimated by the linear regression method, there is a strong Spearman correlation (Figure 15). The reason why a Spearman correlation is used instead of a Pearson correlation, is because there is no linear relationship between the physical positions and map positions and therefore a Pearson correlation, based on ranks, is more suitable. Also this is good evidence that the linear regression works in the mapping of SxN markers.

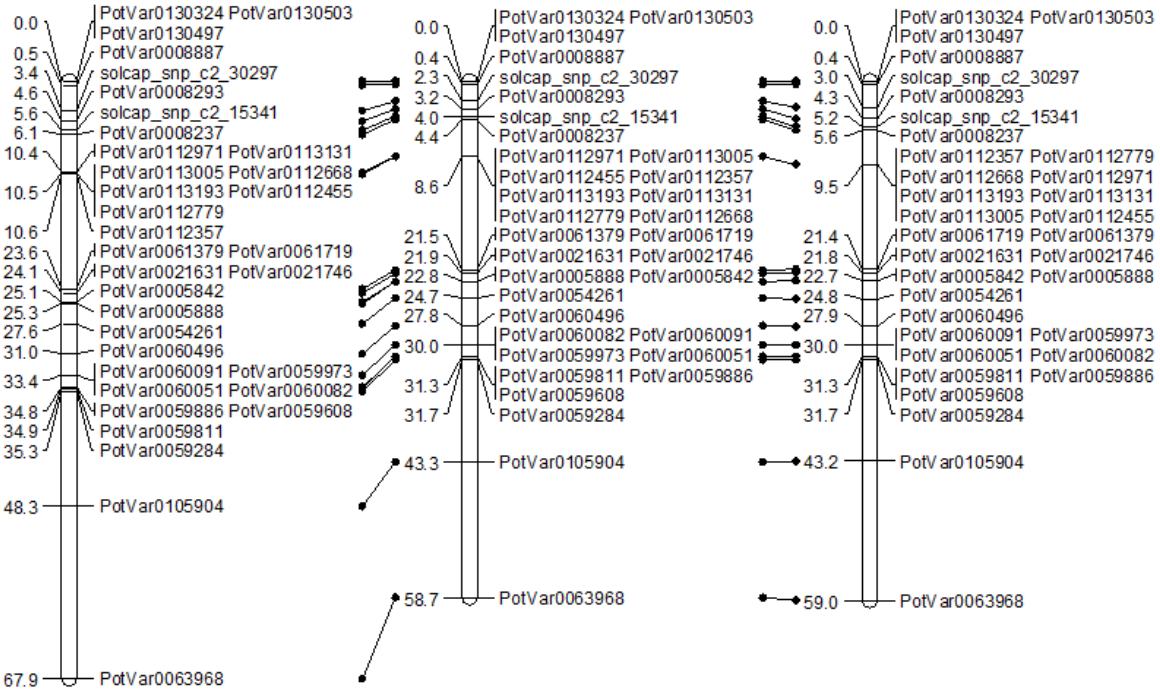


Figure 12. Comparison of three mapping methods on homolog 1 of chromosome 11 of P2 with only SxN markers. Linear regression (Round 2) of JoinMap (left), linear regression method in this thesis (middle) and maximum likelihood of JoinMap (right) are shown. The map positions of the markers are given in cM. Between the same marker on different maps, lines are drawn.

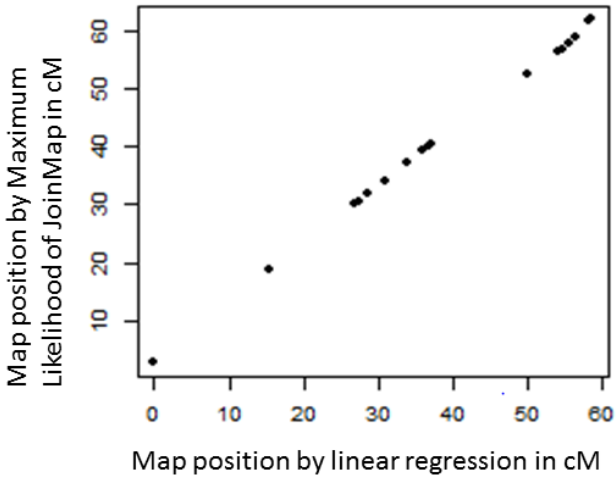


Figure 13. Map positions of common markers from the maximum likelihood map of JoinMap and the linear regression map for homolog 1 for chromosome 11 of P2. The markers map at almost the same positions in both ordering methods as can be seen from the straight line. Both maps are in the reverse orientation when compared to Figure 12. The maximum likelihood maps of JoinMap were considered from the work of Bourke *et al.*, (2015).

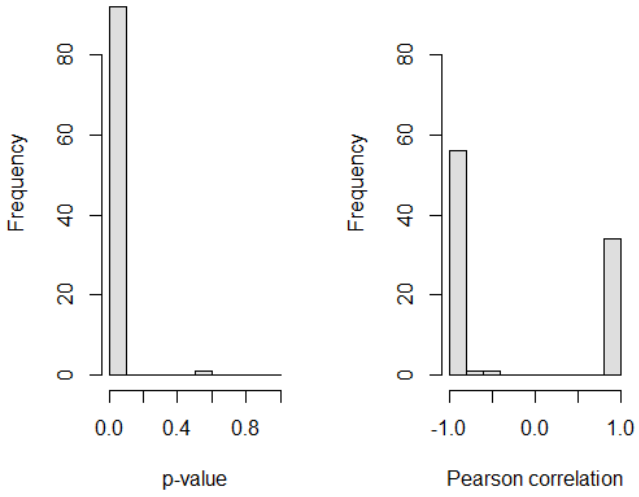


Figure 14. Pearson correlations between map positions of the maximum likelihood method and the linear regression approach of SxN maps. The left plot shows the p-value of the Pearson correlation, which is significant in all cases except one. The right plot shows the Pearson correlations of the maps. Many maps appear to be oriented in the inverse direction, but since the assignment of the starting position (0 cM) is arbitrary, this does not matter.

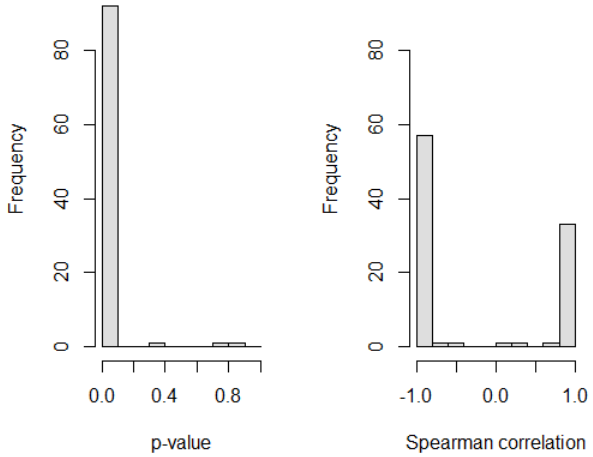


Figure 15. Spearman correlations between maps positions the linear regression approach and physical positions of SxN markers. The left plot shows the p-value of the Spearman correlation. The right plot shows the Spearman correlation of map order with the physical positions.

Maps including other marker types

So far, only SxN markers are considered, but there are more marker types. Therefore the physical position is compared with the ordering of multiple marker types. When the example of homolog 1 of chromosome 11 of P2 is considered again, it can be noted that there is already a decent coverage of the physical chromosome by the SxN markers on the SxN map (Figure 16). The centromere is visible as a region where hardly any recombination happens and the chromosome arms are present as the regions where recombination occurs often. When the DxN maps are calculated, the coverage is already higher and the length of the map is not increased so much. Thereafter, the SxS maps can be calculated. Here there is an increase in map length. It should also be noted that the total map is now inverted, but since the orientation of the maps can be switched, this does not matter. Furthermore, due to the extra information provided by the SxS markers, more DxN markers are now present in the map when compared to the DxN map itself (Table 9). After this, the SxT map was calculated. Again there is a slight increase in map length. Still the relationship between map distances and physical distances is present and clear.

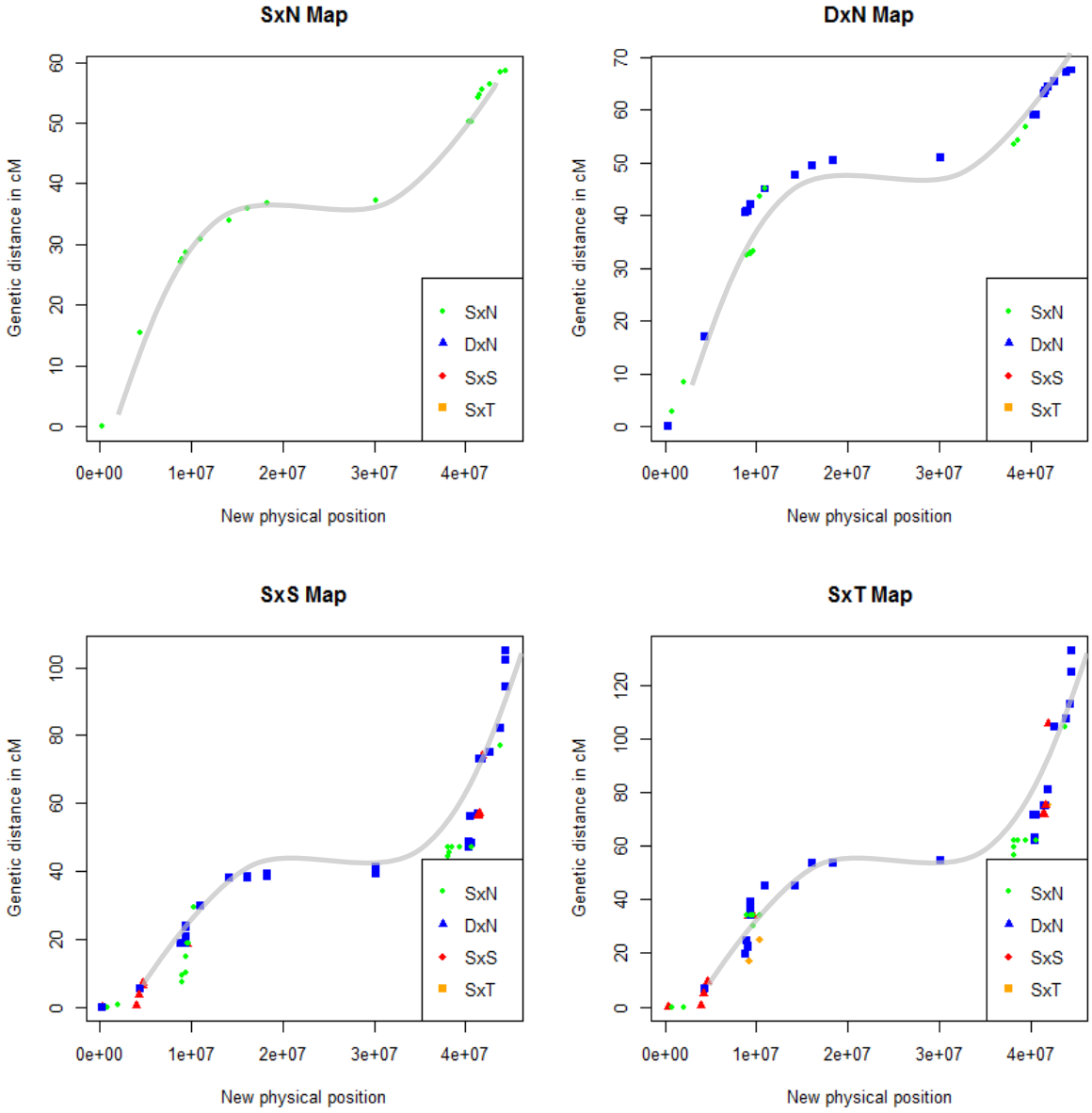


Figure 16. The different map orders are compared with the physical positions of the marker. The top left plot compares the ordering of the SxN map with the new physical positions, which has some small and some large changes when compared to the old physical data (Data; Appendix 10). The top right plot compares the ordering of the DxN map with the new physical positions. The bottom left plot compares the ordering of the SxSmap with the new physical positions. The bottom right plot compares the ordering of the SxT map with the new physical positions. The grey sigmoid line represents a correlation, based on visual inspection (and thus bears no statistical significance), between the physical positions and the map positions. The other homologs of this chromosome and other chromosomes can be found in Appendix 6.

Table 9. Different marker numbers of the four maps of homolog 1 of chromosome 11 of P2. The number of markers per marker type appears to be more or less stable in the different marker type maps.

Map	*Markers*			
	SxN	*DxN*	*SxS*	SxT
SxN	34			
DxN	34	14		
SxS	34	16	11	
SxT	34	16	10	3

New map evaluation methods

Apart from looking at the physical positions for map evaluation, some other methods for map evaluation are used as well. The first method is map evaluation by the use of a heatmap (Van Ooijen, personal communication). In the heatmap (Figure 17), the recombination frequencies and LOD-scores are plotted against the order of the markers. In such a plot, every square represents a recombination frequency or LOD-score of a marker with another marker. The diagonal means nothing, since these are LOD-scores or recombination frequencies from a marker with itself. The low recombination frequencies are correlated with the marker order, since a green patch (low recombination frequencies) follows the diagonal. There is a similar pattern with the LOD-scores, although the pattern is less clear. Furthermore some markers have in general lower LOD-scores than others, which can be due to the marker type. Another thing that can be seen from Figure 17 is that taking markers out on basis on the criterion of having a zero recombination event between two markers is a good criterion. This can be seen by big squares of both recombination frequencies and LOD-scores in Figure 17 below.

Furthermore, the heatmap evaluation can also be used to spot ordering errors. In Figure 18, the heatmap of the recombination frequency, used in mapping of homolog 2 of chromosome 2 of parent 2, is shown. The plot on the left shows the correct order, while the plot on the right contains an artificial wrong marker (Potvar0089282). This incorrect marker was introduced by preventing the removal of markers that failed the Chi-square or jump test in the ordering step (Chapter 5). This heatmap shows that this marker does not fit well in the ordering as can be seen from the high recombination frequency (red line) in an area were all the other markers have a low recombination frequency (green square).

Another method of evaluation is plotting the observed versus the expected distances. In Figure 19, the expected adjacent distances (from the ordering model) are plotted against the observed distances (based on the calculated recombination frequencies) and a straight line can be seen. This is a good indication that the linear model worked. Furthermore, all the expected and observed distances are plotted as well. Here also a straight line can be observed, however, the larger the distance the more it deviates from the line. This is in line with the fact that larger distances have a large error (Hans Jansen, personal communication).

All the maps can be and are evaluated by the three methods proposed here: plotting the map distances against the physical positions (Appendix 5), plotting heatmaps of recombination frequencies and LOD-scores and plotting the observed versus the expected distances (results not shown).

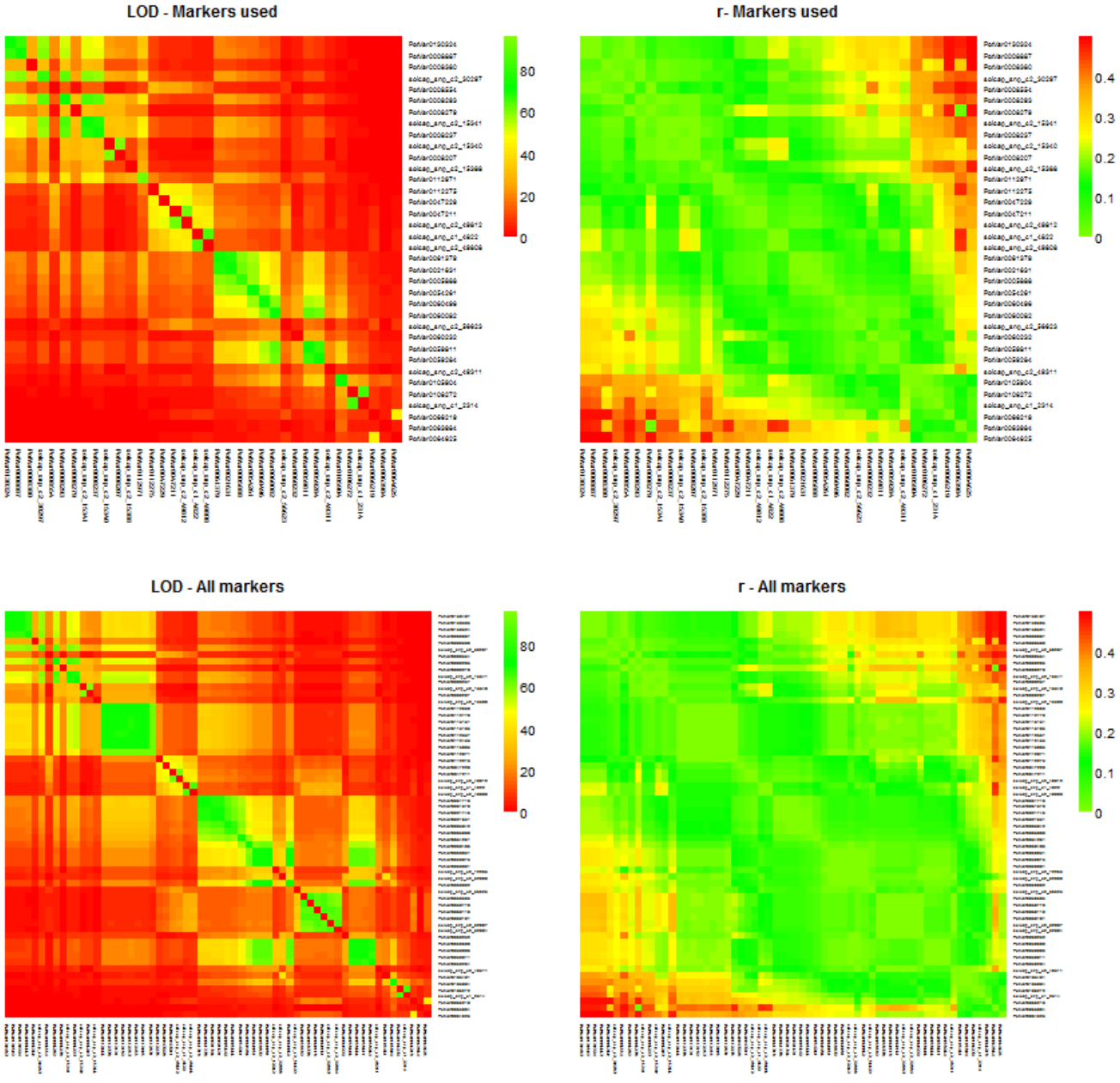


Figure 17. Heatmap of LOD scores and recombination frequencies of all marker pairs of homolog 1 of chromosome 11 of P2. The markers used in the ordering are shown in the two plots above, while all the markers are shown in the plot below.

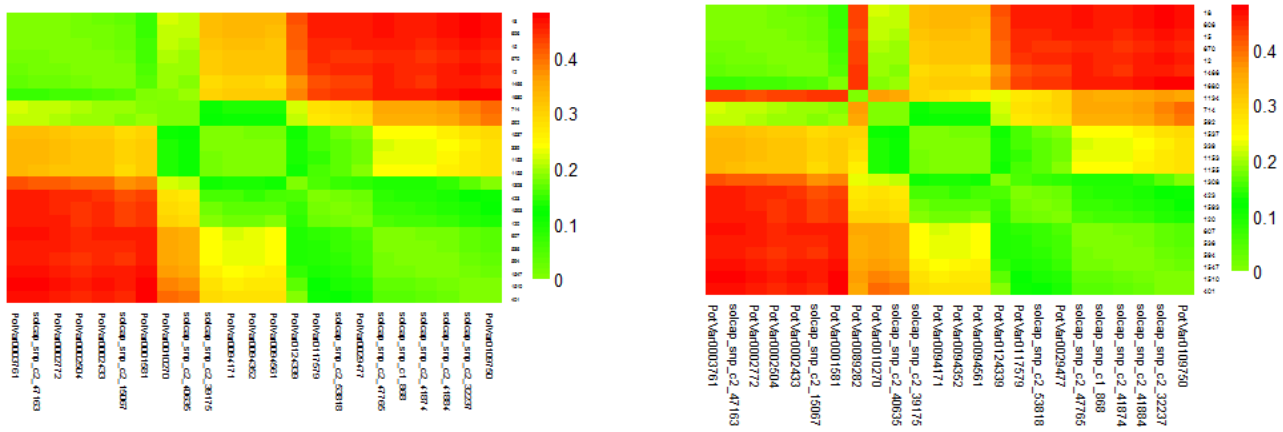


Figure 18. Heatmap of the recombination frequencies used in the ordering of homolog 2 of chromosome 2 of P2. The plot on the right is the correct order, while the plot on the left contains one artificial incorrect marker (Potvar0089282), introduced by not allowing for marker removal during the ordering of markers. From the heatmap it can clearly be seen that this marker is incorrectly mapped.

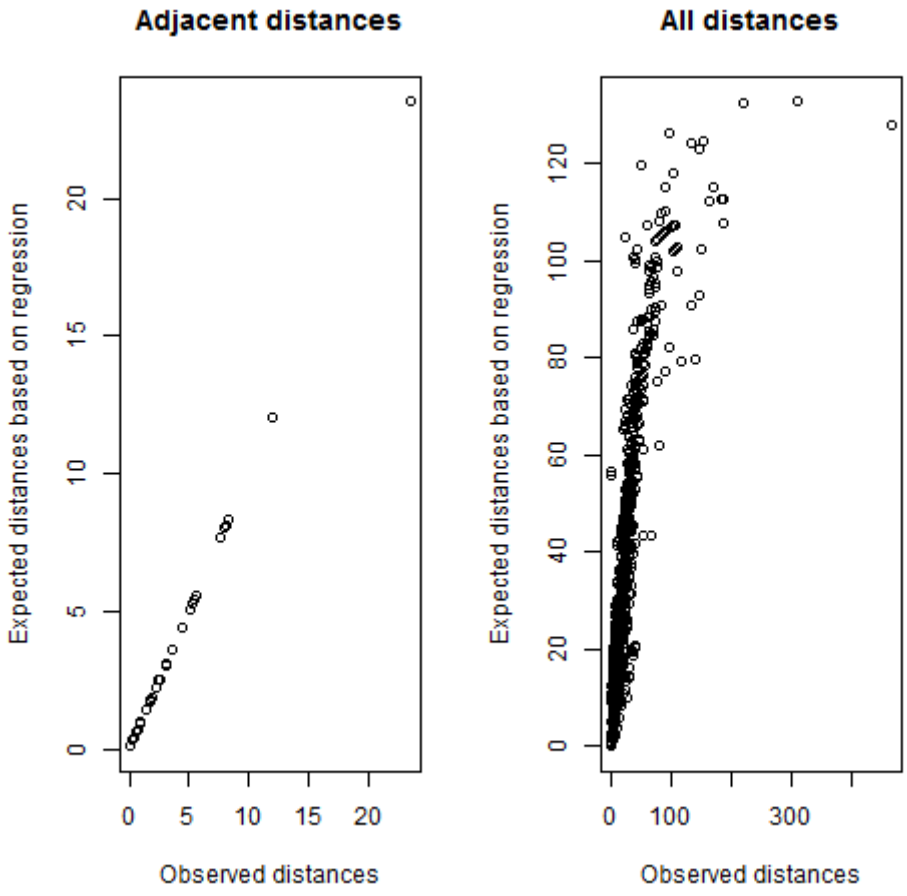


Figure 19. Plot of observed versus the expected distances of homolog 1 of chromosome 11 of P2. The plot on the left presents the adjacent distances only, while the plot on the right presents distances of all marker pairs on the homolog.

Conclusion Chapter 6:

The SxN maps, estimated by the linear regression method described in this thesis, were compared with the maximum likelihood method of JoinMap. Both methods gave comparable results. In addition, the physical positions were also comparable with the map order. Combining these two finding with the new map evaluation tools, leads to the conclusion that the linear regression method used here is capable of mapping different marker types.

Chapter 7: Integration

Summary Chapter 7:

The homolog maps, estimated in the previous chapter, are integrated in this chapter. LPmerge is used for the integrated of the homolog maps. LPmerge uses a graph-theory approach to integrate and solve conflicting orders. This is in contrast to JoinMap, which uses a statistical pooled approach. The timing difference between the two methods is tremendous. The integrated chromosomes maps of LPmerge gave good correlation with the underlying homolog maps and the physical positions. The integrated maps covered in total 1406.13 cM for 12 chromosomes and contained 5165 markers.

Programmes to integrate maps

In the previous chapter, the maps of the homologs are calculated. For effective QTL-analysis, an integrated map of those homologs is desired. There are several programmes that can integrate maps of different populations into one consensus map. In this chapter, the homologs are thus treated as if they came from different populations.

Currently, different approaches have been developed to make a consensus map based on maps of different populations. The first approach is to visually align the maps by hand (Yap *et al.*, 2003). Of course this proves to be very unpractical for large datasets. Luckily, the other approaches are automated.

The second approach relies on the recombination frequencies and LOD-scores and is thus directly based on the genotypes and this is called a statistical pooled approach (Jackson *et al.*, 2005). JoinMap uses this approach. In JoinMap all the pairwise recombination frequencies are used to create an integrated map with the linear regression approach (Van Ooijen, 2006). This also requires the repulsion estimates for markers on different homologs. As was already mentioned in Chapter 1, some recombination frequencies for repulsion can be negative, which are then set to zero. Doing so is a loss of information and might shorten the integrated map (Hackett *et al.*, 1998). Furthermore, the approach by JoinMap proves to be time-consuming with a large number of markers, for example JoinMap took 3 months of calculations for the construction of a consensus map of 1800 markers (Wu *et al.*, 2008). Even due to the drawback of timing, JoinMap is used for the integration of linkage maps of certain species, for example pineapple (de Sousa *et al.*, 2013). Another programme, MetaQTL, which also uses the weighted regression approach, was used for the construction of an integrated map of potato (Danan *et al.*, 2011).

Another approach to integrate maps is to use the maps themselves, rather than the underlying recombination frequencies and LOD scores. This approach is used by MergeMap (Yap *et al.*, 2003) and uses graph-theory and regards the maps as a directed graph.

In graph-theory, the markers are represented as nodes and the distances as edges. In the approach proposed by Yap *et al.*, (2003), the individual linkage maps are scanned for bridge-markers. In case of a tetraploid, the bridge markers are the DxN markers (bridge for homologs) and SxT and SxS markers (both a bridge for parents).

Thereafter, the bridge markers are used as anchors and merged. Once the maps are merged based on bridge-markers, the software looks for inconsistencies and presents them as cycles (non-linear paths) in the graph. The software presents the integrated maps as a graph which connects the well-ordered (or merged) markers with lines and the inconsistencies as cycles. The reason that the software presents it in such a way instead of a single linkage map is that presenting the consensus map as a single linkage map may hide inconsistencies with the underlying homolog maps (Yap *et al.*, 2003). Although such a graph-map is useful to spot inconsistencies easily, it is not very useful for QTL-analysis since it does not present a single integrated linkage map. Thus it is useful to solve the inconsistencies of the integrated graph by linearization or simplification to a linear graph (Endelman, 2011). However, by doing so, it might create an order in the consensus map that is not present in any of the individual linkage maps.

Therefore, new software, such as DAGGER (Endelman *et al.*, 2014), has been developed to cope with this problem. DAGGER finds the best consensus map by minimizing the residual mean sum error (RMSE) between the individual linkage maps and the consensus map. However, one practical disadvantage of DAGGER is that it shrinks the consensus maps considerably and another disadvantage of DAGGER is that it cannot handle ordering conflicts.

Its successor, LPmerge, solved these problems (Endelman & Plomion, 2014). One advantage of LPmerge in comparison to other merging programmes is that is removes constrains rather than markers when there are inconsistencies between the underlying linkage maps. By using LPmerge and MergeMap to integrate different maps of maritime pine it was found out that MergeMap gave longer consensus maps than LPmerge, while the ordering was similar (Plomion *et al.*, 2014). Furthermore, LPmerge has been used in other species, such as cassava (International Cassava Genetic Map Consortium, 2014). Although LPmerge has been used to integrate populations of tetraploid wheat (Yu *et al.*, 2014), it has not been used yet for the integration of homologs. Here LPmerge was used for the development of an integrated map of the 8 homolog maps per chromosome.

LPmerge minimises the RMSE, residual mean square error, by means of linear programming between the individual homolog maps and the integrated map to find the best order of markers for the integrated map (Endelman & Plomion, 2014). It is advised to select the consensus map with the lowest RMSE. The error terms of the consensus map are based on the interval size. The interval ranges from 1 to the maximum interval size and LPmerge allows the user to change the maximum interval size (with a default value of 1 to 3). An interval size of 1 means that only adjacent pairs on the original maps are considered for the error estimation while higher interval sizes mean that also markers further away are considered.

Integration of homolog maps

For chromosome 1 the SxS map of homolog 1 of P1 was used since the SxT map showed an increase of 50cM when compared to the SxS map, furthermore, for homolog 4 of P2 the SxS map was used since there was an error during the ordering of the SxT map, for the other homologs the SxT map was used. For chromosome 2, the SxS map of homolog 1 of P2 was used since there was an error during the ordering of the SxT map, for the other homologs the SxT map was used. For chromosome 3, the SxS map of homolog 3 of P1 and homolog 1 of P2 were used since there was an error during the ordering of the SxT map, also for homolog 4 of P1 the SxS map was used since the SxT map was not consistent with the SxS map, for the other homologs the SxT map was used. For chromosome 4 the SxT maps were used for all homologs. For chromosome 5, the SxS map of homolog 2 of P2 was used since there the SxT map lost an entire chromosome arm when compared to the SxT map, for the other homologs the SxT map was used. For chromosome 6, the SxS map of homolog 1 of P1 was used since there was an error during the ordering of the SxT map, for the other homologs the SxT map was used. For chromosome 7 the SxS map of homolog 4 of P1 was used since the SxT map showed an increase of 40cM when compared to the SxS map, for the other homologs the SxT map was used. For chromosome 8 the SxT maps were used for all homologs. For chromosome 9 the SxT maps were used for all homologs. For chromosome 10, the SxS map of homolog 2 of P1 and homolog 2 and 3 of P2 were used since there was an error during the ordering of the SxT map, for the other homologs the SxT map was used. For chromosome 11, the SxS map of homolog 2 of P2 was used since there was an error during the ordering of the SxT map, for the other homologs the SxT map was used. For chromosome 12 the SxT maps were used for all homologs.

The individual homolog maps were put in the correct orientation with respect to each other, since LPmerge is orientation-dependent (personal observation; results not shown). This is done based on the (Spearman) correlation of the order of the homolog map with the physical position. When a correlation larger than 0 is found, the map is already in the good orientation, but when a correlation lower than 0 is found, the map should be reversed. It should be noted that the Pearson correlation between maps themselves could also be used to put the maps into the right orientation. During integration the maximum interval size was varied from 1 to 4 and the best consensus map was selected based on the lowest RMSE and the smallest consensus map length (Endelman, 2011). In practice, a maximum interval size of 1 was selected for all chromosomes.

Evaluation of the integration process

A way to visualize the quality of the integrated map is to plot the underlying homolog maps against the integrated map, which gave a good correlation between the maps, for the example of chromosome 11 (Figure 20). This means that the order between the markers on the homologs is maintained on the integrated map. More importantly than a general correlation are potential switches between the positions of markers. No large rearrangements of marker order are found (Figure 20). This means that the constraints that were removed by LPmerge to make the consensus map are in correspondence with the underlying homolog maps. The Pearson correlation can be calculated for all the homolog maps against the integrated maps. For all the chromosomes there is a good correlation between the homolog maps and the integrated map (Figure 21; Appendix 16).

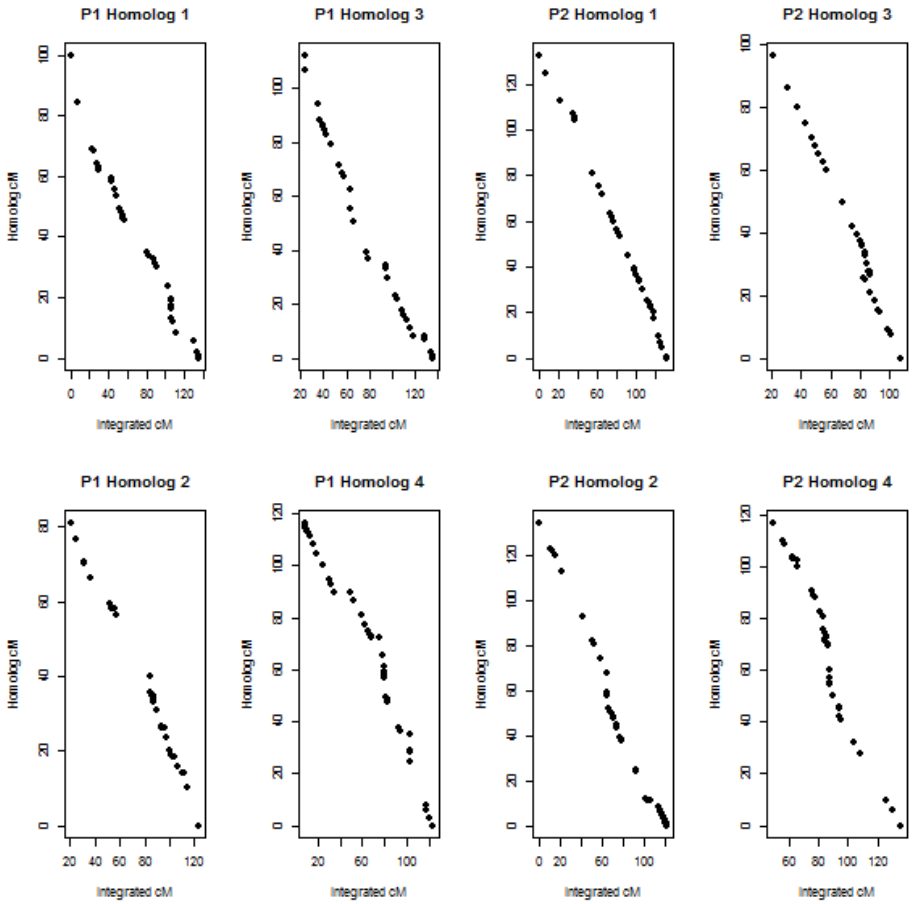


Figure 20. The map positions of the markers on the homolog maps are plotted against the map positions in the integrated map of chromosome 11. The homolog maps have a good correlation with the integrated map. The plots of the individual homolog maps against the integrated maps of other chromosomes can be found in Appendix 16.

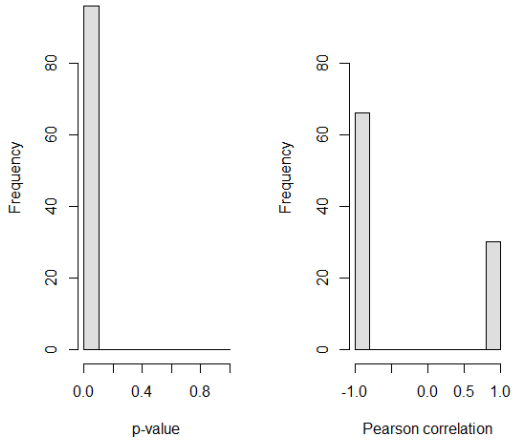


Figure 21. The Pearson correlations between map positions of the underlying homolog maps and the integrated map. The left plot shows the p-value of the Pearson correlation, which is significant in all cases. The right plot shows the Pearson correlation of the maps.

When the integrated map of homolog 11 is plotted against the physical positions together with the homolog maps (Figure 22), a number of things can be noted. The first thing that comes to mind is the coverage of the markers in the plot. All the regions (centromere and the arms) are covered well by markers. The second thing that can be noted is the relative smoothness of the curve, when considering that 8 homolog maps were integrated. Another thing that can be noticed is that the physical position of one marker, from homolog 2 of P2, around 70cM on the integrated map is out of range of all the other markers. This can indicate that the physical position of this marker is not good (and probably unrealistic) and needs to be revised. In addition, markers that did not have any physical information were treated as if they had a physical position of 0 bp. By plotting those markers, there relative physical position can be figured out based on the integrated map. Such an example can be found around 100 cM, meaning that the relative position of this marker should be at about $4 * 10^7$ bp.

Figure 22 is only one example, but the other integrated chromosomes can be evaluated in a similar fashion (Table 10; Figure 23). The first thing that comes to mind when looking at all the integrated chromosomes is that some integrated maps appear to have two centromeres. This can pinpoint to conflicting homolog maps or a lack of bridge markers in the centromere.

Furthermore, literature on previous linkage maps can be compared with the integrated chromosome maps. Chromosome 6 is known for its short arm (Van Os *et al.*, 2006), which can be seen from Figure 23. Chromosome 5 is metacentric (Van Os *et al.*, 2006), which means that both arms are equally long. Chromosome 2 is telocentric (Park *et al.*, 2007), which is indicated with a centromere in the telomere and thus one long arm. Chromosome 12 is also telocentric according to Park *et al.*, (2007), but cytogenetic studies suggest that this is not the case (Gavrilenko, 2007), which is in correspondence with the integrated map.

Another way of looking at the quality of the integrated map, is by looking at the markers that are actually loci of the same gene. The 6 loci of D_locus_(DFR) are all located on chromosome 2 at 80.43 cM, the two R2 loci are both located on chromosome 4 around 30 cM, the 6 solcap_TUBER markers are all located on chromosome 10 around 56cM and the three Plocus_F35H are all located on chromosome 11 at 102.37 cM (Appendix 9). The fact that all the loci of different genes are mapped together on the integrated map indicates that the mapping of the homolog maps in combination with integration performed well.

Based on the Pearson correlation between the homolog maps and the integrated map, the comparison between the integrated map with the physical information, the comparison with literature, and mapped loci of the same genes, it can be concluded that the integrated maps are of good quality. The integrated maps covered in total 1406.13 cM for 12 chromosomes and contained 5165 markers (Table 10; Figure 23). The majority of the markers were SxN markers and the other marker types were used as bridge markers. The coverage (N markers / map length in cM) was on average 3.71. This is a major increase in marker coverage when considering the previous integrated map (Hackett *et al.*, 2013), which had a coverage of only 1.22 (Appendix 13).

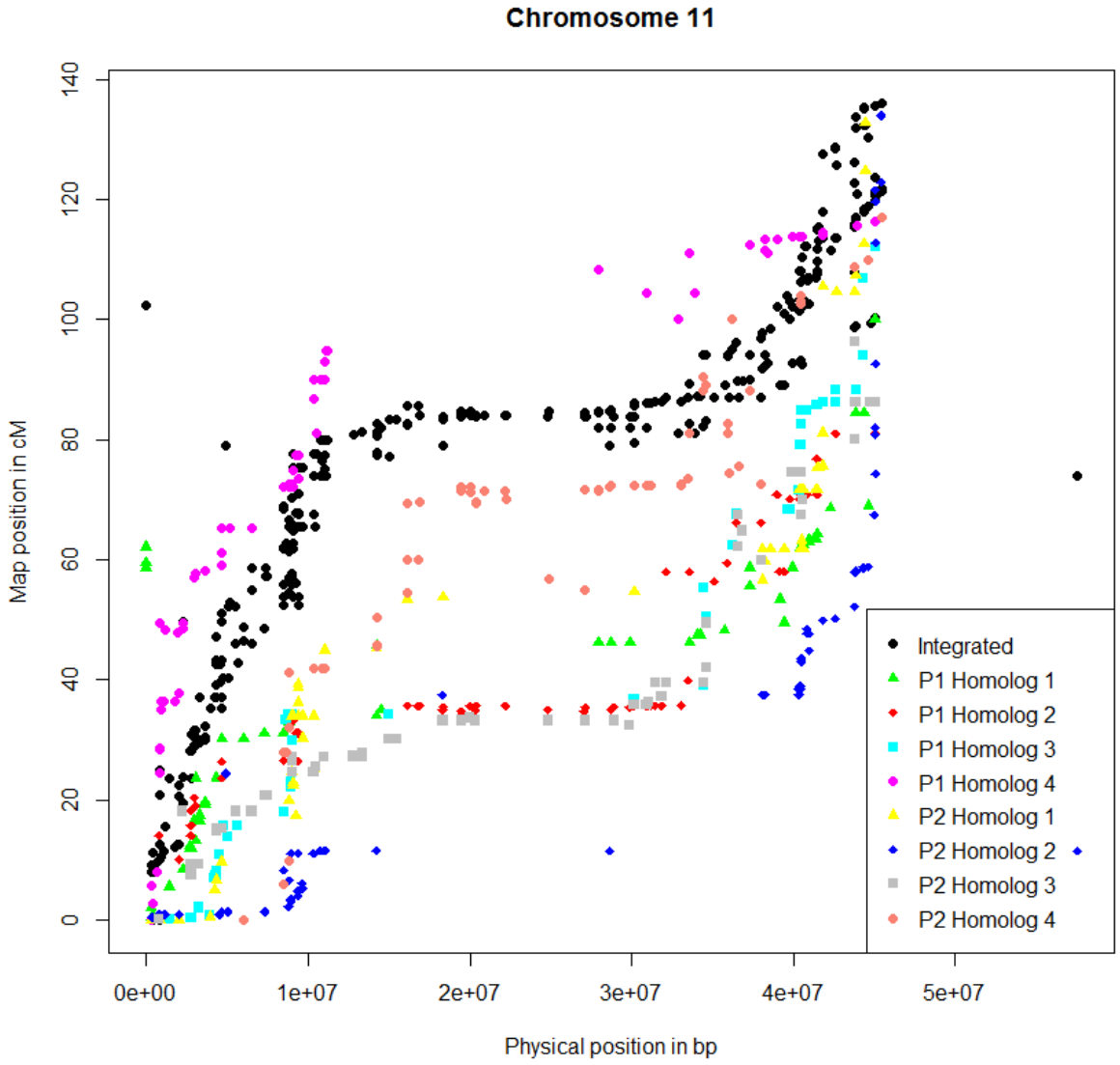


Figure 22. Map positions of the integrated map and homolog maps against the physical positions of chromosome 11. The map positions of the integrated map are plotted against the physical positions. The original map positions of markers on the individual homolog maps are plotted against the physical positions as well.

Table 10. Overview of integrated chromosomes. This table shows the Residual Mean Square Error (RMSE) and standard deviation (sd) from the integration of 8 homologs into an integrated map per chromosome by LPmerge. The number of markers and total map length are shown together with the size of gaps. The coverage of markers per map distance and base pairs is shown as well. The physical position of the markers come from the sequence information (Vos *et al.*, 2014;The Potato Genome Sequencing Consortium, 2011). The Spearman correlation between the physical positions and the integrated map positions is shown as well. The number of markers per integrated chromosome per marker segregation type is presented in this table.

Chromosome	Mean RMSE	sd	Markers	Map length in cM	Gaps > 10cM	Gaps> 1cM
1	20.44	10.58	624	141.7		44
2	24.89	15.04	544	118.9	1	30
3	16.71	8.33	459	125.57		38
4	23.88	15.78	478	151.26		42
5	14.9	10.06	545	101.75		29
6	18.99	9.91	352	121.2		33
7	8.24	4.39	447	94.78		22
8	11.08	8.33	450	102.85		27
9	16.2	10.35	369	119.06		39
10	15.38	4.24	213	109.83	1	33
11	20.11	11.27	396	136.1		39
12	13.91	11.95	288	83.13		30
Total (sum or average)	*17.0608333*	*10.01917*	*5165*	*1406.13*	*2*	*406*

Chromosome	Coverage N/cM	Coverage N/MB	Spearman-correlation	p-value	SxN	DxN	SxS
1	4.40366973	9.984	0.981313	0	338	95	129
2	4.57527334	12.65116	0.981313	6.83e-259	359	46	118
3	3.65533169	18	0.975320	6.092e-302	262	95	65
4	3.16012165	9.192308	0.977070	6.32e-322	267	74	103
5	5.35626536	15.13889	0.935467	1.90e-247	353	93	55
6	2.90429043	8.8	0.979327	5.28e-245	219	45	78
7	4.71618485	14.19048	0.968993	2.55e-272	227	93	91
8	4.37530384	16.36364	0.960020	7.44e-250	228	46	78
9	3.09927768	12.09836	0.955169	4.31e-196	197	72	72
10	1.93936083	5.195122	0.902943	2.47e-79	110	48	38
11	2.90962528	12.375	0.947498	3.37e-197	229	57	66
12	3.46445327	7.384615	0.975454	5.38e-190	165	64	39
Total (sum or average)	*3.71326316*	*11.78113*	0.96165725	2.24e-80	*2954*	*828*	*932*

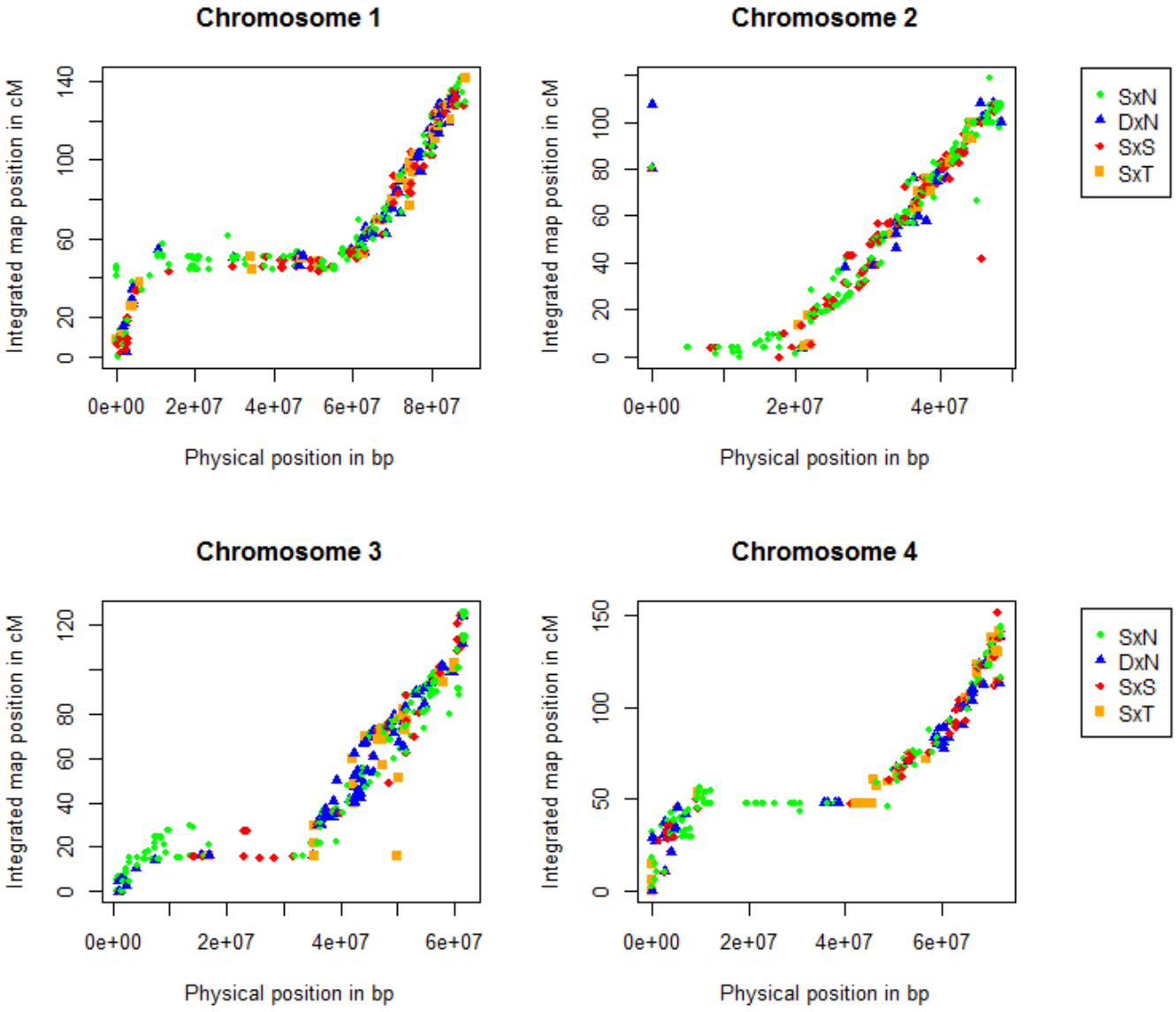


Figure 23. Integrated map positions per chromosome plotted against the physical positions. The marker segregation types are shown with their corresponding map positions and physical positions. Physical positions with missing values were set at 0 bp to allow those markers to be plotted. In this way one could estimate very roughly the physical position based on the genetic position on the integrated map.

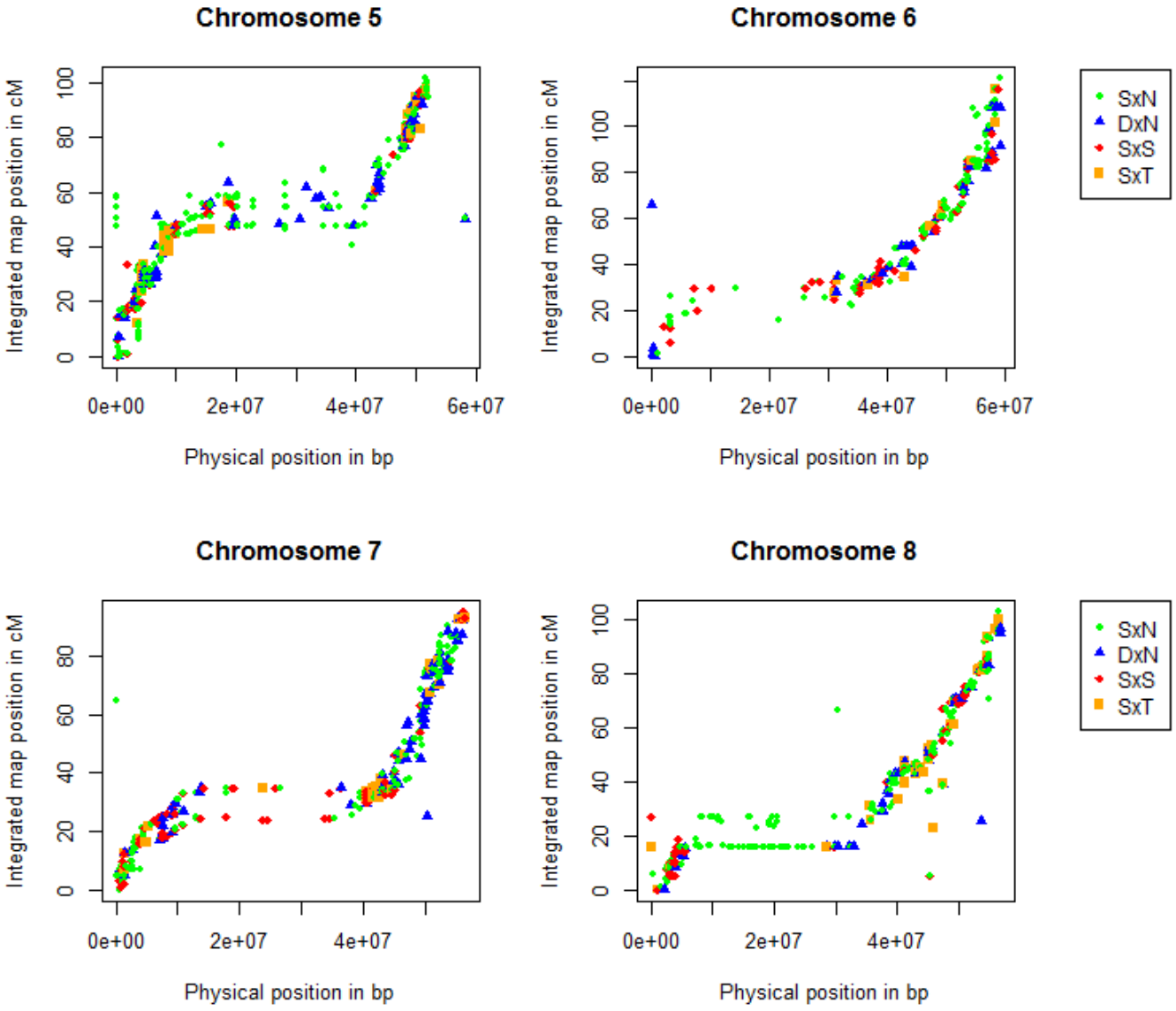


Figure 23. Continued

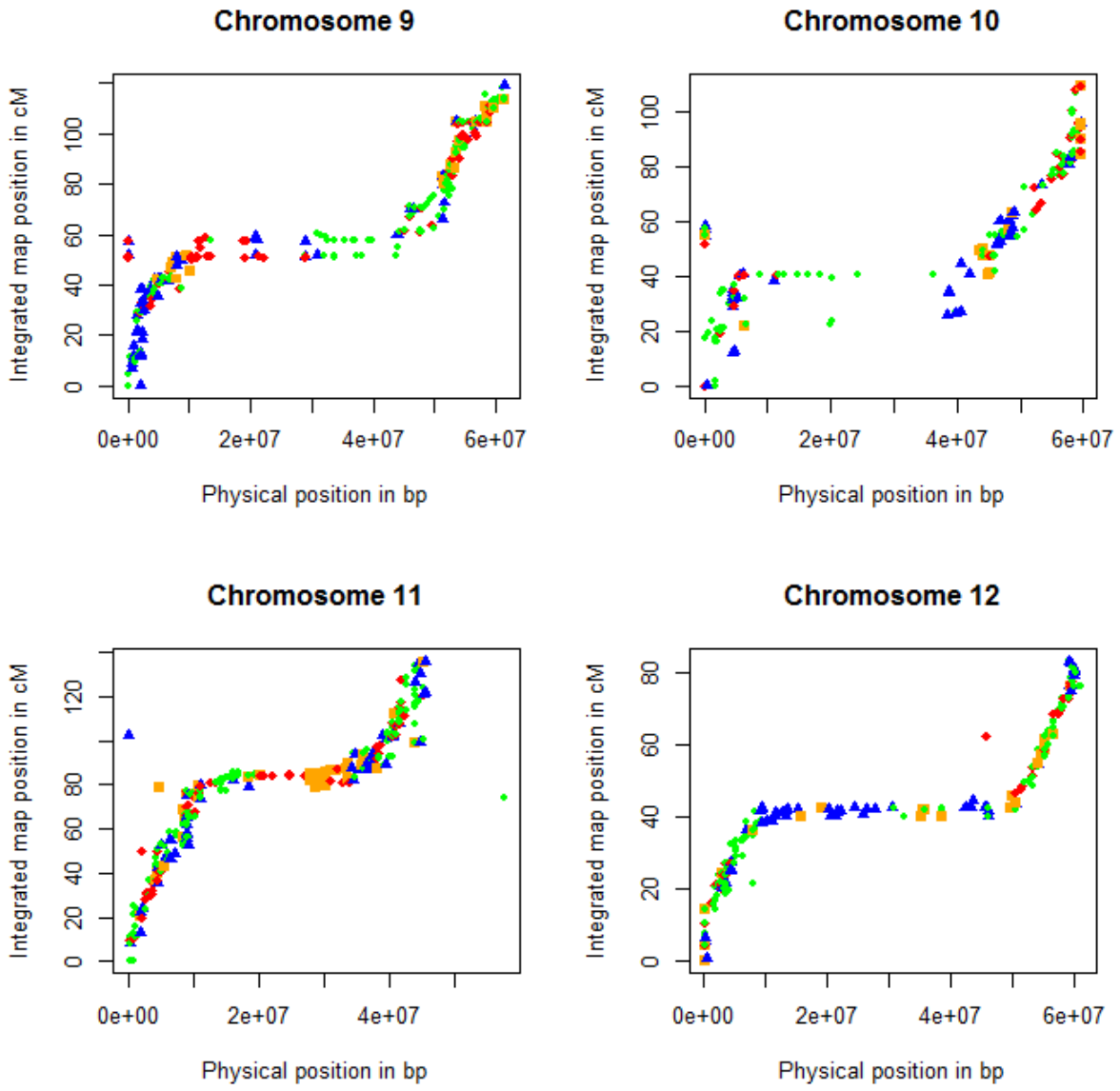


Figure 23. Continued

Conclusion Chapter 7:

LPmerge was used to integrate the homolog maps. Integration of homolog maps with LPmerge was extremely fast in terms of computational time. The integrated map covered in total 1406.13 cM for 12 chromosomes and contained 5165 markers. The integrated map showed good correlation with the individual homolog maps. Furthermore, it showed a good correlation with the physical positions. In addition, it can allow for a rough estimation of the physical position for markers with no assigned physical position.

Discussion and future prospects

Linkage mapping pipeline in R

Currently genetic and statistical tools to analyze polyploids species are either lacking, very basic (Dufresne *et al.,* 2014) or cannot handle large number of markers (Hackett & Luo, 2003). However, it is important that genetic analysis on polyploidy organisms can be performed, since many crop species, such as potato, are polyploids. Therefore there is a desire to make a pipeline that covers all the steps from marker development to QTLs in polyploids. In this thesis, a mapping pipeline in R was built from dosage scored marker data to an integrated map for tetraploid potato. The strategy to build the integrated map involved several steps, starting from the calculation of the recombination frequencies between SxN markers and ending in integrating homolog maps. In the Discussion and Future Prospects, all the steps of the mapping pipeline are discussed with relation to the performance, literature or other programmes, and speculation with regards to errors and violation of the assumptions. Finally, the significance of the thesis overall is explained with regards to future developments in tetraploids.

Mode of inheritance

In Chapter 1, the recombination frequencies and LOD-scores between SxN markers were calculated. Many SxN markers were evaluated with respect towards the mode of inheritance. Based on the repulsion recombination frequency estimates, it could be concluded that potato is an autopolyploid, as indicated by Bradshaw (1994) and no preferential pairing occurs (Assumption 7). Although, other methods for testing the mode of inheritance could be used (Vukosavljev *et al.*, 2014), this method worked well for potato.

The method presented here can be applied to other tetraploid species as well and was used for *Alstroemeria*. The preliminary results of *Alstroemeria* indicated that a certain degree of preferential pairing is present (Appendix 15). Other lines of evidence, such as the inheritance of DxS markers, indicate that indeed preferential pairing occurs (Shahin, personal communication), however, on which chromosome(s) and to what degree preferential pairing occurs is not known yet.

Since the recombination frequencies between SxN markers are needed for most software, the method to investigate the mode of inheritance via SxN markers is a desirable method. Another way of investigating the mode of inheritance within this pipeline would be to check the ratio between coupling and repulsion linkages, which might provide a crude estimate for the amount of preferential pairing (Wu *et al.,* 1992).

The mode of inheritance was investigated based on repulsion recombination frequency estimates. Under the tetrasomic model, as used for autotetraploid species, the repulsion estimate of the recombination frequency can be negative. In some cases the recombination frequency of both repulsion and coupling phase were out of the 0 to 0.5 range for recombination frequency estimates. It is common practice to estimate the phase as repulsion between the two SxN markers and set the recombination frequency at 0 (Hackett *et al.,* 1998), which is essentially a loss of information. Wu *et al.,* (1992) indicated that negative recombination frequency estimates might indicate a violation of the assumed number of homologs. Another possible explanation for the phenomena of negative recombination frequency estimates could be the huge standard error that repulsion linkages have regardless of the population size (Hackett *et al.,* 1998).

A way of illustrating the low information content of repulsion linkages, due to large standard errors, is that the repulsion recombination frequencies have a much lower LOD-score when compared to coupling linkages. Combining the large standard error with a low LOD-score, it can therefore be concluded that it is not wise to use these estimates in the map integration process, which does happen in the statistical pooled approach of JoinMap for example. In this thesis, the repulsion estimates are not used in the map construction and integration (see below).

Clustering SxN markers into linkage groups

In Chapter 2, the LOD-score of linkage was used to cluster the SxN markers into linkage groups. The algorithm described by Van Ooijen & Jansen (2013a) was used in this thesis as well as by JoinMap. Both programmes gave identical results, although in JoinMap the LOD of independence was used instead the LOD of linkage. Whether the algorithm will cluster the markers in the same way when other linkage thresholds, such as the test of linkage of Mather (described in Chapter 1) or the G^2-test of JoinMap, are used, is currently unknown.

When the same method was applied to *Alstroemeria*, the SxN markers did not cluster until SxN markers with more than 10% missing values were excluded from the data. This indicates that this method used here is vulnerable to single (or multiple) unreliable markers. Ronin *et al.,* (2010) recognize this problem as pseudo-linkage, which means that two markers of different linkage groups have lower recombination frequencies (or higher LOD-scores) than markers on the same linkage group. In the approach of Ronin *et al.,* (2010) markers are clustered in linkage groups for different LOD-score thresholds and at the same time ordered. Jansen (personal communication) suggested to use another method of clustering SxN markers into linkage groups, namely based on the recombination frequency. In this approach, markers with a low recombination frequency are grouped together while markers with a high recombination frequency are excluded. Whether clustering markers based on the recombination frequency is less vulnerable to single marker deviations is currently not known. For the clustering of markers into linkage groups only SxN markers were used. However, whether it is possible to use the same approach for all the marker types at once is currently not known.

In addition to comparing the clustering method of this thesis with the clustering method of JoinMap, the clustering method was also compared with the information of the physical chromosomes. The physical chromosomes and the clustering method were not identical. This could indicate that some markers are wrongfully assigned to chromosomes. Another explanation is that markers are duplicated in the genome and thus are located on two chromosomes (a violation of assumption 6). If indeed markers are located on two chromosomes, the calculation of the recombination frequencies and LOD-scores will be wrong for those markers, since the dosage scores are actually a mixture of two markers. It is therefore likely that in those situations the markers will not map well. Although it was not investigated if such markers are present on the current SNP array, it is very unlikely that the violation of this assumption will have an effect on the integrated map, since there are only a few markers that are wrongfully assigned to linkage groups based on the physical chromosomes (and only a fraction of those are likely to be a duplicated marker).

Clustering SxN markers into homologs

In Chapter 3, the SxN markers were assigned to homologs. Currently, software to assign SxN markers to homologs is not available. Previously, homolog assignment of SxN markers was based on the ordering of SxN markers of a linkage map with JoinMap (or other diploid mapping programmes) and identifying the correct phase from the order (Maliepaard, personal communication; Hackett *et al*., 2013). In this thesis a method to assign SxN markers to homologs was developed and this method uses the phase information (coupling or repulsion) of SxN markers. This method produces a phase-tree which a user can cut into four or more homologs (or sub clusters). For most chromosomes this led to four distinctive homologs. However, for some homologs the distinction was not clear and therefore the phase-tree was cut in five sub clusters (or artificial homologs). To put two sub clusters together into one biologically meaningful homolog, another source of information was used, namely the linkage between SxN and DxN markers. The SxN with DxN linkages contained enough information to put two sub clusters together into one real homolog for most chromosomes except two. For these two chromosomes, other sources of information were used, such as the physical positions of the SxN markers. The phase-tree and SxN with DxN linkage proved to be useful methods to separate the homologs from each other. Although this methodology is not perfect yet, it is a step in the good direction, especially when considering previous methods to separate the homologs did not exist before.

Currently, it has not yet been investigated how the phase-tree approach will work under different degrees of preferential pairing. In species with a degree of preferential pairing, the homologs are not as distinctive as in autotetraploid potato. This might prove to be a problem in terms of the formation of sub clusters in the phase-tree. However, a true allotetraploid (complete preferential pairing) species, such as wheat, could be handled as a diploid and therefore this problem will only exist from species with a degree of preferential pairing.

Other marker types

In Chapter 4, the recombination frequencies, LOD-scores and the phase was estimated for all marker segregation types (SxN, DxN, SxS, SxT) combinations. The SxT markers were assigned to chromosomes and homologs in this chapter, while SxS and DxN markers were already assigned to chromosomes and homologs in the previous chapter. Hackett *et al.,* (2013) simulated the recombination frequencies of the different marker combinations. In this study the simulated recombination frequency of a SxS marker with a SxT marker differed greatly from the actual recombination frequency and had the lowest LOD-score. This corresponds with the fact that the LOD-scores of SxS with Sxt markers were very low in some phases (Appendix 7). In addition to the low LOD-scores, Meyer *et al.,* (1998) found that SxS markers in mixed phase with each other had a high standard error, but on the other hand SxS markers or SxT markers in coupling phase show a high LOD-score (Hackett *et al.,* 2013; Appendix 7). The same was found for SxS with SxN markers in repulsion (Meyer *et al.,* 1998). Additionally, Hackett *et al.,* (1998) found that also DxN with DxN markers in mixed and repulsion phase had a high standard error. This is another indication that the recombination frequency estimates of markers in mixed and repulsion phase may not be reliable, although in some cases the repulsion estimates might be useful (Mester *et al.,* 2003b). A recommendation by Bourke (personal communication) was to set the LOD-score of uninformative phase situations at 0. What the effect of setting the LOD-score at 0 in the mapping procedure will be when implemented has yet to be investigated.

The two marker types that are not considered in this thesis, DxS and DxD, need such an implementation since also here the LOD-scores are low (Hackett *et al.*, 2013) and are not informative (Meyer *et al.*, 1998). Although these marker types could be useful for map integration and provide extra coverage to interesting regions, such as QTL regions, with the current approach I would say that those marker types are too uninformative to be mapped well. Furthermore, it is doubtful if these marker types would be beneficial since the marker density of the integrated map is already high.

Adjusting estimators of the recombination frequencies

When the recombination frequencies are calculated, it is good to keep possible violation of the assumptions and possible errors into account. For example, it is known that double reduction occurs in potato (Bourke *et al.*, 2015; Haynes & Douches, 1993), but one of the assumptions is that this not happen or does not influence the mapping of markers much (Assumption 8). What the effect is of the violation of such an assumption is currently not known and it would be interesting to see its effect in both simulation and real data studies. Preliminary results show that the formation of quadrivalents, leading to double reduction, does not influence the estimation of recombination frequency of SxN markers in coupling (Bourke, personal communication).

A way of accounting for errors is to adjust the recombination frequency estimators for the errors and violations of the assumptions. For example, Liu (1997b) developed a method to adjust the estimator of the recombination frequency for skewedness in a diploid F2 population by introducing two distortion parameters. Without doubt, a similar method can be applied to tetraploids as well. Currently, no software available can handle these kind of skewedness models, however it would be relatively straightforward to implement a similar model for tetraploids in the pipeline of linkage mapping described in this thesis

Apart from adjusting for skewed markers in the recombination frequency calculation, other deviations can be handled when the estimator of the recombination frequency is adjusted. For example, a model has been developed to account for degrees of preferential pairing and double reduction by introducing extra parameters into the recombination estimator (Wu *et al*., 2002b; Wu *et al.*, 2004b). In this way, the pairwise recombination frequency for allotetraploids can be calculated. Such recombination frequency estimators could allow the linkage mapping pipeline, described in this thesis, to be expanded to allotetraploids as well. In addition, Rhemsmeier (2013) includes five parameters, including preferential pairing and multivalent formation, into the calculation of the recombination frequency. Göring & Terwilliger (2000) developed estimators for the recombination frequencies in diploids that allow for the presence of genotyping errors (see below), which could potentially also be implemented in the recombination frequency estimators of tetraploids. Furthermore, there are several other deviations that could be implemented, such as unequal recombination rates in both parents (Assumption 11; Plomion & O'Malley, 1996). However, so far, this is not done and this is a challenge for the future.

Ordering with linear regression, time-efficiency and co-segregating markers

In Chapter 5, the ordering of markers by the linear regression approach was explained. The linear regression uses the recombination frequencies between markers to estimate the map distances. The squared LOD-score functions as a weight in the linear regression. The time the linear regression method approach takes to map all the markers increases exponentially with the number of unique (not co-segregating) markers to be mapped. This can be problematic in the future, since there is a tendency to use more markers (see below) or in case of large populations (less co-segregating markers due to many recombination events). It is therefore needed to also implement other mapping algorithms within the same pipeline as presented here. Not only will this very likely speed up the process of mapping, but will allow the user to choose a method he or she desires. Furthermore, another beneficial effect of having two (or more) mapping algorithms that can be selected within the same pipeline is that the orders estimated by different mapping algorithms can be compared for (in)consistencies.

In addition, efficient programming in R might speed up the computational process in R (Visser *et al.,* 2015). The code written in R can be optimized by an experienced programmer and this is definitely a challenge for the future.

Another way of improving the speed of the linear regression method is by taking out co-segregating markers. In this thesis, a marker was considered co-segregating with another marker when the recombination frequency was zero. However, as was noted above, this might lead to false positives when there are marker type and phase combinations which are uninformative and thus another way of taking out co-segregating markers is desired. Another viewpoint on taking out co-segregating markers is that currently the number of markers is surpassing the mapping resolution (based on the population size as well as other parameters) and therefore only a few markers can be genuinely mapped (Ronin *et al*., 2010). According to the authors it is therefore necessary to bin markers. The question then becomes how to select the right markers for the estimation of a skeleton map. Wenzl *et al.,* (2006) for example bin markers based on the so-called segregation signatures of markers, while Van Os *et al.,* (2006) use a different but similar approach with a bin signature. A method for successfully binning marker has yet to be implemented in the R pipeline.

Furthermore, during the mapping procedure thresholds are considered, such as a value of 3 for the jump-test. What the effect of these thresholds is on the map order is currently not known and is worth investigating. A simulation study with a known marker order might reveal the sensitivity for the different threshold used in this thesis.

Although the points mentioned above, linear regression has the advantage that it only needs the distances, which are converted from recombination frequencies, and the LOD-scores. This indirectly means that the linear regression approach is not only suitable for tetraploids, but also for higher ploidy levels, as long as the recombination frequencies and LOD-scores are calculated. So far this has been done for hexaploid sweet potato (Kriegner *et al.,* 2003) and octoploid sugarcane (Aitken *et al.*, 2007) with JoinMap's regression approach for example. Similarly, mapping those species could easily be done with the linear regression method proposed here in R when the recombination frequencies between markers from higher polyploidy levels are calculated.

Homolog maps and map evaluation

In Chapter 6, the marker types, SxN, DxN, SxS and SxT, were ordered and presented as homolog maps. One SxN map was compared with both ordering methods, linear regression and maximum likelihood, of JoinMap. The three ordering methods produced the same order although there were small differences in the map distances. The maximum likelihood method was the fastest of the three ordering methods considered in this example. The order of the regression method presented in this thesis was most similar with the order of the maximum likelihood method of JoinMap. When all the SxN homolog maps were compared with the order estimated by the maximum likelihood approach of JoinMap, it was found that both methods produced maps which are comparable in order and size. In addition, the physical positions were used as a verification of the map order.

Furthermore, the other marker segregation types were mapped. These maps were compared with the physical positions. The physical map positions and the linkage map positions were strongly correlated. This is an indication that the ordering by the linear regression method works for the other marker segregation types as well. One note should be made that the map length appears to increase, although not quantified, when more marker and marker types are added (see below). An explanation for this could be that markers in the mixed phase are not very informative as previously discussed, but are used in the ordering.

Apart from comparison with JoinMap and the physical positions, the homolog maps were also evaluated by two new methods. The first method is plotting the LOD-scores and recombination frequencies by means of a heatmap. The second method is plotting the observed distances, the transformed recombination frequencies, against the expected distances from the order. The observed and expected distances should roughly be equal. Both methods allow the user to visually check the ordering process.

Integration of homolog maps with LPmerge

In Chapter 7, the homolog maps were integrated with the R-package LPmerge. LPmerge uses a graph-theory approach to integrate individual maps. The graph-theory approach is incredibly fast, especially when compared to JoinMap, where the integration takes a long time when the marker number is high (Wu *et al.*, 2008). The integrated maps showed a high correlation when compared to the individual homolog maps. Furthermore, the physical positions showed a good correlation with the integrated map too.

The integrated map with a cumulative length of 1406.13 cM for 12 chromosomes and contained 5165 markers, and thus has a high coverage. Furthermore, it has very few gaps. According to Watanabe (1994) the ultimate goal of marker development is the saturation of the genome with a maximum gap size of 1cM. Although, the integrated map has gaps larger than 1cM and thus saturation is not final yet, it is getting close (Table 21; Appendix 17).

Comparison of the integrated map and maps found in literature

Isidore *et al.*, (2003) estimated that the cumulative length of the potato genetic map should be between 600 cM and 1100 cM, while on the other hand Gebhart *et al.*, (1991) estimated that the cumulative length should be between 1200 cM and 1300 cM. Still, the integrated map presented here with 1406 cM surpasses both estimates. To evaluate the integrated map length, the genetic map presented here is compared with genetic maps in the literature (Table 11). The first tetraploid map was estimated by Meyer *et al.*, (1998) and covered 909 cM and 486 cM for the respective parents (which could indicate that the recombination frequencies in both parents are not equal; assumption 11). The most recent tetraploid map in the literature is the integrated map of Hackett *et al.*, (2013). This map covers 1087 cM and misses some homologs. Prashaw *et al.*, (2014) estimated the most recent diploid map, which covers only 753.9 cM, which is a decrease in map length when compared to previous diploid potato maps. Furthermore, recently a consensus map has been estimated based on different maps present in the literature and covers 1260 cM (Danan *et al.*, 2012). What can be noted is that the length of all these maps differs. It can therefore be said that there is no fixed estimate for the total length of a genetic map of potato and that the quest for the true genetic map still continues. Still the map presented here is the longest potato map, but not in the *Solanum* genus, for which diploid tomato has the longest map (Table 11).

One of the reasons why the map presented here is the longest potato map, can be due to the fact that the population size is the largest. During simulation studies it is found that when the population size decreases, the cumulative map length also decreases (Hackett *et al.*,, 1998). In addition, the difference in the true position and the map position increases when the population size increases. The limited number of informative meiosis in a small population could cause errors (DeWan *et al.*, 2002). This appears not to be the case in this particular population, since the mapping population is large. Based on the past literature, there was no correlation of total potato map length (including the map of this thesis) and the population size (Pearson correlation 0.247, p-value 0.464; Table 11). What is causing the conflict between the simulation study and the published genetic maps is currently not known.

What can be seen in Table 11 though, is that there is a correlation between the number of markers used and the total map length (Pearson correlation 0.665, p-value 0.0094), between the number of markers and the publication year (Pearson correlation 0.639, p-value 0.0138) and between the population size and the publication year (Pearson correlation 0.639, p-value 0.0139). It appears that the number of markers in the map is more a measurement for the cumulative map length than the population size. Consequently, correctly binning of markers shortens linkage maps (Ronin *et al.*, 2010).

Table 11. Overview of linkage maps of potato found in literature, the integrated map of this thesis and linkage maps of other *Solanum* species. The type of the map, population size, length and the number of markers are used as a statistic for comparing the maps. Furthermore, authors and the publication years are included in the table as well.

Authors	Publication year	Type	Population size	Total length (cM)	N Markers
Potatoes					
Gebhardt *et al.*	1991	diploid	67	1034	304
Tanksley *et al.*	1992	diploid	155	684	134
Jacobs *et al.*	1994	diploid	67	1120	270
Meyer *et al.*	1998	tetraploid	94	909.9	231
Meyer *et al.*	1998	tetraploid	94	486.6	106
Menéndez *et al.*	2002	diploid	189	750	447
Feingold *et al.*	2005	tetraploid	42	792	55
Luo *et al.*	2006	tetraploid	228	888	201
Danan *et al.*	2011	consensus	-	1260	2141
Felcher *et al.*	2012	diploid	?	965.3	944
Felcher *et al.*	2012	diploid	?	792.1	637
Hackett *et al.*	2013	tetraploid	190	1087.5	1301
Prashar *et al.*	2014	diploid	186	753.99	2157
This thesis	2015	tetraploid	237	1406.13	5165
Other *Solanum* species					
Sim *et al.*	2012	Tomato (diploid)	79	1669.9	3503
Sim *et al.*	2012	Tomato (diploid)	160	1154.6	3687
Sim *et al.*	2012	Tomato (diploid)	183	1049.2	4491
Gramazio *et al.*	2014	Eggplant (diploid)	91	1085	234
Iorizzo *et al.*	2014	*S. Bulbocastanum* (diploid)	?	644.9	409

Effect of errors and violation of assumptions on mapping

One of the reasons that more markers might increase the map length is because with more markers there is a higher change on errors. One of these errors is assigning a wrong dosage to a marker which can have a huge impact on the accuracy of the map by inflating the map length (Cheema & Dicks, 2009). Cartwright *et al*. (2007) explain that every 1% error rate inflates the map with 2 cM. Brzustowicz *et al.* (1993) even found that a 3% error rate can double the map length. It is good to note that the error rate can be estimated for a specific SNP array (Saunders *et al.*, 2007), although estimating the error rate for a specific marker is often labour intensive, it is possible (Hoffman & Amos, 2005). When the global error rate, for a specific SNP array, is known, the true map length can be estimated from the estimated length and the number of mapped markers (Brzustowicz *et al.*, 1993).

In addition to wrong dosage scoring, missing data can lead to incorrect marker orders, especially in regions with a high marker coverage (Hackett & Broadfoot, 2003). Even though, on a local level the marker order might be wrong due to missing data, it is doubtful that it will distort the global order (Maliepaard, personal communication). Markers with many missing values were not removed before ordering or before calculation of the recombination frequency during this thesis. Considering that markers with missing values can lead to an incorrect order, it may be wise to have a pre-selection of the markers (Pompanon *et al.*, 2005) before the markers enter the mapping pipeline described in this thesis. An example of a pre-selection is a 10% missing value threshold, as was used in *Alstroemeria* (see above; Appendix 15), meaning that markers with more than 10% missing values are excluded prior to the analysis.

Hackett & Broadfoot (2003) mention that missing data in combination with segregation distortion (violation of Assumption 3) will shorten the map when the linear regression method of JoinMap is used, however this is in contrast to my personal observations (results not shown). Although, under normal conditions, the linear regression method of JoinMap is longer than the linear regression method used in this thesis and the maximum llikelihood method of JoinMap (Figure 12). Furthermore, Hackett & Broadfoot (2003) also mention that segregation distortion does not affect the map order much, but this is in contrast with other studies (Cheema & Dicks, 2009). Liu (1997b) showed that small recombination frequencies have a larger bias for segregation distortion while for larger distances the tolerance against skewedness goes up. Small recombination frequencies are of most importance in the linear regression approach and thus these findings could be worrying. However, one would still want to use the small distances in the linear regression approach, since those are most informative and large map distances are more prone to errors when compared to small map distances (Jansen, personal communication).

Another reason for the difference in map length could be that the integrated map presented in this thesis does cover more bits of the genome and previous maps are missing regions, for example telomeric regions. However, if the previous maps are missing certain genomic regions is not known since no comparison between those genetic maps and the physical positions has been made yet.

In addition, during genetic mapping a lot of tests are performed. Although during this thesis multiple-testing was taken into account, errors due to multiple testing are likely to have occurred and this could also lead to inconsistencies on the map (Ripol *et al.*, 1999). Furthermore, ordering errors of bridge markers could be problematic in some cases, although LPmerge is able to remove ordering conflicts quite easily (Endelman & Plomion, 2014).

The reasons why errors in the map order are troublesome is because it could complicate the ability to map QTLs or isolate genes (DeWan *et al.*, 2002). However, a side note should be made here that small local errors in the order would likely not influence the ability to detect QTLs, but map inversions at a larger distance might. It is not very likely that there are many errors in the integrated map, since there is a good correlation between the physical positions and the linkage map, a good correlation between the SxN maps with the previous SxN map (Bourke *et al.*, 2015), the homolog maps are corresponding with the integrated map and the other evaluation methods gave no indication that the ordering might be wrong. Still, it would be interesting to see the source of possible errors and the effect on the map ordering procedure presented in this thesis. This could be done, for example, by simulating tetraploid populations with PedigreeSim (Voorrips & Maliepaard, 2012) and deliberately introduce different kind of errors.

QTL analysis

As was mentioned in the Introduction, the estimation of an integrated linkage map is one step towards QTL analysis on the tetraploid level. The advantage of doing a QTL analysis on an integrated map instead of homolog maps itself, is that the QTL analysis based on the integrated map has greater power and higher accuracy. An estimated position of a QTL with a low accuracy is a major obstacle in the application of the results of the QTL analysis (Korol *et al.*, 2012). The QTL mapping with only homolog maps need larger populations to detect the same QTL effects (Hackett *et al.*, 2001). Therefore, progress was made to estimate integrated linkage map of potato. With the marker dense linkage map made in this thesis, QTL analysis can be done and it may provide detailed information about the location of QTLs (Hackett *et al.*, 2014).

QTL mapping is a combination of linkage mapping and traditional quantitative genetics (Liu, 1997e). During QTL analysis, a significant association between traits and markers is searched for. Significant association between traits and markers may be evidence that a QTL is located nearby. The integrated marker information of the consensus map is combined in the calculation of haplotype probabilities along with the map positions to be used in the QTL analysis. This leads to greater power to find QTLs. Wu *et al.*, (2004a) developed a model for QTL analysis in outcrossing tetraploids, such as potato.

Hackett *et al.* (2014) presents a method to do integrated QTL analysis on 12 potato chromosomes. The QTL analysis was done by a combination of a Hidden Markov Model, to estimate the haplotype probabilities, and weighted regression on those genotype probabilities. Several options for the modelling of QTLs are possible in autotetraploids, such as a main effect model (Hackett *et al.*, 2013) or a mixture model (Bradshaw *et al.*, 2004). Further research will very likely show what kind of approach is most suitable for certain QTLs in potato.

A way to make QTL analysis even more powerful is to use pedigree-information (Bink *et al.*, 2002). The dosages of 3 grandparents and 1 great-grandparent are available for this population (Maliepaard *et al.*, n.d.). When more information is required, this can possible be found in public databases (Van Berloo *et al.*, 2007). By combining the integrated map with pedigree-information it will be possible to find QTLs with higher power and precision.

In addition to the ability to map QTLs, it is also possible to map Segregation Distortion Loci (SDL), such as the self-incompatibility locus located on chromosome 1 (Gebhardt *et al.*, 1991), with a similar method as mapping QTLs (Vogl & Xu, 2000).

Conclusion

In this thesis, a mapping pipeline was developed for autotetraploid species such a potato. Four different marker types were assigned to chromosomes and homologs. The markers on homologs were mapped with a linear regression approach. The homolog maps showed good correlation with the physical positions. In addition, the SxN maps showed a high correlation with the maps estimated by JoinMap. The homolog maps were integrated with the R-package LPmerge. LPmerege was extremely fast and uses a graph-theory approach. The methods were applied to a SNP dataset of tetraploid potato. From the comparison of the integrated map with the maps of other species, the genome sequence and other evaluation methods, it can be concluded that the integrated map presented here has a good quality. The integrated map presented in this thesis has a high coverage and can be used for haplotyping, QTL analysis and as a reference linkage map. The methods to estimate the map are working well for tetraploid potato and can therefore be applied to other autotetraploids as well.

Recommendations

In the Discussion and Future Prospects possibilities were discussed to improve the linkage mapping procedure described in this thesis. In the Recommendations, these possibilities and opportunities are summarized.

- Implement methods to test for degrees of preferential pairing within the pipeline from marker development to QTL-analysis for tetraploids.
- Develop a method to deal with and investigate the cause of recombination frequencies out of the 0-0.5 range (negative recombination frequencies).
- Investigate how the clustering of markers in linkage groups works when other thresholds than the LOD of linkage are used.
- Investigate what the effect is of single pseudo-linkage marker is on the clustering of markers into linkage groups.
- Investigate if the clustering of markers into linkage groups still works when other marker types than SxN are used.
- Investigate what the effect is of duplicated markers on the calculation of the recombination frequencies and LOD-scores.
- Investigate how the clustering of markers into homologs performs under degrees of preferential pairing.
- Investigate what the effect of setting the LOD-score at 0 when the phase is uninformative.
- Investigate a good way to deal with uninformative marker types, such as DxD and DxS
- Implement parameters for preferential pairing, formation of multivalents, skewedness, unequal recombination frequencies, etc. into the estimator of the recombination frequency.
- Implement more ordering algorithms in the linkage mapping pipeline.
- Investigate how to properly deal with co-segregating markers or how to implement binning in a descent way.
- Investigate the sensitivity of the thresholds used in the whole mapping pipeline.
- Investigate the effect of segregation distortion, missing values, genotyping errors, multiple testing, etc. on the ordering.
- Estimate the (genotype) error rate of the SNP array used.
- Investigate why the integrated map is one of the longest maps in the *Solanum* genus.
- Investigate what kind of pre-selection is necessary for linkage mapping.
- Implement a haplotyping and QTL-analysis in the pipeline that spans from marker development to QTL-analysis.
- Make the R-scripts more time-efficient and turn the R-scripts into a freely available package.

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Appendix 1: Editing the datasets

As mentioned in Programmes, Data and Assumptions, the initial datasets have been edited slightly in Excel for practical reasons. How the datasets are edited is mentioned for each dataset here below:

The SxN dataset for P1 (P1_Allsimxnull.xlsx) is edited by converting the dosages 2 to 0 for markers for which the parents have dosages of 3 and 0 (triplex x nulliplex) and converting the dosage 2 to 0 for markers for which the parents have dosages of 4 and 1 (quadruplex x simplex). Furthermore, the markers that have 1 as physical chromosome are converted to ST4.01ch01 as physical chromosome. In the same way 4 is converted to ST4.01ch04, 5 is converted to ST4.01ch05, 8 is converted to ST4.01ch08, 9 is converted to ST4.01ch09, chr02 is converted to ST4.01ch02,chr04 is converted to ST4.01ch04, chr11 is converted to ST4.01ch11 and Chr5 is converted to ST4.01ch05. Thereafter, the file was saved as "P1_all_simxnull.csv."

The SxN dataset for P2 (P2_Allsimxnull.xlsx) is edited by converting uu and – to NA, converting the dosages 3 to 1 and 2 to 0 for markers for which have parents have dosages of 4 and 1 (quadruplex x simplex), converting the dosage 2 to 0 for markers for which the parents have dosages of 3 and 0 (triplex x nulliplex), converting the dosages 4 to 0 and 3 to 1 for markers for which the parents have a dosages of 4 and 3 (quadruplex x triplex). Four markers PotVar0009488, PotVar0090283, PotVar0078532, solcap_snp_c2_37622) were removed from the dataset, since the parental dosages were missing and this made it hard to estimate to which dosages these markers should have been converted. Furthermore, the columns which contained information about the missing values were removed. In addition, the markers that have chr04 as physical chromosome are converted to ST4.01ch04 as physical chromosome. Also, markers that had Unknown as physical chromosome were converted to NA. After the editing, the file was saved as "P2_all_simxnull.csv."

The DxN dataset (P1_P2_All_DxN.xlsx) consisted of two sheets, one for each parent. Sheet 1 contains information of the duplex x nulliplex data of P1, which is edited by which is edited by converting uu and – to NA and converting the dosages 4 to 2, 3 to 1 and 2 to 0 for markers for which have parents have dosages of 4 and 2 (quadruplex x duplex). Furthermore, the columns which contained information about the missing values were removed. In addition to that, three markers (PotVar0029408, Potvar0068142 and Potvar0088599) were removed from the dataset since the parental dosages were missing and this made it hard to estimate to which dosages these markers should have been converted. . Furthermore, the markers that have chr10 as physical chromosome are converted to ST4.01ch10 as physical chromosome. Also chr07 is converted to ST4.01ch07. Furthermore, markers that had Unknown as physical chromosome were converted to NA. After the editing, the file was saved as P1_All_DxN.csv.

Sheet 2 is the DxN data for P2, which is edited by converting uu and – to NA and converting the dosages 4 to 2, 3 to 1 and 2 to 0 for markers for which have parents have dosages of 4 and 2 (quadruplex x duplex). Furthermore, the columns which contained information about the missing values were removed. In addition, the markers that have Chr09 as physical chromosome are converted to ST4.01ch09 as physical chromosome. After the editing, the file was saved as "P2_All_DxN.csv."

The SxS dataset for both parents (P1_P2_All_sim_x_sim.xlsx) is edited by converting Unknown to NA as physical chromosome. In the same way Chr9 is converted to ST4.01ch09. PotVar0102642 and PotVar0131737 were removed from the dataset because almost all dosages were missing values. After the editing, the file was saved as "P1_P2_All_sim_x_sim.csv."

In the dataset with the new physical position, the physical positions which were missing (#N/B) were set as 0. The advantage of this is, is that the missing physical position could potentially be inferred from the linkage maps positions. Another reason is that R will systematically fail when it encounters a non-numeric value (#N/B) in a place where there should be a numeric value. After editing, the file was saved as "Position info all infinium markers_NBRemoved.csv."

Appendix 2: Preferential pairing

In Chapter 1 the mode of inheritance of potato was investigated. It was concluded that potato indeed has tetrasomic inheritance. However, a few marker pairs tested significantly for the preferential test and of course it is interesting to see why. One hypothesis is that a skewed marker could be pulling the other markers in the pairs towards testing significant for preferential pairing. Therefore, the markers in the preferential pairing pairs are tested for skewedness by using a Binomial test (with H_0=n1/(n0+n1)=0.5; Table 12). From Table 12 it can be concluded that only a few markers are skewed. This is even more clear, when the frequency of the occurrence of a SxN marker in a preferential pair is plotted against the p-value for skewedness per physical chromosome (Figure 24). The preferential pairing markers of chromosome 2 of P1 are not skewed, but abundant, while the preferential pairing markers of chromosome 1 and 10 are few but skewed. The same pattern holds for P2, where the markers of chromosome 11 are not skewed and the marker pair of a marker on chromosome 4 and 10 contains a skewed marker (one of these markers is wrongfully assigned to the physical chromosome and this can be seen in Appendix 3). From this it can be concluded that the hypothesis, a single skewed marker is pulling other markers towards a situation that looks like preferential pairing, is not true in all preferential pairing cases. What can be seen however, is that single markers are pulling other markers. However, why this happens is currently unknown and not investigated further in this thesis.

Table 12. SxN markers that tested significantly for preferential pairing. This table included the marker name, the p-value for skewedness, the frequency of occurrence in a "preferential pairing" pair, the physical chromosome and the physical position in base pair.

Marker Name	p-value	Frequency	Parent	Physical chromosome	Physical positions (in bp(
PotVar0039036	0.18809044	6	P1	2	22151711
PotVar0039050	0.103459235	6	P1	2	22005405
PotVar0039021	0.134177819	5	P1	1	64376174
solcap_snp_c1_12024	0.007799616	4	P1	10	45944735
PotVar0032906	0.371980256	3	P1	1	64376110
PotVar0038914	0.068716964	3	P1	2	22153416
PotVar0039112	0.068716964	3	P1	2	22001826
PotVar0039162	0.118818527	3	P1	2	20906832
PotVar0039293	0.152838641	3	P1	2	20903543
PotVar0039503	0.214123258	3	P1	2	20838296
PotVar0039524	0.423773691	2	P1	2	20838027
PotVar0010678	0.224546142	1	P1	2	38654566
PotVar0010735	0.845223367	1	P1	2	38503391
PotVar0032910	0.037428085	1	P1	2	22151971
PotVar0032928	0.037428085	1	P1	1	64376527
PotVar0119199	0.603397237	1	P1	10	49584903
solcap_snp_c1_11535	0.603397237	1	P1	10	49553136
solcap_snp_c2_13751	0.026349714	1	P1	1	64614014
solcap_snp_c2_19223	0.210176728	1	P1	10	38722264
solcap_snp_c2_19225	0.103459235	1	P1	10	38723959
PotVar0054060	0.70637084	5	P2	11	14227149
PotVar0021602	0.69559142	1	P2	11	18319898
PotVar0054058	0.89623426	1	P2	11	14227218
PotVar0058240	0.02487583	1	P2	10	57479587
PotVar0101542	0.69559142	1	P2	4	4925258
PotVar0101550	0.69559142	1	P2	4	4925336
PotVar0109580	0.16967645	1	P2	4	6336502
PotVar0113358	0.60030616	1	P2	11	28638721

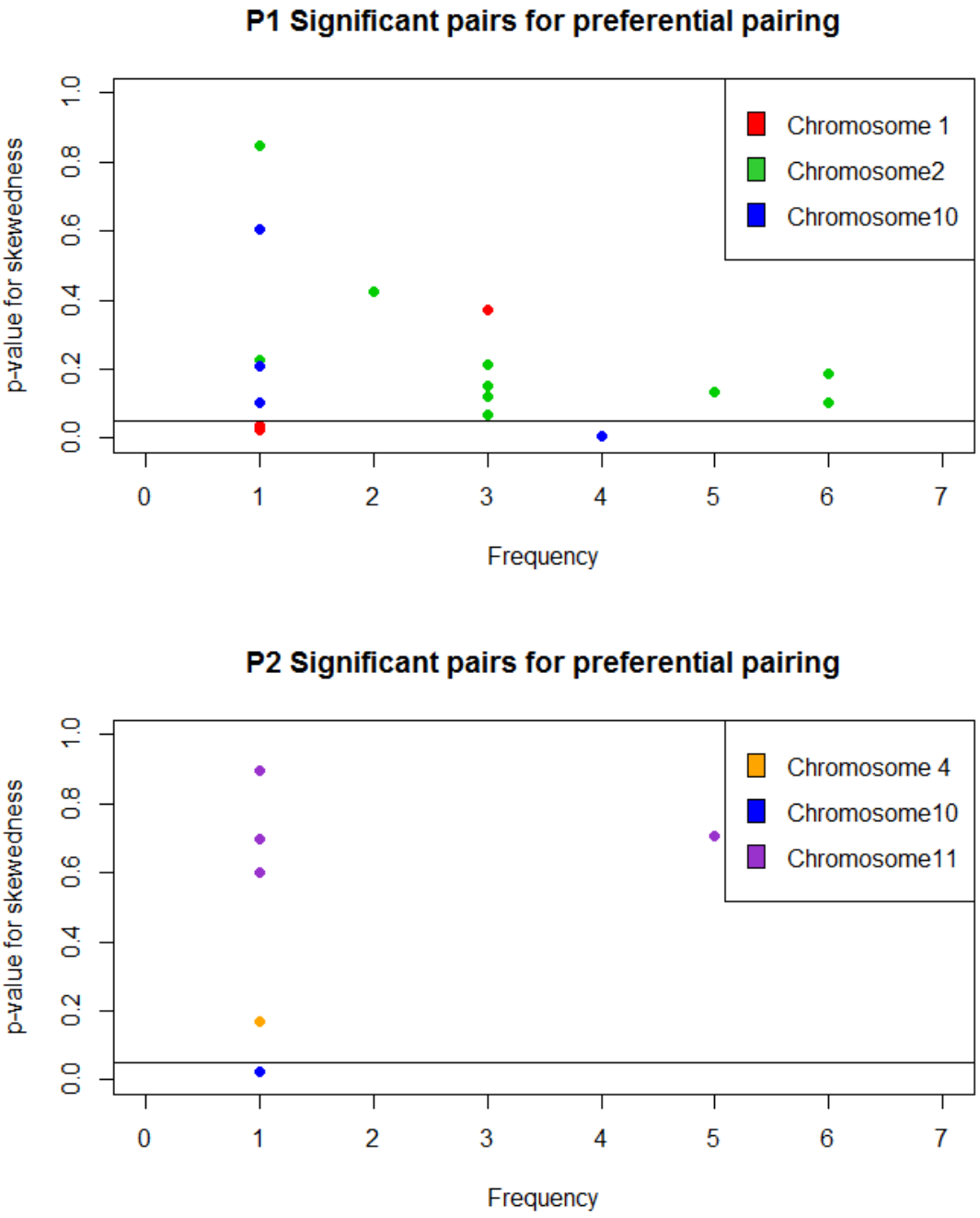


Figure 24. The frequency of occurrence of a SxN marker in a preferential pairing plotted against the p-value for skewedness per physical chromosome. It can be noted that not all preferential pairing markers on a certain chromosome are skewed.

Appendix 3: Clustering of SxN markers along linkage groups

In Chapter 2 the SxN markers were assigned to chromosomes (or linkage groups). Thereafter, the clustering method was compared with the physical chromosomes and the clustering of JoinMap. This appendix presents the consistencies and inconsistencies of the clustering method.

The SxN markers of P1 were clustered at a LOD of 5. Two markers were not clustered (PotVar0079248 and PotVar0059901). The comparison with the physical chromosomes is good (Table 13) and the comparison with JoinMap clustering (Table 14) is perfect. The SxN markers of P2 were clustered at a LOD of 5.15. Two markers were not clustered (PotVar0055484 and PotVar0077706). The comparison with the physical chromosomes is good (Table 15), however, 7 markers were not used in the comparison since those were not assigned yet to physical chromosomes. Between the physical chromosomes and the clustering methods, some inconsistencies exist. Therefore, these SxN markers are investigated a bit further (Table 16). However, most markers were located at the same chromosome in the updated physical chromosomes and public databases.

Table 13. Comparison of clustering of SxN markers of P1 with the physical chromosomes. Both methods of clustering markers are similar, although some inconsistencies exist.

	Cluster												
Chromosomes	1	2	3	4	5	6	7	8	9	10	11	12	**Total**
1	2	156											158
2			153										153
3				109									109
4					144				1				145
5						191						1	192
6							76						76
7								105	1				106
8	182		1									2	185
9									115				115
10		2								83			85
11	2	1									137		140
12			1			1						79	81
Total	186	159	155	109	144	192	76	105	117	83	137	82	**1545**

Table 14. Comparison of clustering of SxN markers of P1 with the JoinMap clustering. Both methods of clustering markers are similar.

	Cluster												
JM Chromosomes	1	2	3	4	5	6	7	8	9	10	11	12	**Total**
1		159											159
2			155										155
3				109									109
4					144								144
5						192							192
6							76						76
7								105					105
8	186												186
9									117				117
10										83			83
11											137		137
12												82	82
Total	186	159	155	109	144	192	76	105	117	83	137	82	**1545**

Table 15. Comparison of clustering of SxN markers of P21 with the physical chromosomes. Both methods of clustering markers are similar, although some inconsistencies exist.

	Cluster												
Chromosomes	1	2	3	4	5	6	7	8	9	10	11	12	**Total**
1					181				1				182
2	234												234
3		224											224
4			4					132	2	2			140
5										188			188
6		1		1			152						154
7			129			1							130
8				103									103
9											106		106
10					1			1			1	43	46
11									126	1			127
12			1			85							86
Total	234	225	134	104	182	86	152	133	129	191	107	43	**1720**

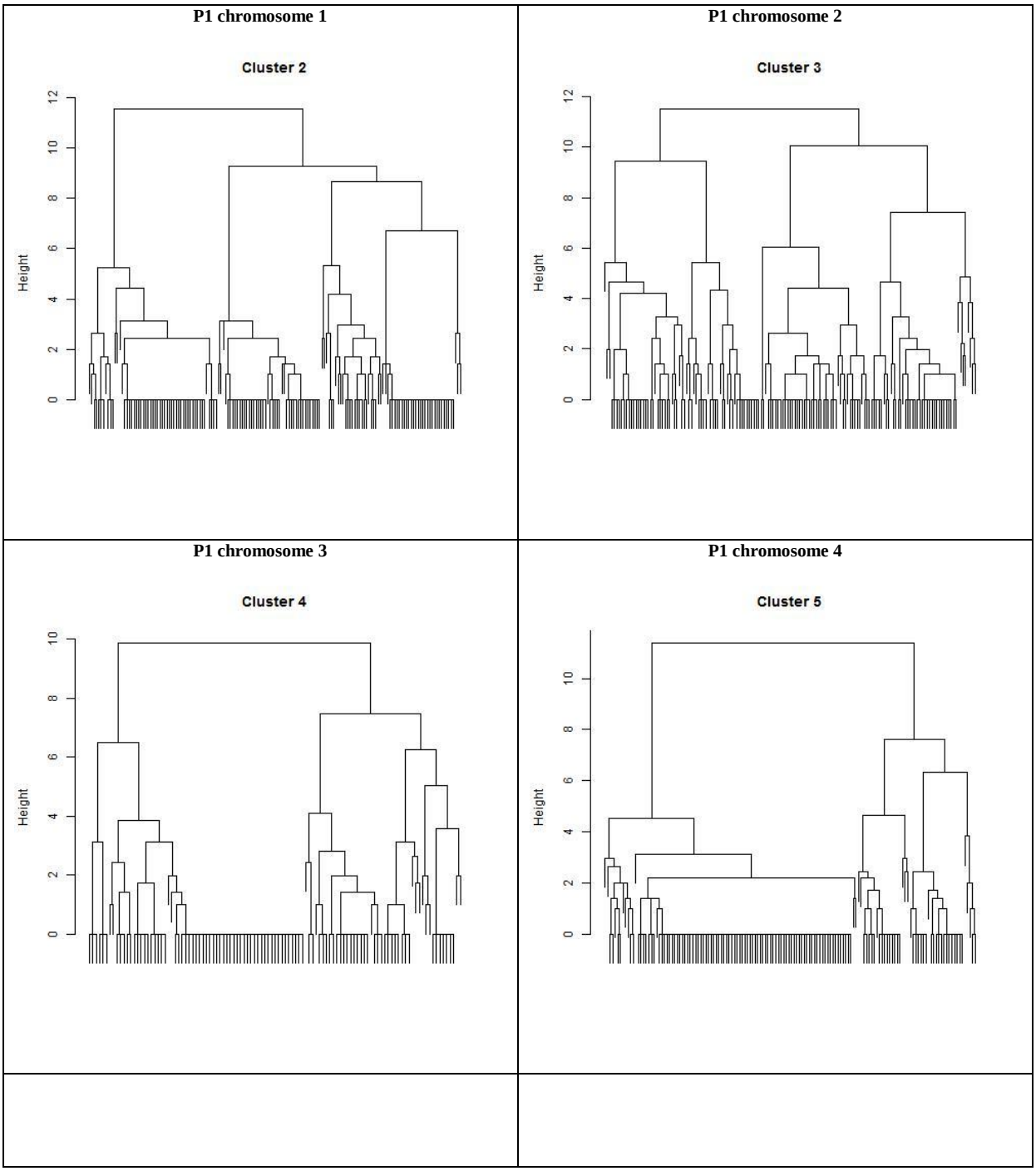
Table 16. SxN markers with inconsistencies between clustering and physical chromosomes. The markers were searched for in a public database and those results are presented under note.

Marker name	Parent	Physical Chromosome	Clustering Chromosome	Note
PotVar0081045	P1	1	8	
solcap_snp_c2_54581	P1	1	8	Still on chromosome 1*
solcap_snp_c2_32337	P2	1	11	On chromosome 1 and 11*
PotVar0050913	P1	4	9	
PotVar0032614	P2	4	7	
PotVar0032617	P2	4	7	
PotVar0032700	P2	4	7	
PotVar0032779	P2	4	7	
PotVar0101542	P2	4	11	
PotVar0101550	P2	4	11	
PotVar0084430	P2	4	5	
PotVar0084432	P2	4	5	
PotVar0125939	P1	5	12	
PotVar0085038	P2	6	3	
PotVar0069362	P2	6	8	
solcap_snp_c2_4567	P1	7	9	Still on chromosome 7*
PotVar0022107	P2	7	12	
PotVar0125072	P1	8	2	
PotVar0124931	P1	8	12	
PotVar0124993	P1	8	12	
PotVar0014240	P1	10	1	
PotVar0118576	P1	10	1	
PotVar0014615	P2	10	1	
PotVar0058240	P2	10	4	Skewed preferential pairing marker: Table 13
PotVar0118577	P2	10	9	
PotVar0118200	P1	11	8	
PotVar0118202	P1	11	8	
PotVar0071270	P1	11	1	
PotVar0047235	P2	11	5	
solcap_snp_c2_42265	P1	12	2	On chromosome 12 and 2*
PotVar0007814	P1	12	5	
PotVar0037615	P2	12	7	
* based on http://potato.plantbiology.msu.edu/cgi-bin/gbrowse/potato/ (Retrieved on 15-1-2014)				

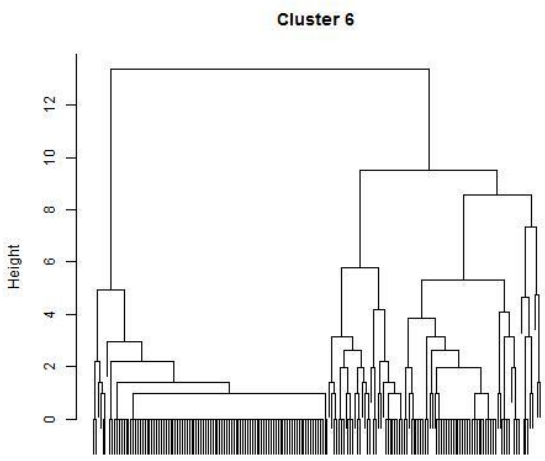
Appendix 4: Hierarchical phase trees

In Chapter 3, the SxN markers were assigned to homologs based on a phase-tree, DxN linkage and sometimes other information sources. Only the phase-tree of chromosome 11 of P2 was shown. Therefore, the phase-trees are presented here for further information (Figure 25).

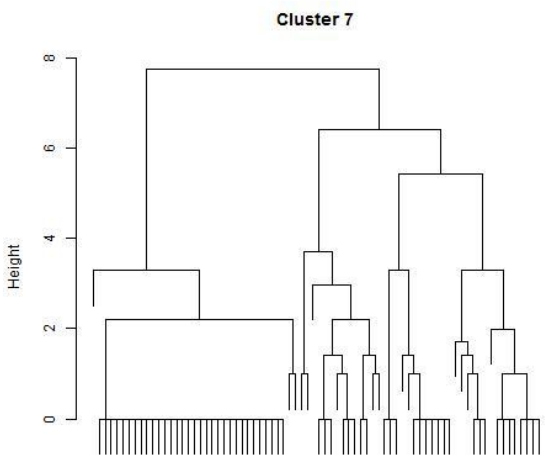
Figure 25. Hierarchical phase-trees of all the chromosomes. Most chromosomes split nicely in four chromosomes.



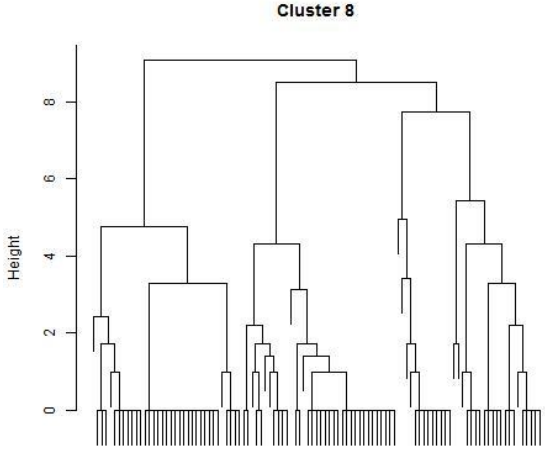
P1 chromosome 5



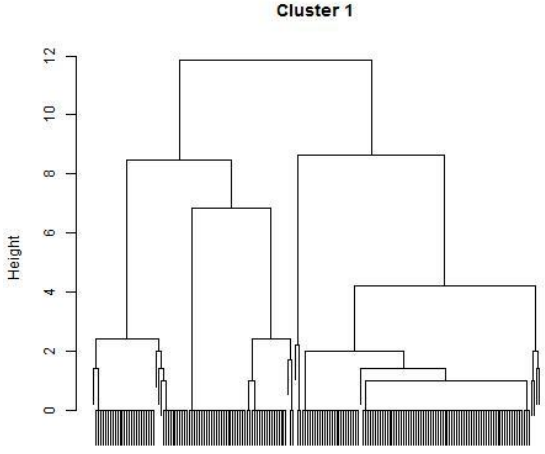
P1 chromosome 6



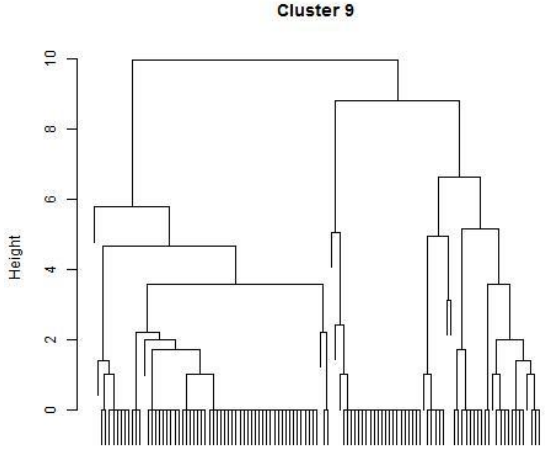
P1 chromosome 7



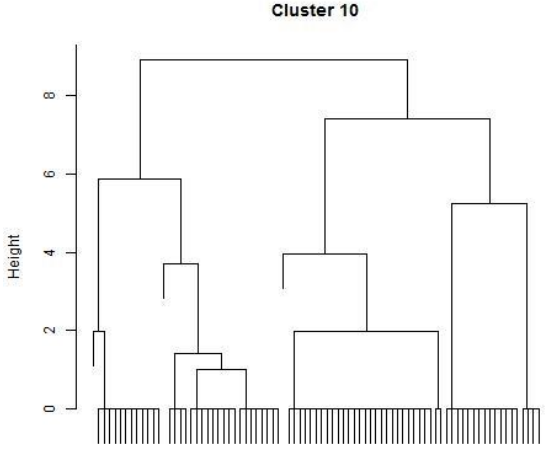
P1 chromosome 8



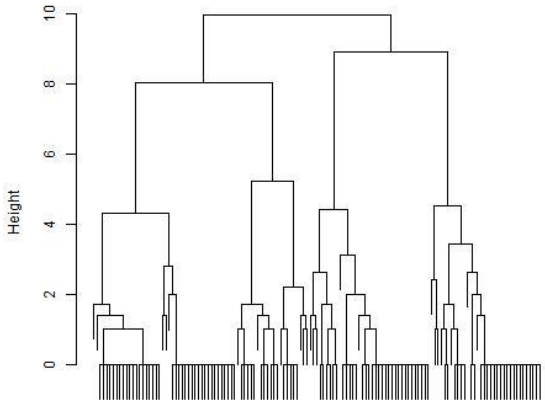
P1 chromosome 9



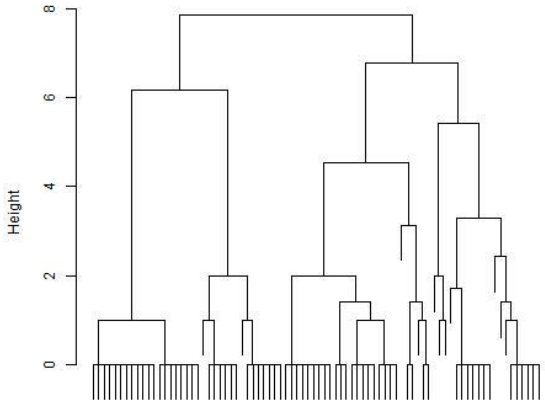
P1 chromosome 10



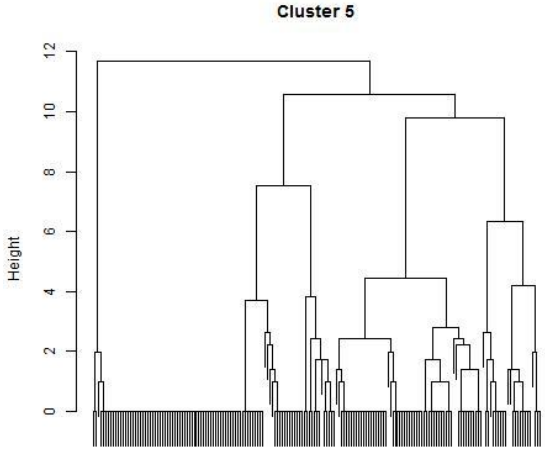
P1 chromosome 11



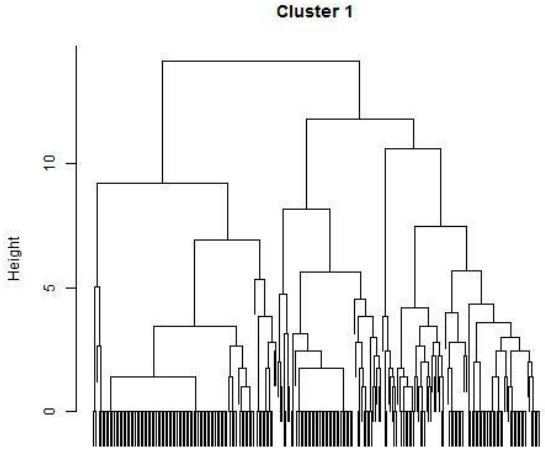
P1 chromosome 12



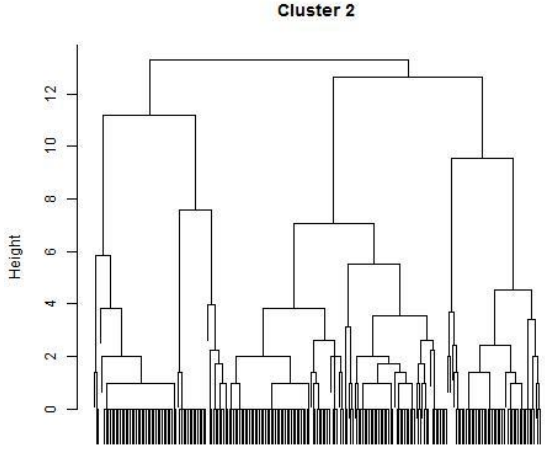
P2 chromosome 1



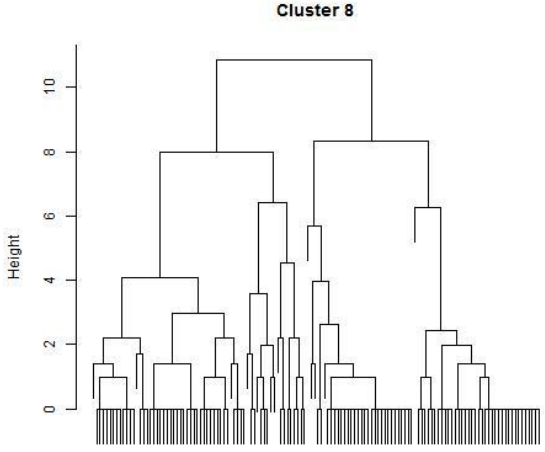
P2 chromosome 2



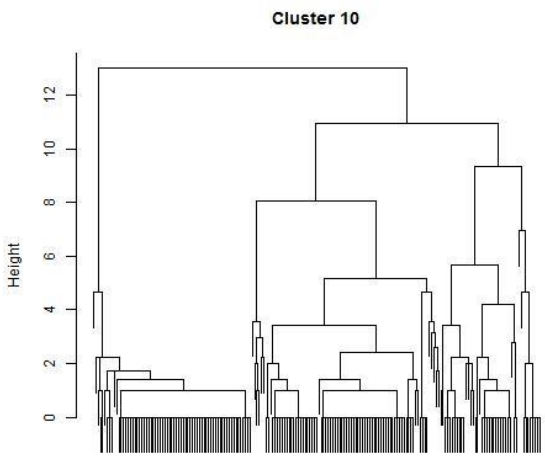
P2 chromosome 3



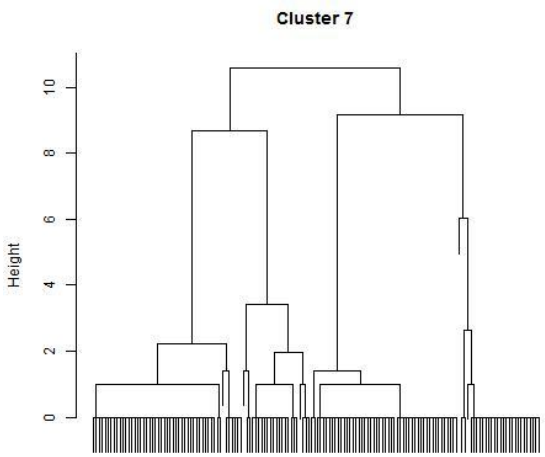
P2 chromosome 4



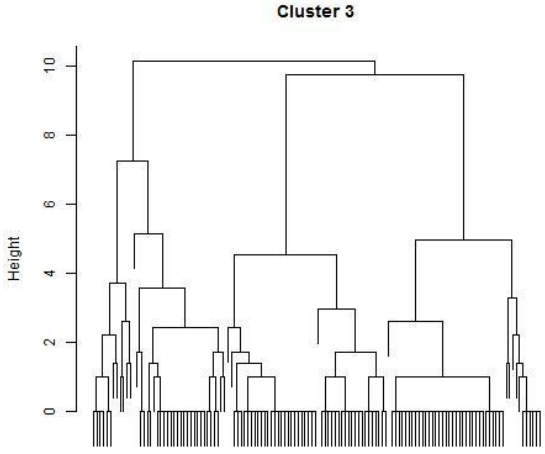
P2 chromosome 5



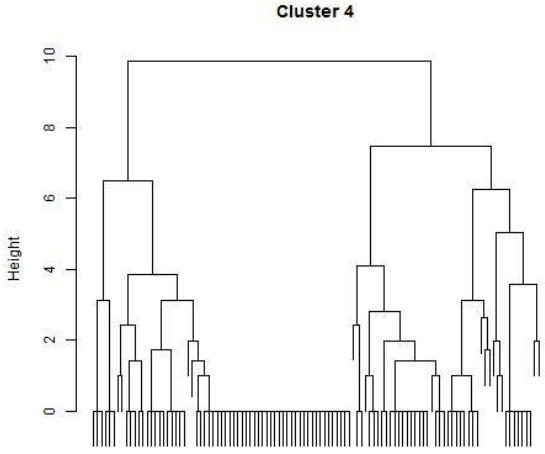
P2 chromosome 6



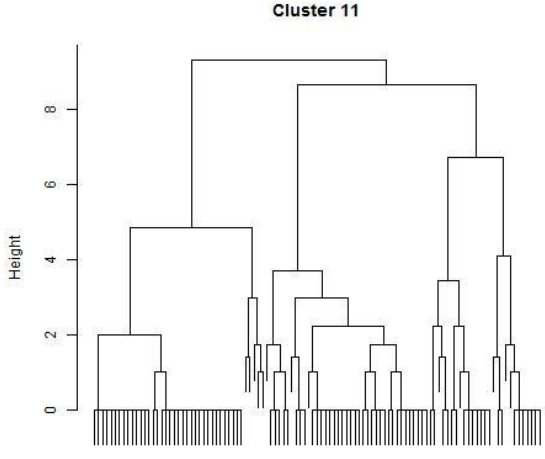
P2 chromosome 7



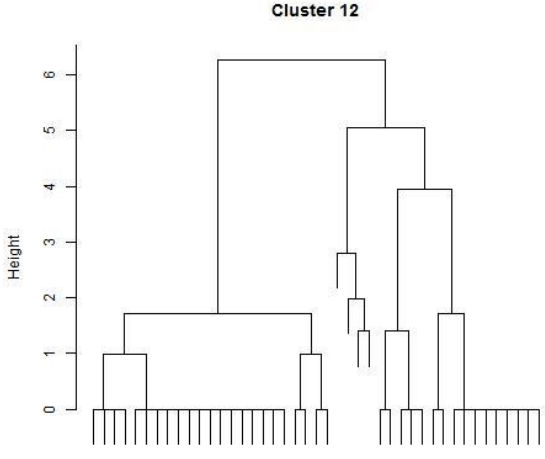
P2 chromosome 8

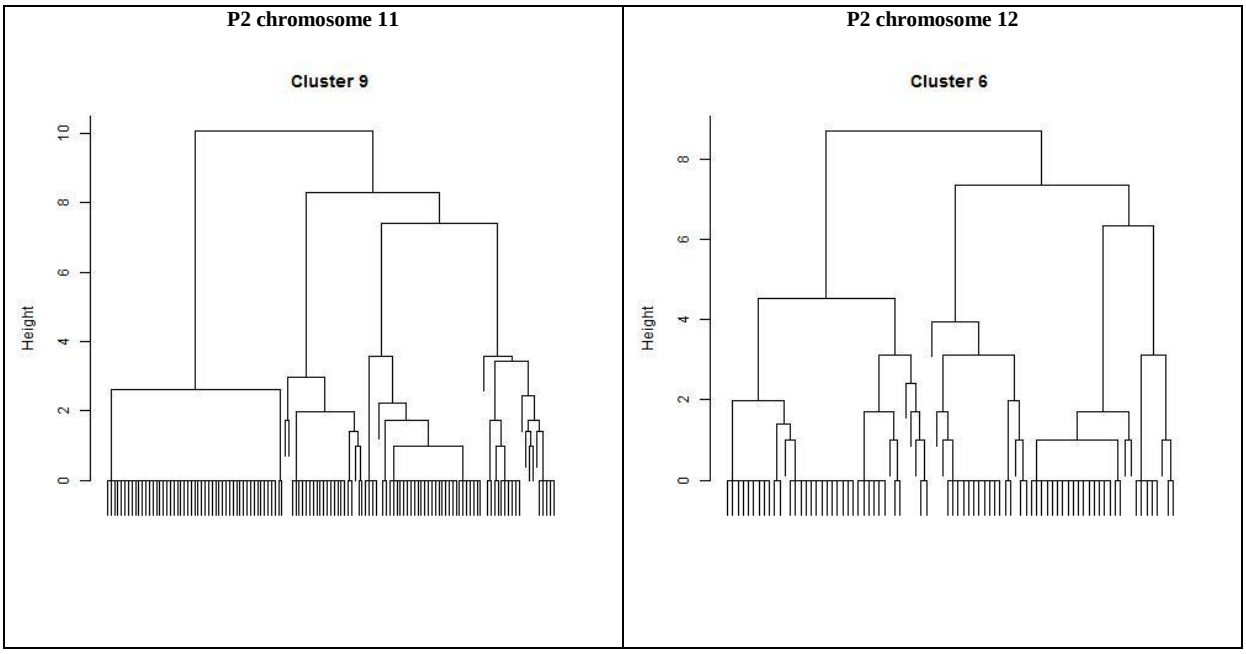


P2 chromosome 9



P2 chromosome 10





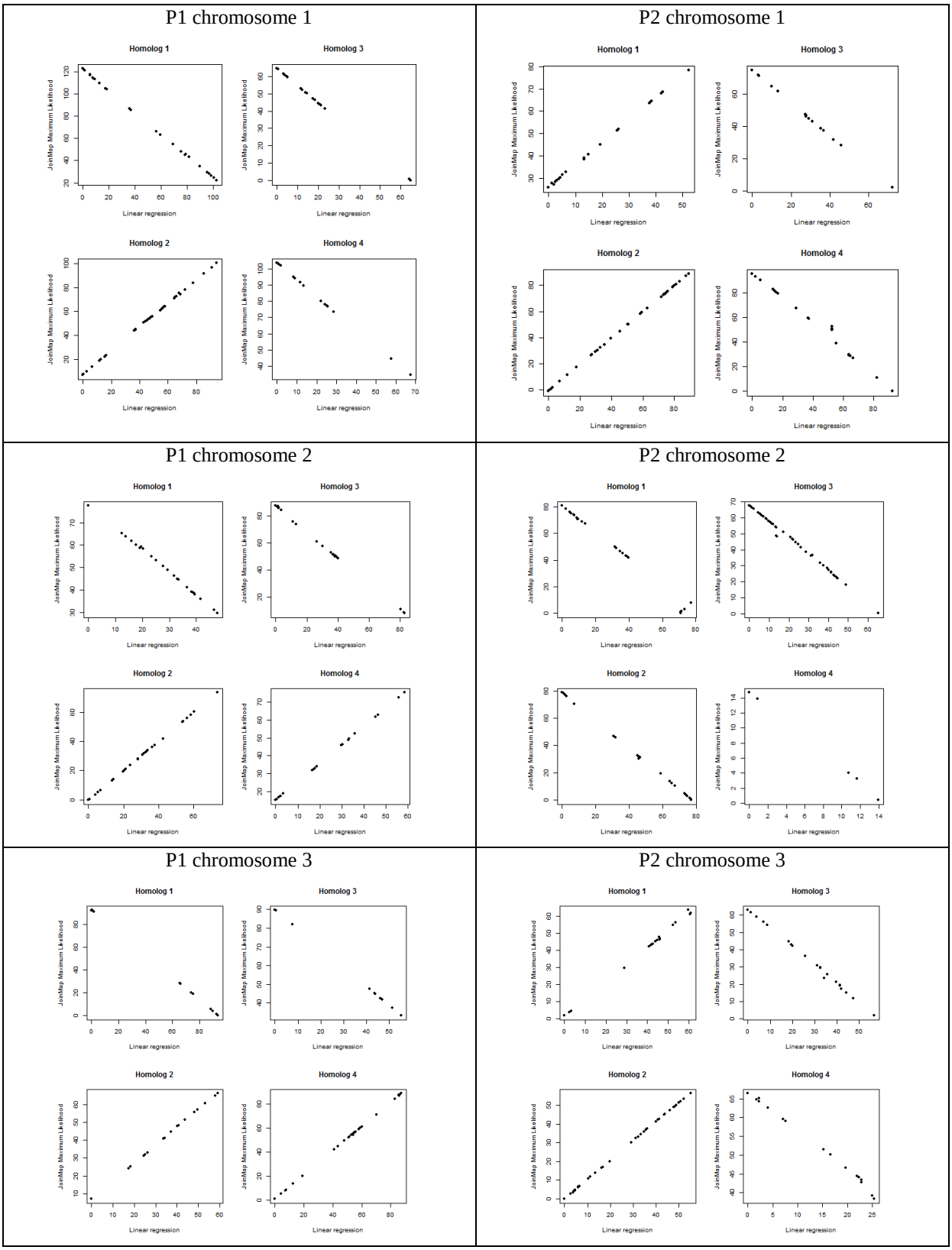
Appendix 5: Comparison of ordering by JoinMap and ordering of this thesis

In Chapter 6, the SxN maps were compared between two mapping methods, namely the maximum likelihood method of JoinMap and the linear regression approach of this thesis. This appendix expands further on the comparison of JoinMap and the ordering method used during this thesis. The number of SxN markers mapped by the maximum likelihood method of JoinMap and the linear regression method used in this thesis are roughly equal (Table 16), although some inconsistencies exist. Furthermore, when the map distances of the common markers are plotted against each there is a good correlation of the two (Figure 26).

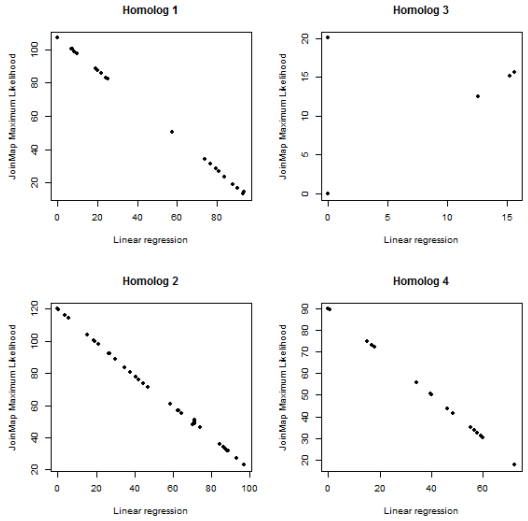
Table 16, Next page. Number of SxN markers ordering by the maximum likelihood method of JoinMap and the ordering by the method used in this thesis. The numbers of the homolog (1 to 4) are translated to letters (A to D) because the assignment of homologs was different between JoinMap and the clustering method here.

Chromosome	JoinMap maximum likelihood				Linear regression				Difference			
P2	**A**	**B**	**C**	**D**	**A**	**B**	**C**	**D**	**A**	**B**	**C**	**D**
1	25	60	60	36	24	59	60	37	-1	-1		1
2	74	16	54	88	74	8	54	88		-8		
3	110	26	46	42	110	26	46	42				
4	32	37	17	46	32	38	13	46		1	-4	
5	67	32	77	15	69	34	69	12	2	2	-8	-3
6	23	51	28	50	23	51	28	50				
7	12	47	27	46	12	48	28	46		1	1	
8	12	36	29	23	12	37	31	24		1	2	1
9	15	39	12	41	10	39	5	41	-5		-7	
10	5	4	11	23	4	0	11	23	-1	-4		
11	23	34	20	51	23	34	21	51			1	
12	8	39	19	20	8	37	19	19		-2		-1
P1	**A**	**B**	**C**	**D**	**A**	**B**	**C**	**D**	**A**	**B**	**C**	**D**
1	43	33	26	53	44	34	26	55	1	1		2
2	44	34	31	46	44	34	31	46				
3	17	23	12	57	17	23	12	57				
4	5	97	21	20	5	96	21	20		-1		
5	32	100	8	49	32	84	9	50		-16	1	1
6	12	35	15	14	12	35	15	14				
7	21	36	12	34	21	36	12	34				
8	40	99	20	26	39	98	20	27	-1	-1		1
9	7	61	24	23	7	62	24	23		1		
10	21	18	13	29	22	18	13	28	1			-1
11	34	36	21	44	34	37	22	44		1	1	
12	15	26	20	20	15	27	20	20		1		

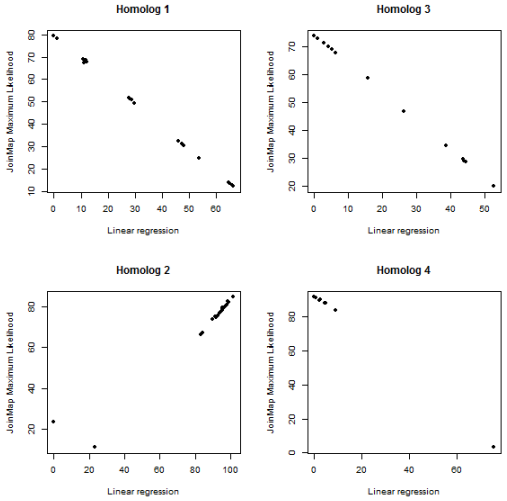
Figure 26. Map positions of common SxN markers in both SxN map of the linear regression method of this thesis and the maximum likelihood method of JoinMap. The map positions are plotted against each other.



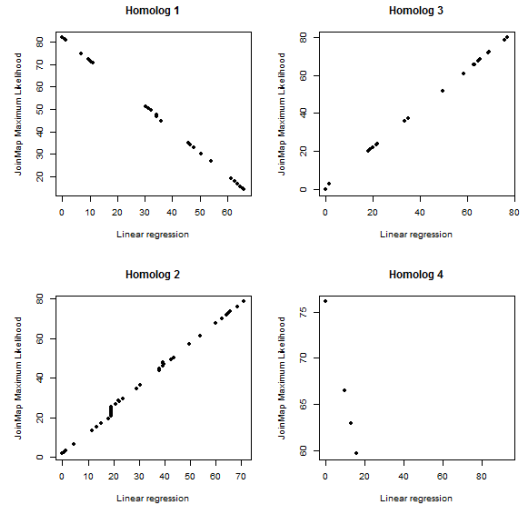
P1 chromosome 4



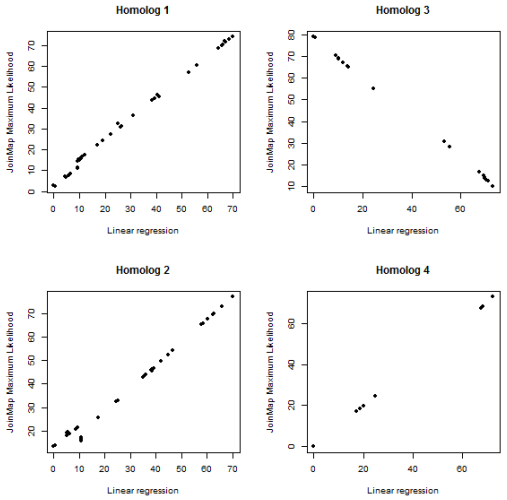
P2 chromosome 4



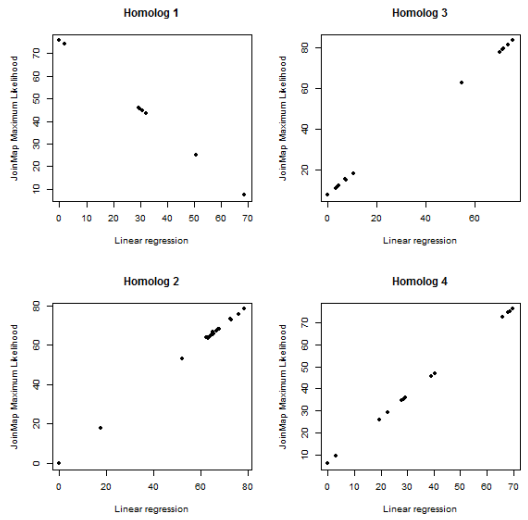
P1 chromosome 5



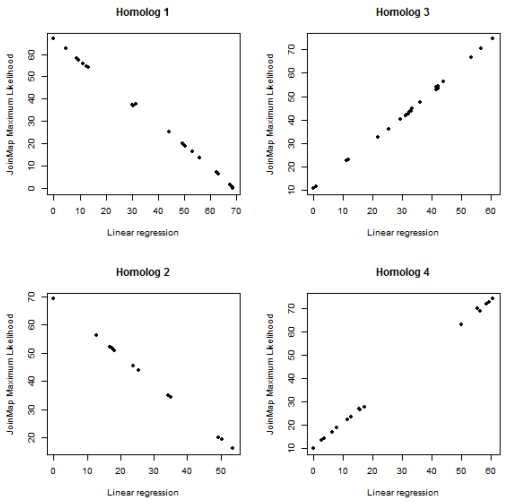
P2 chromosome 5



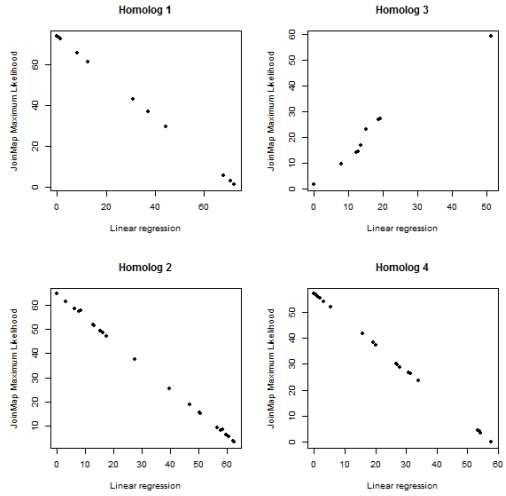
P1 chromosome 6



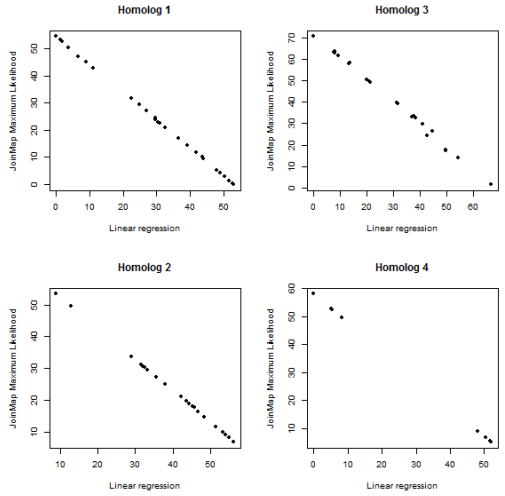
P2 chromosome 6



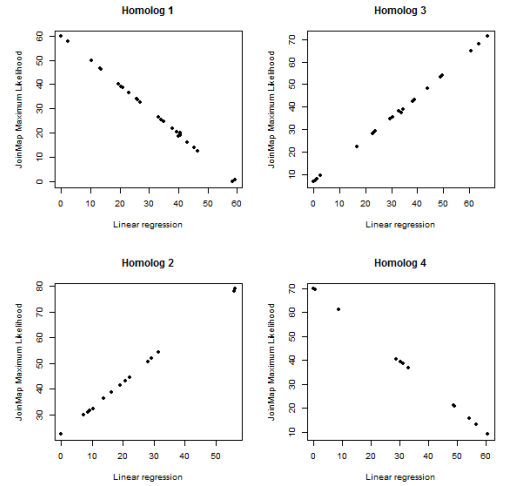
P1 chromosome 7



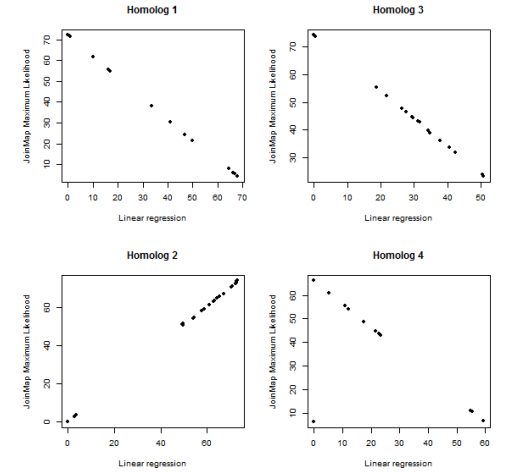
P2 chromosome 7



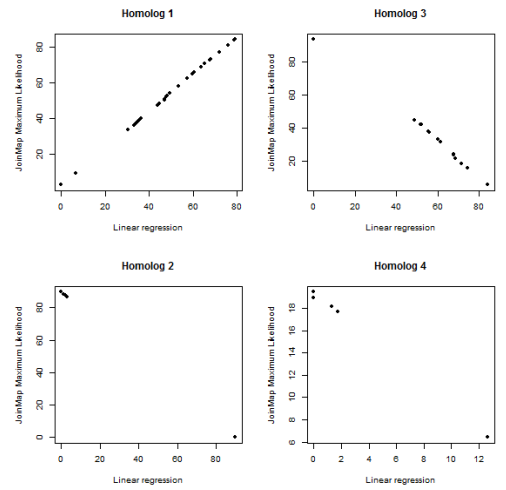
P1 chromosome 8



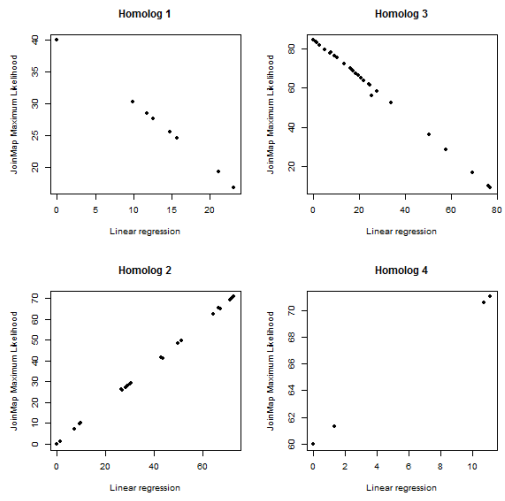
P2 chromosome 8



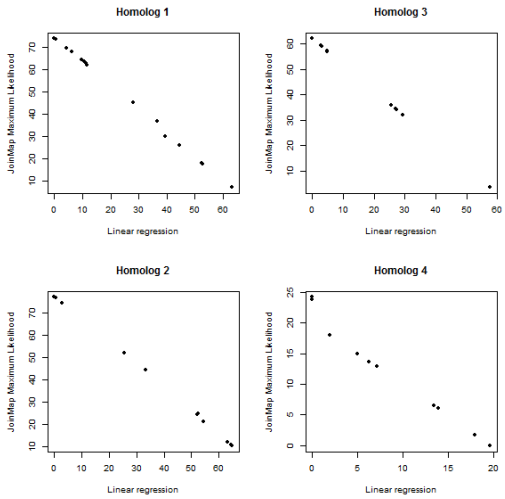
P1 chromosome 9



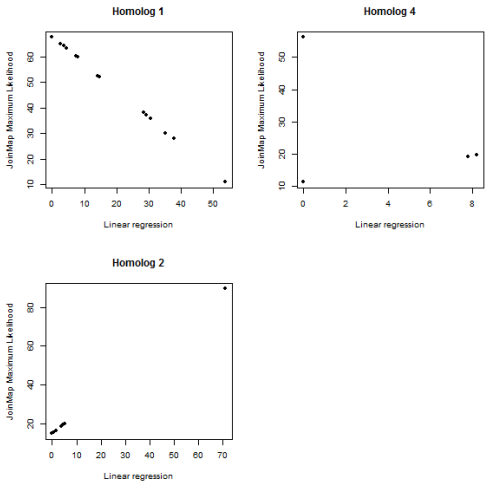
P2 chromosome 9



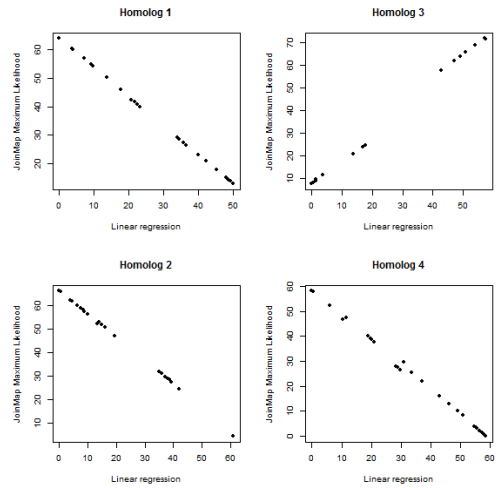
P1 chromosome 10



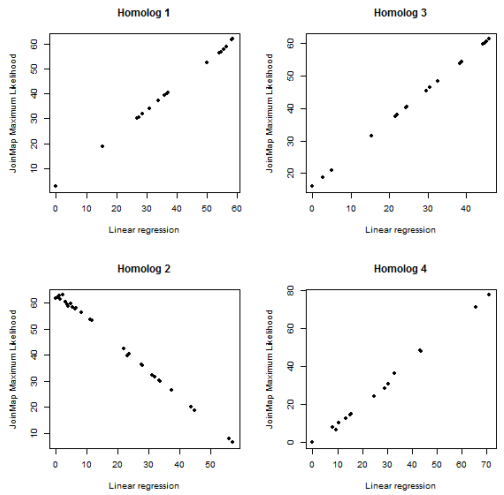
P2 chromosome 10



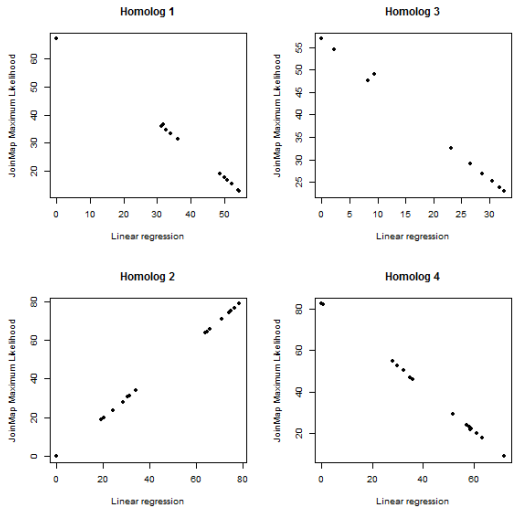
P1 chromosome 11



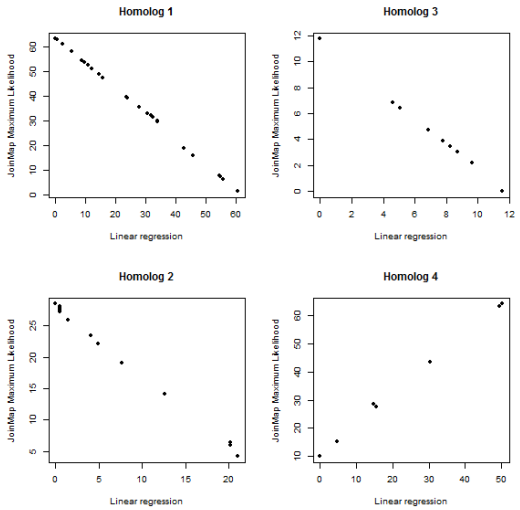
P2 chromosome 11



P1 chromosome 12



P2 chromosome 12



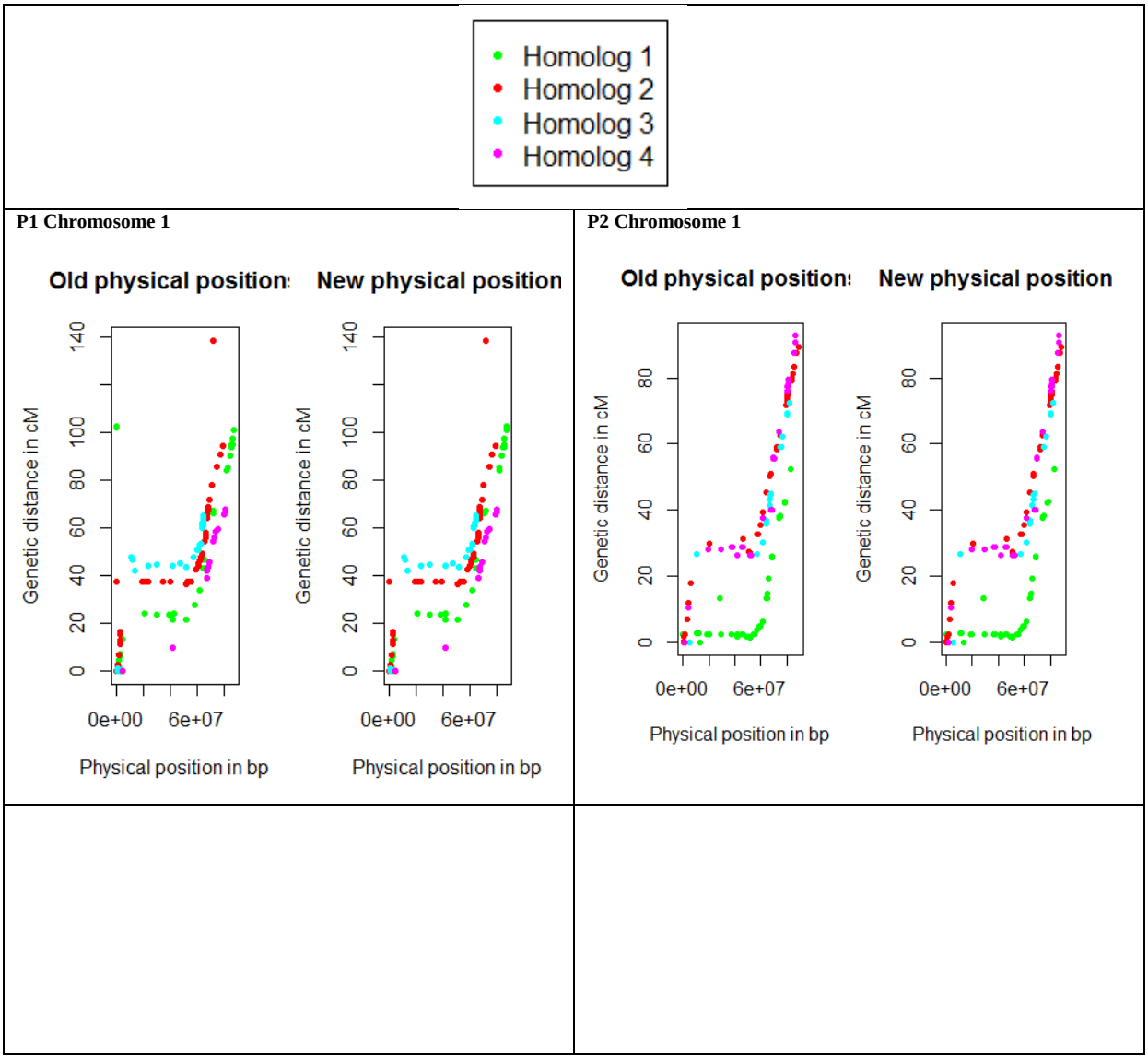
Appendix 6: Comparison between the physical positions and map positions

In Chapter 6, different maps were estimated. The SxN map contains only SxN markers, the DxN map contains SxN and DxN markers, the SxS map contains SxN, DxN and SxS markers and the SxT map contains all marker types considered in this thesis. In this thesis, those maps are compared with the physical positions for further information.

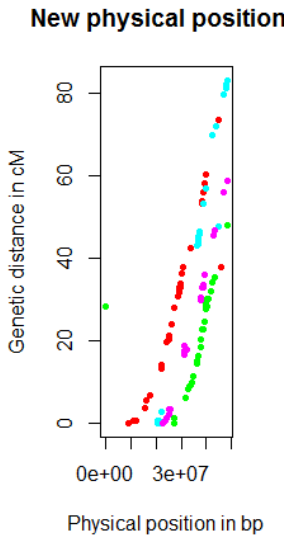
SxN maps

The SxN maps, containing only SxN markers, are compared with the physical positions (Figure 27).

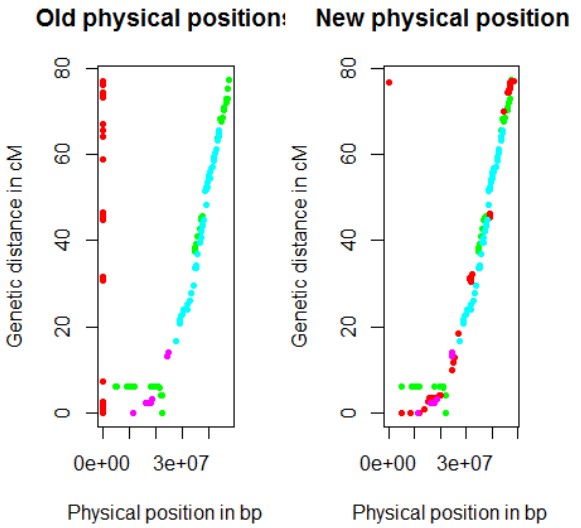
Figure 27. The comparison of the map position of the SxN map with the physical positions. The old and new physical positions are compared with the map. In some cases, the comparison between the map and the old physical positions is wrongfully presented as a vertical line. This means that a non-numerical value is present as physical position.



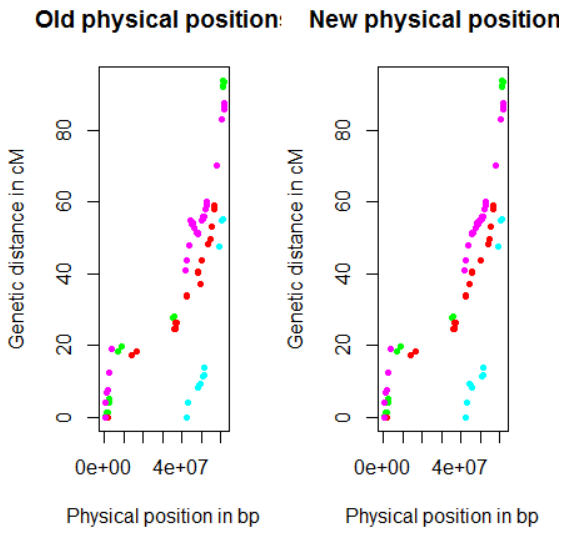
P1 Chromosome 2



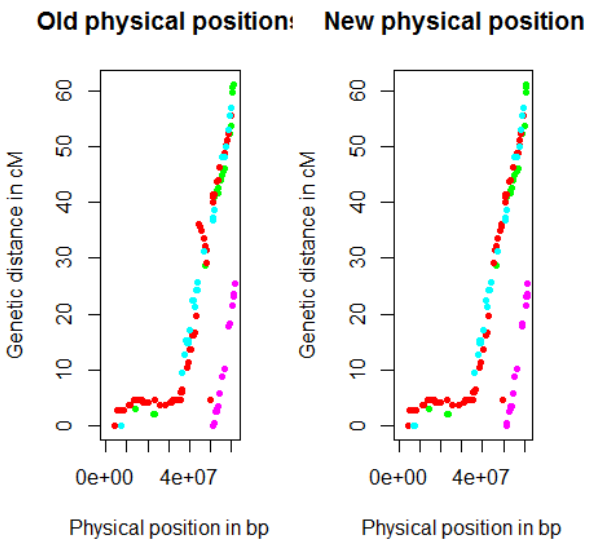
P2 Chromosome 2



P1 Chromosome 3



P2 Chromosome 3



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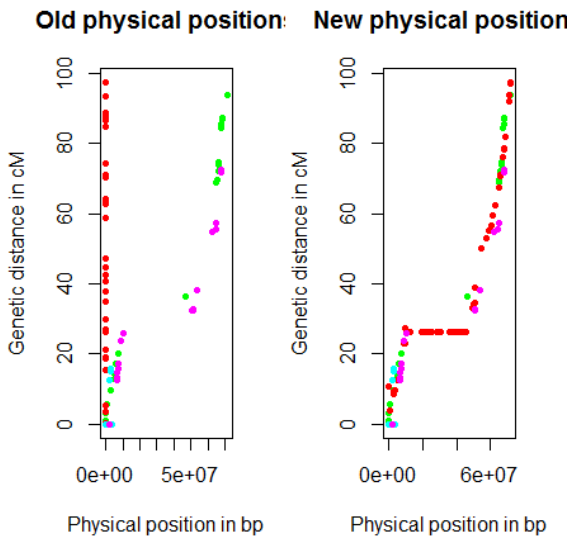
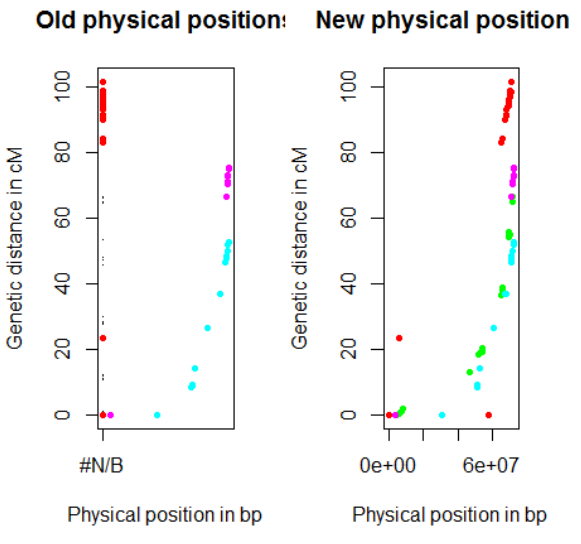
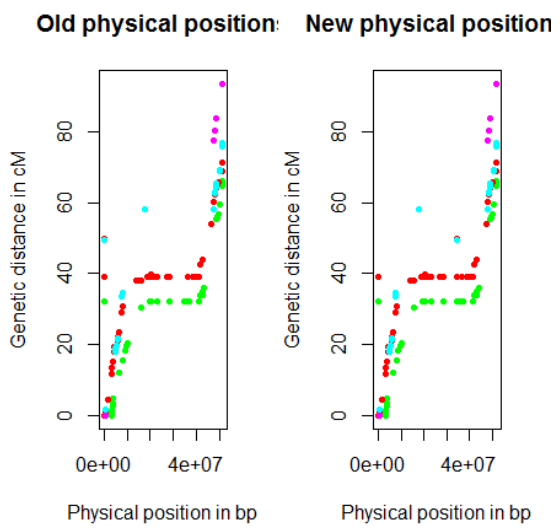


P2 Chromosome 4



P1 Chromosome 5



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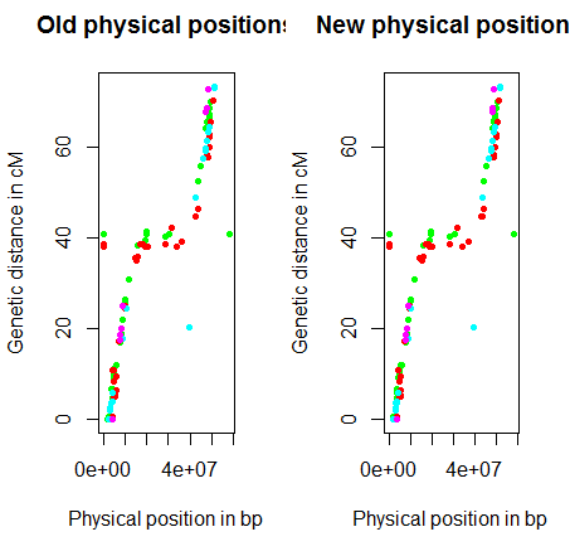

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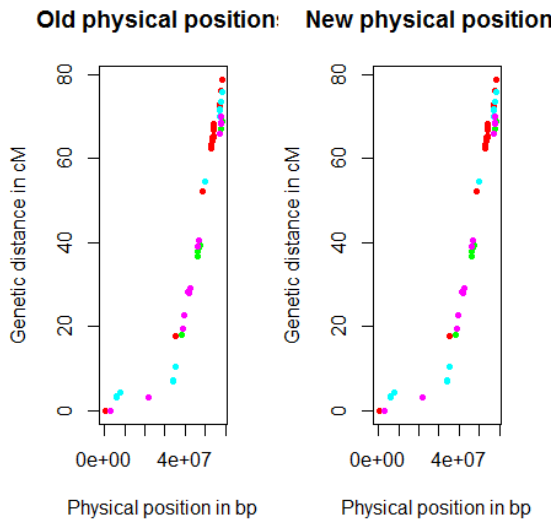
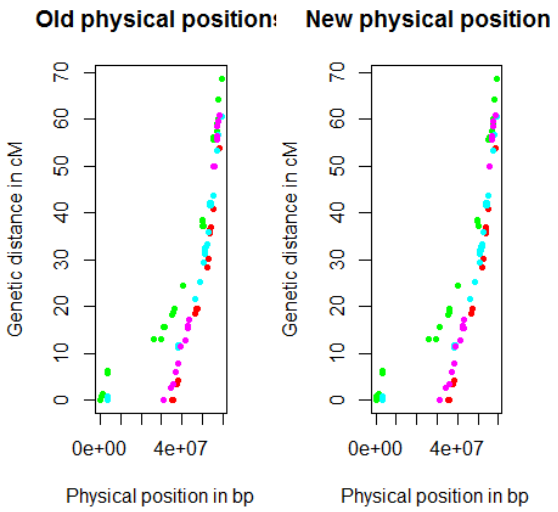


P2 Chromosome 6



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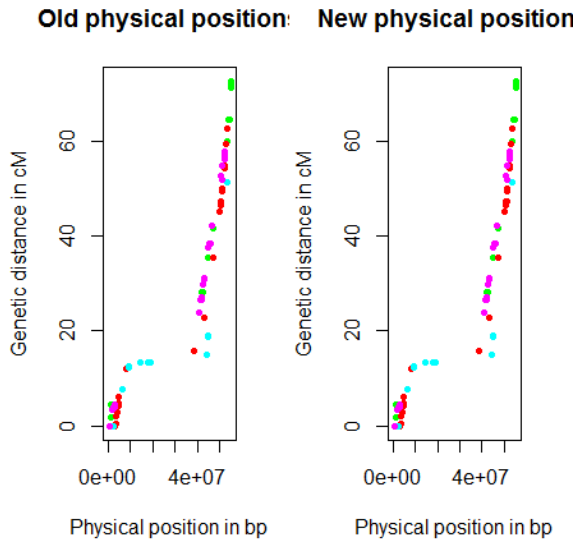

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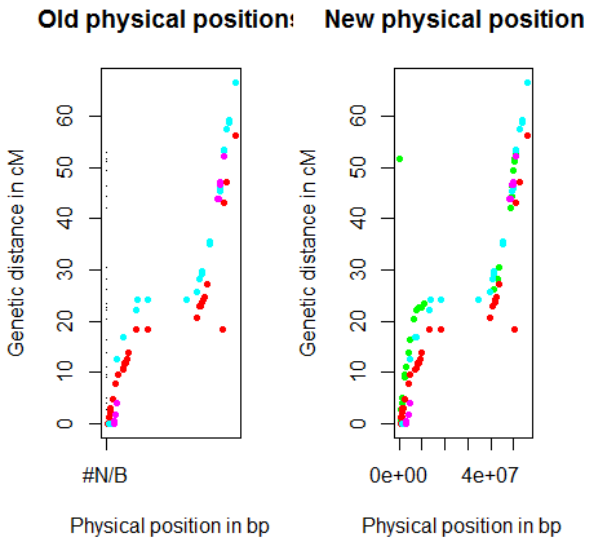
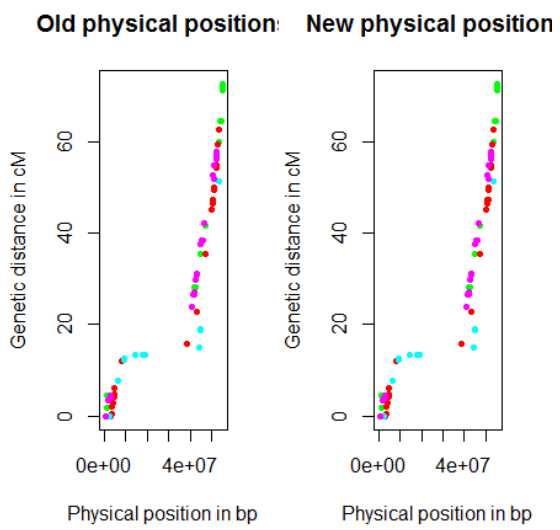
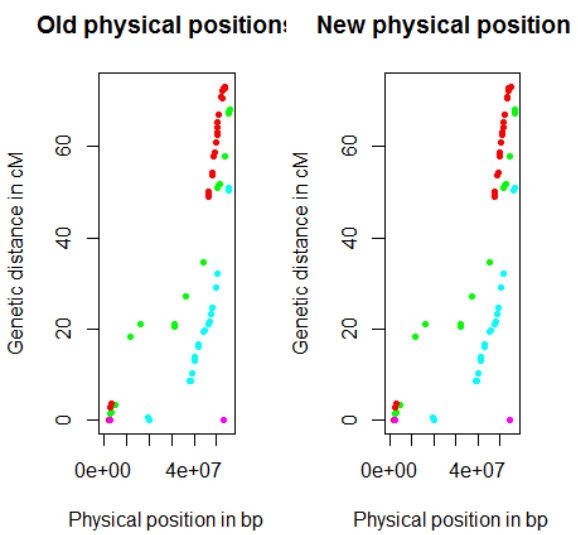


P1 Chromosome 8



P2 Chromosome 8



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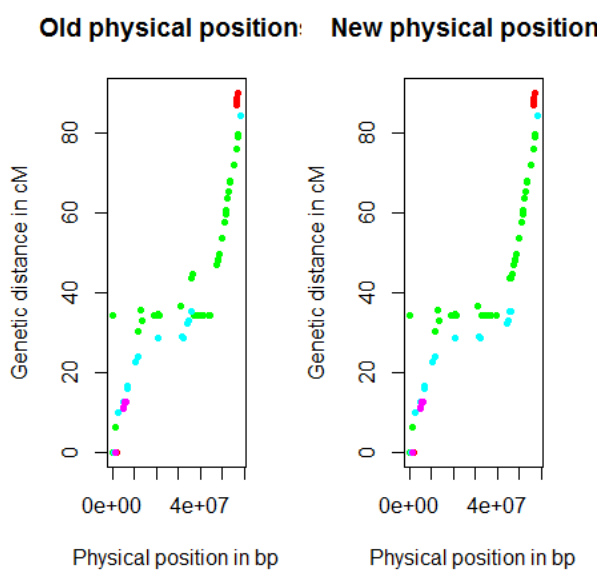

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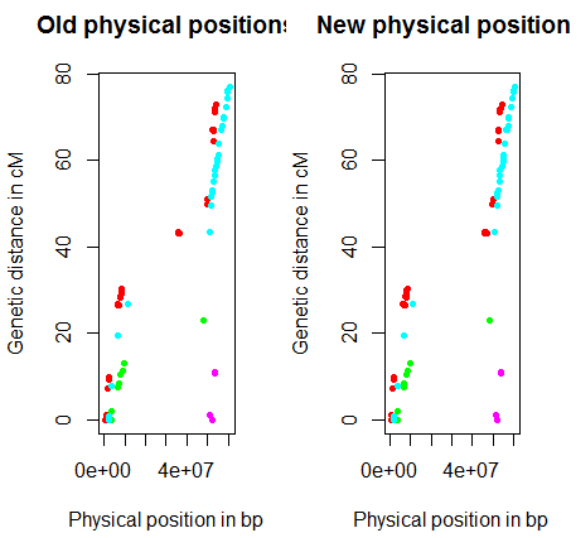

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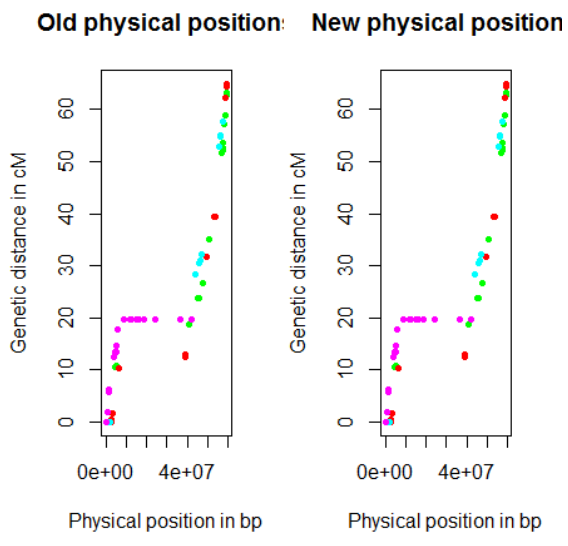

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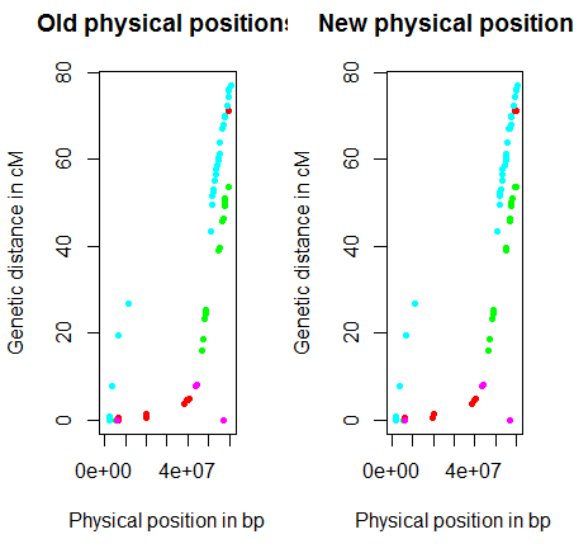
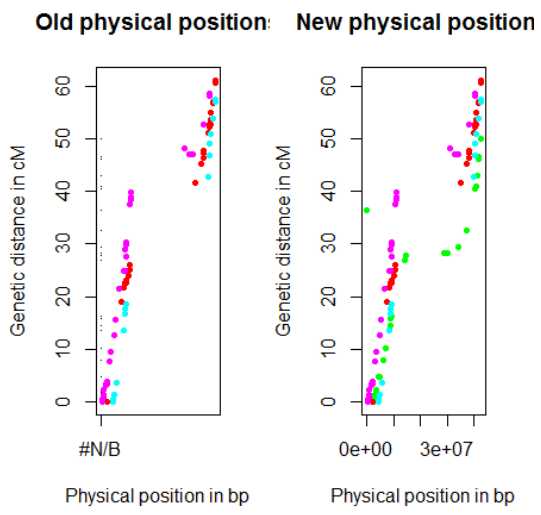


P1 Chromosome 11



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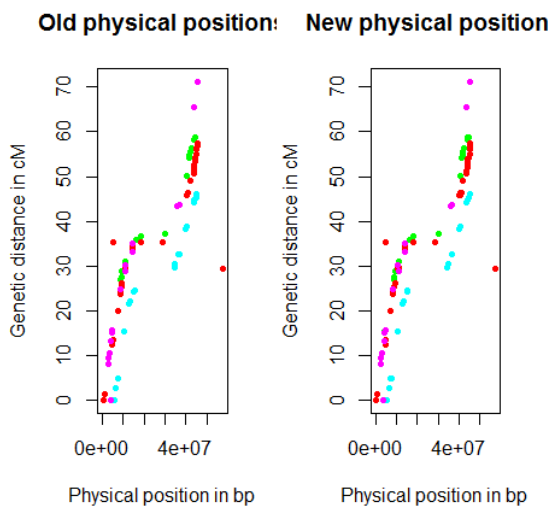

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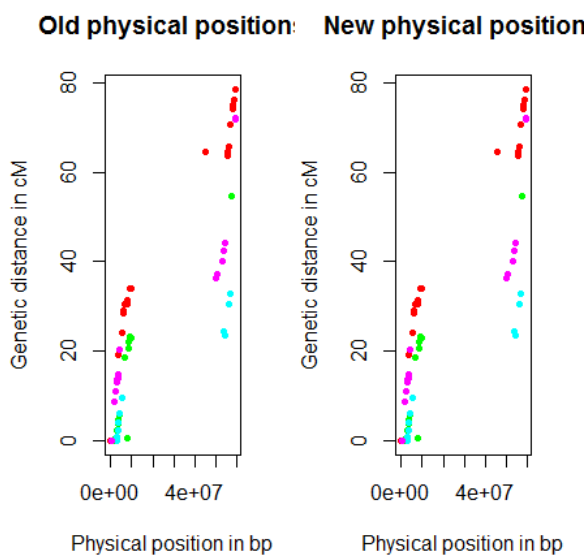

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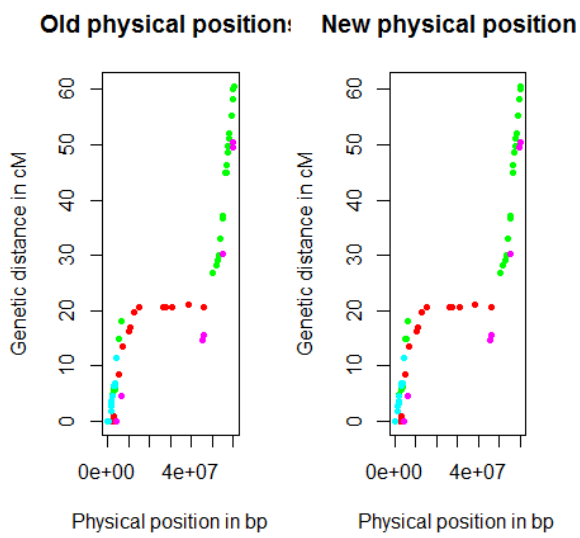
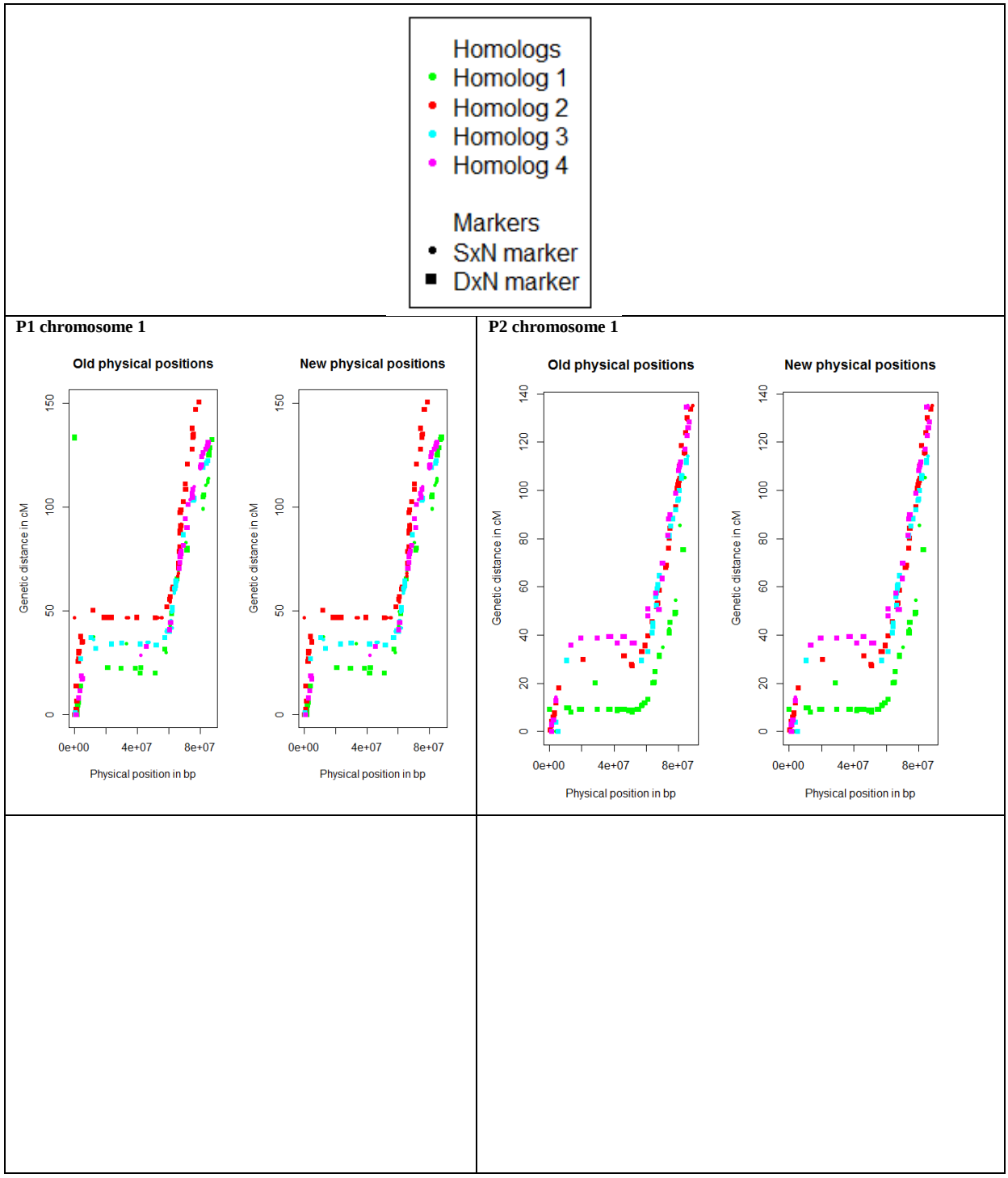


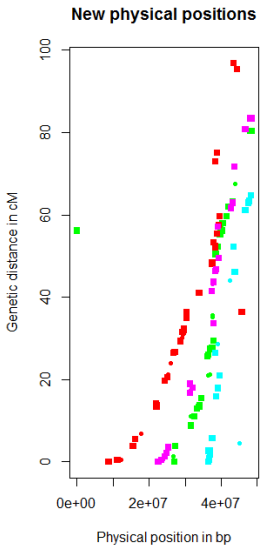
DxN maps

The DxN maps, containing SxN and DxN markers, are compared with the physical positions (Figure 28).

Figure 28. The comparison of the map position of the DxN map with the physical positions. The old and new physical positions are compared with the map. In some cases, the comparison between the map and the old physical positions is wrongfully presented as a vertical line. This means that a non-numerical value is present as physical position.



P1 chromosome 2



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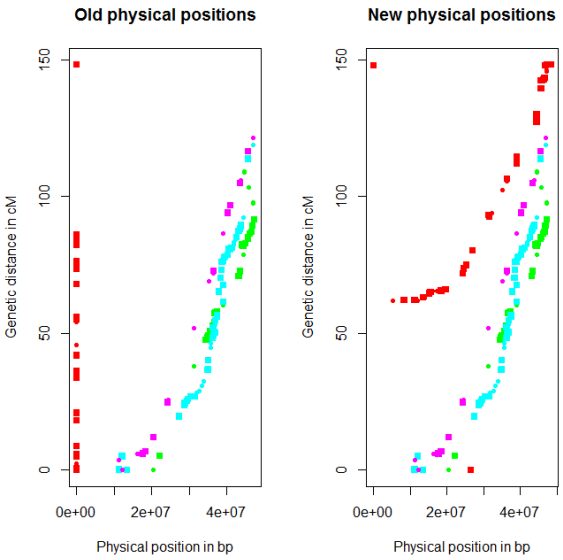

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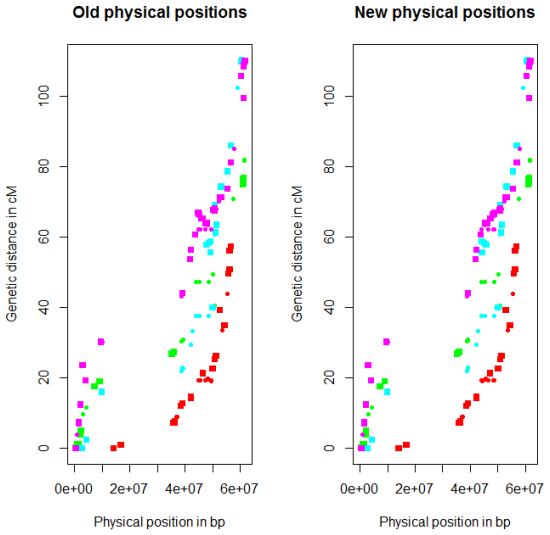

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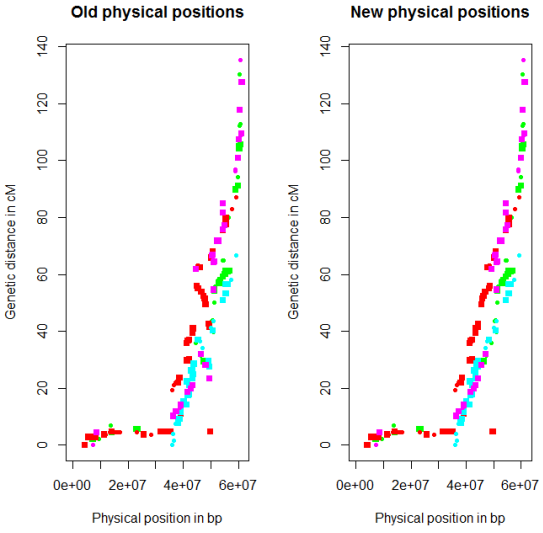
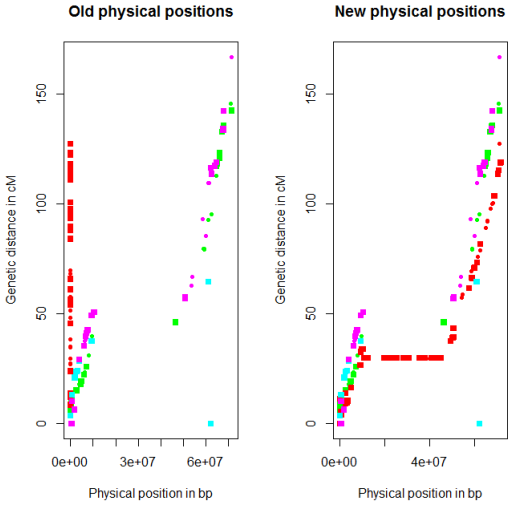


P1 chromosome 4



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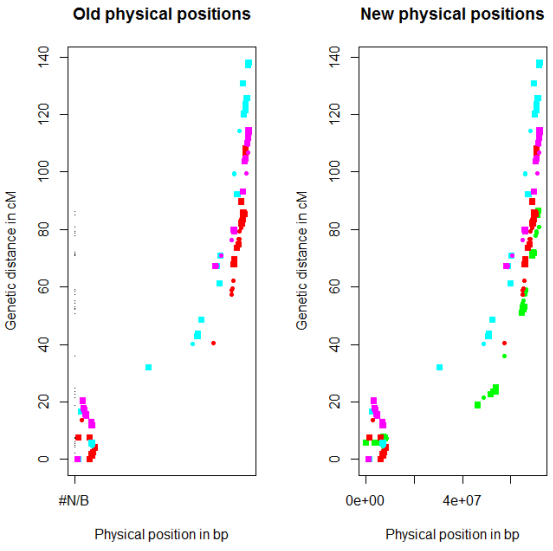
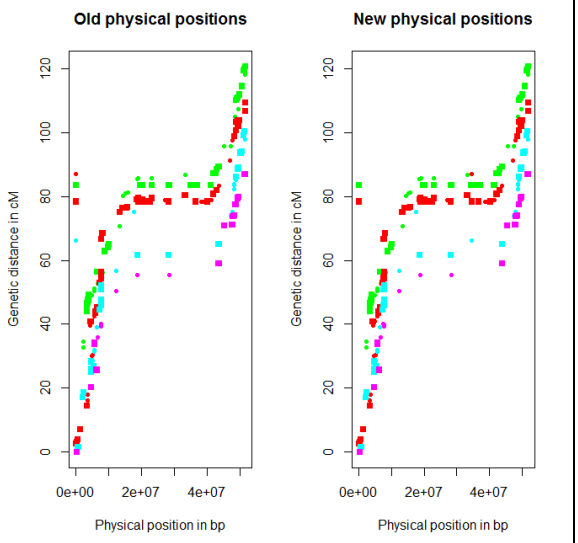


P1 chromosome 5



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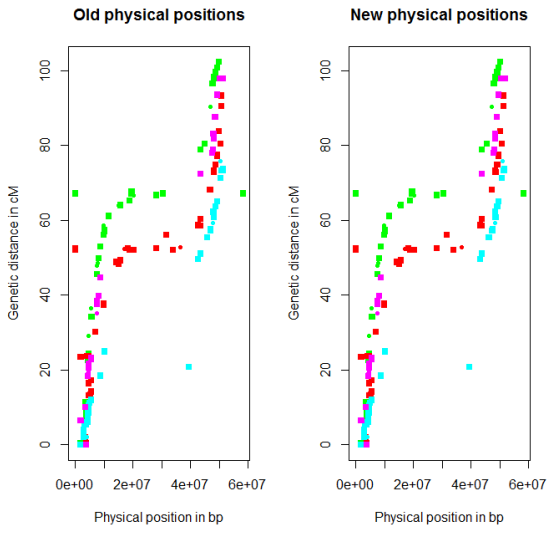
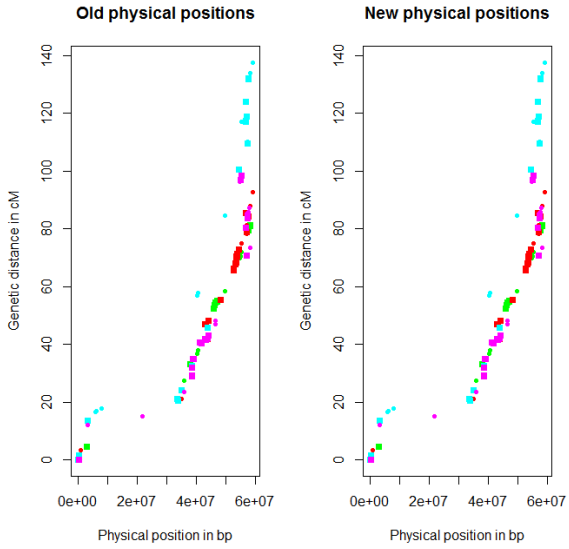


P1 chromosome 6



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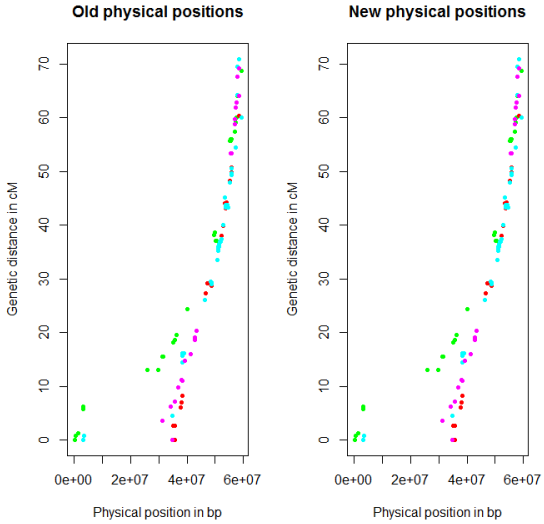

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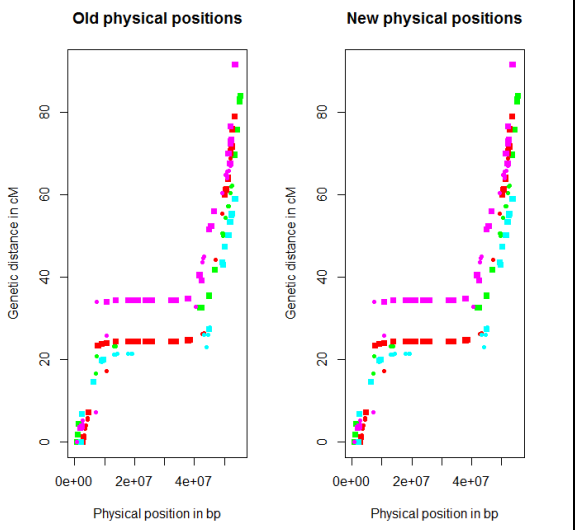
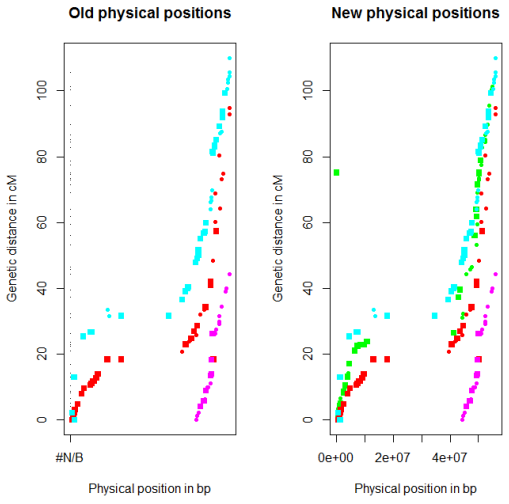
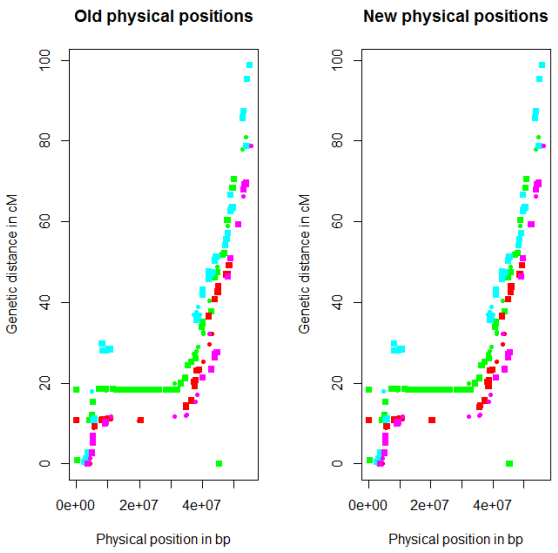


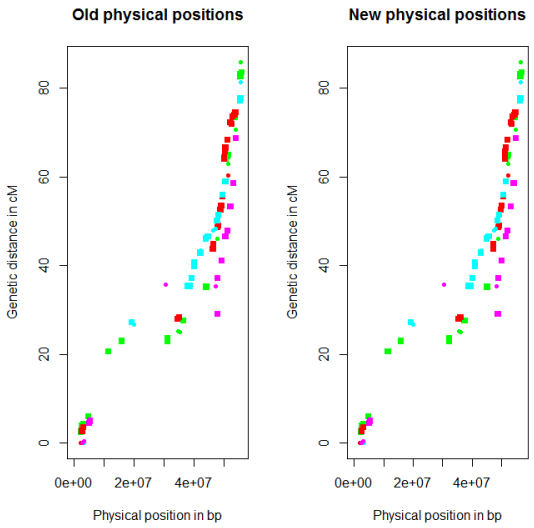
P2 chromosome 7



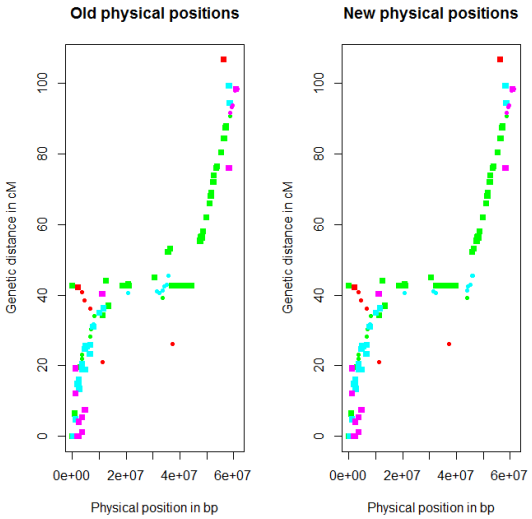
P1 chromosome 8



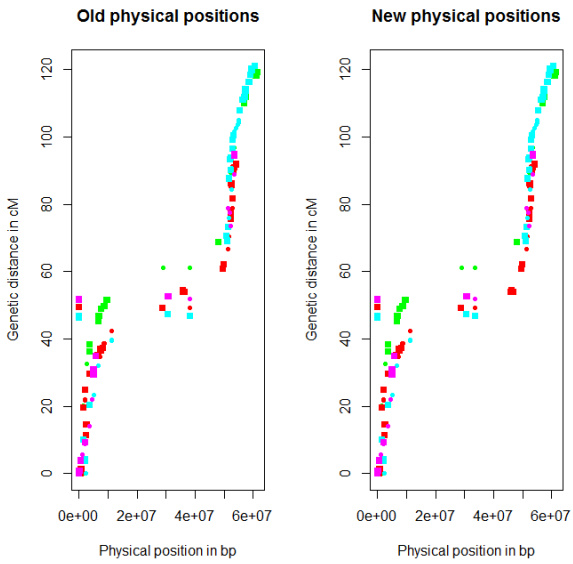
P2 chromosome 8



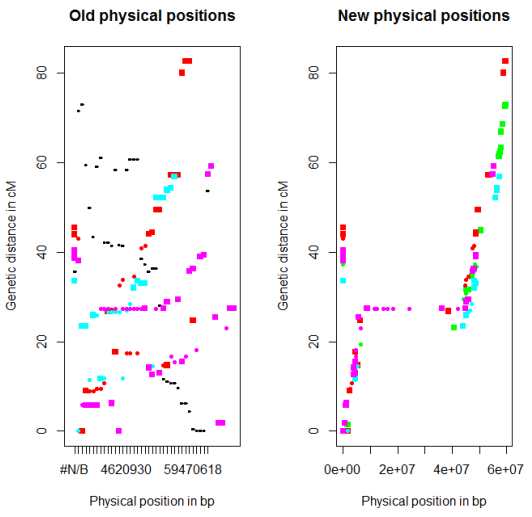
P1 chromosome 9



P2 chromosome 9



P1 chromosome 10



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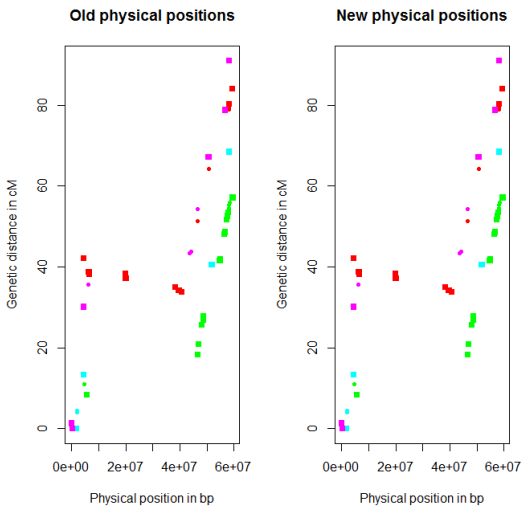
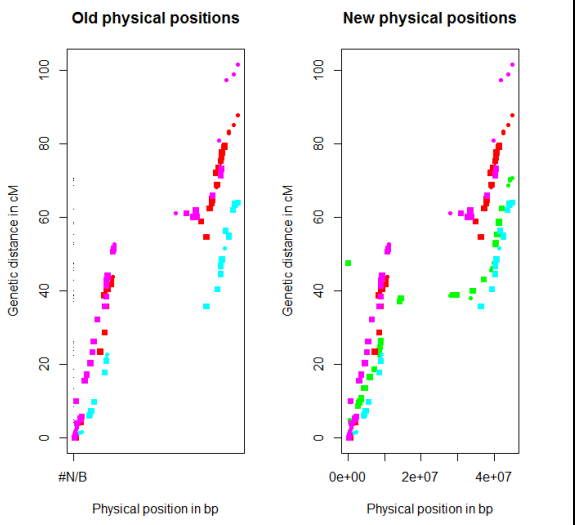


P1 chromosome 11



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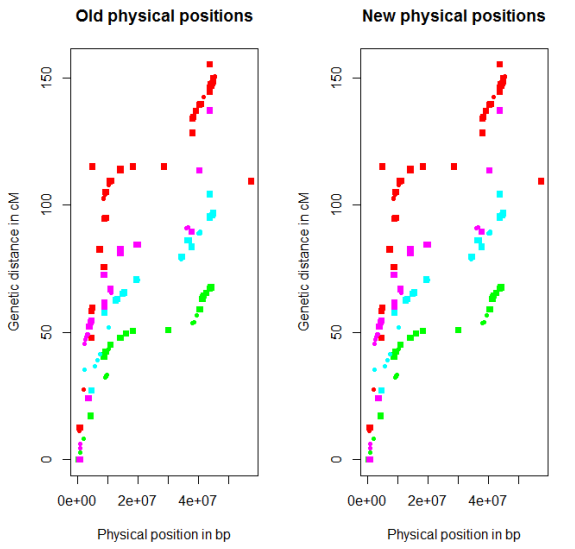

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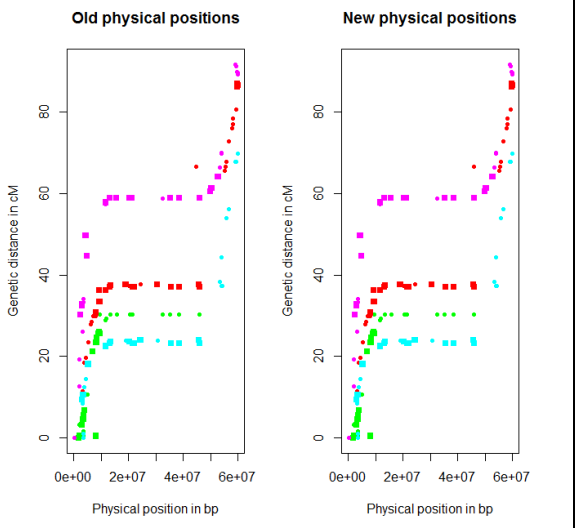

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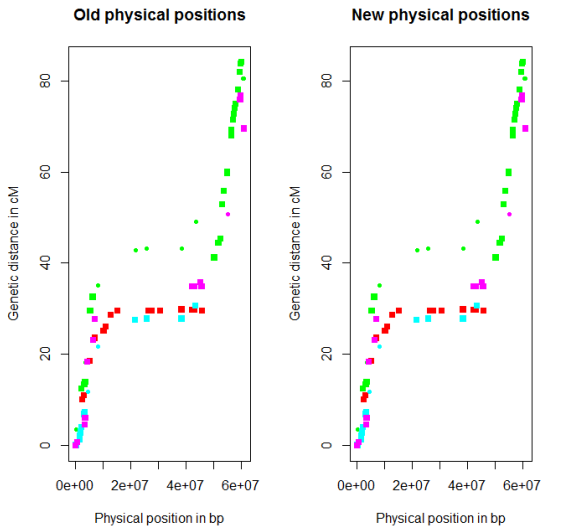
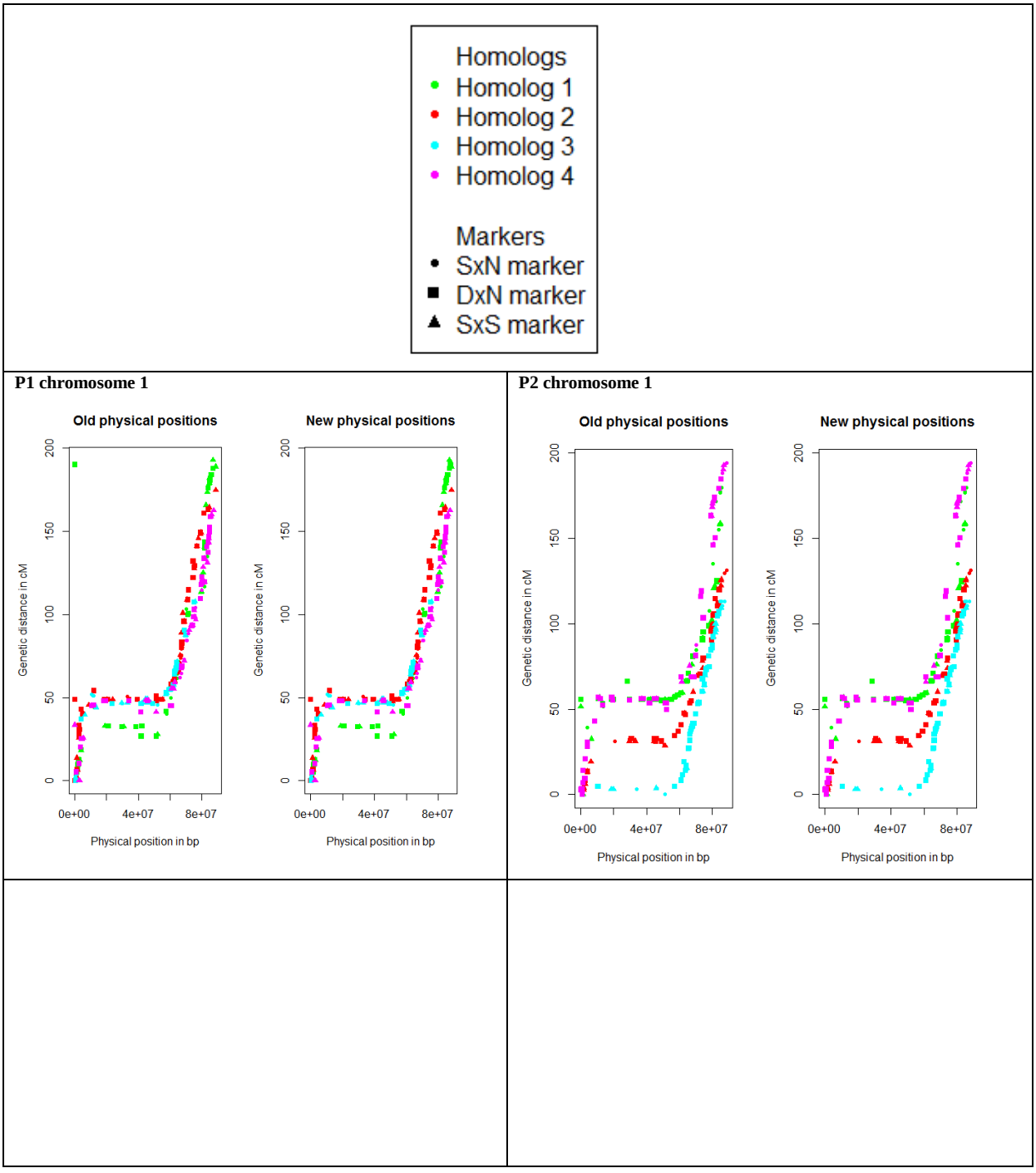


SxS maps

The SxS maps, containing SxN, DxN and SxS markers, are compared with the physical positions (Figure 29).

Figure 29. The comparison of the map position of the SxS map with the physical positions. The old and new physical positions are compared with the map. In some cases, the comparison between the map and the old physical positions is wrongfully presented as a vertical line. This means that a non-numerical value is present as physical position.



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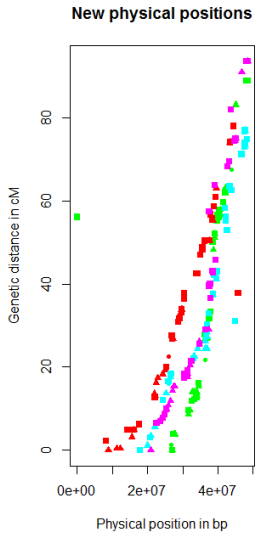

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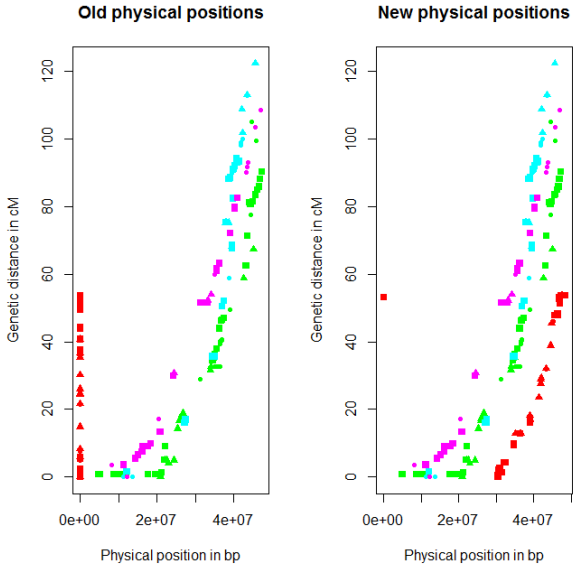

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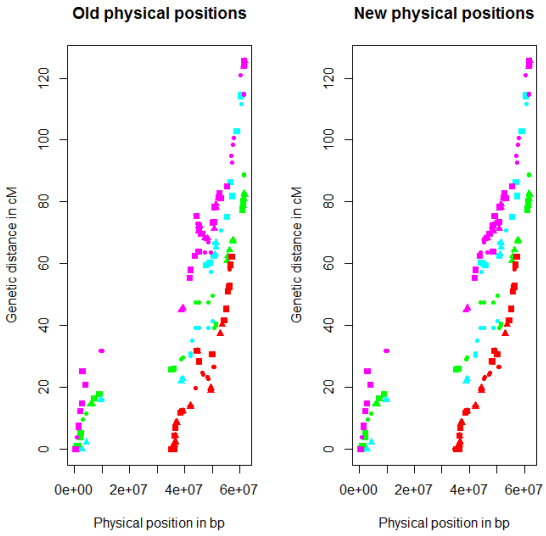

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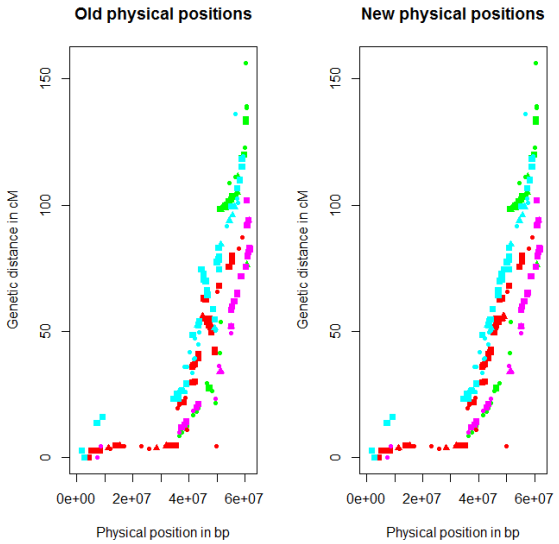

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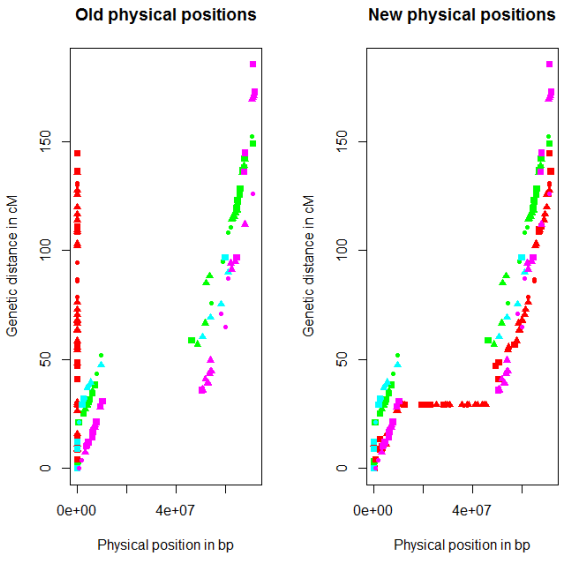

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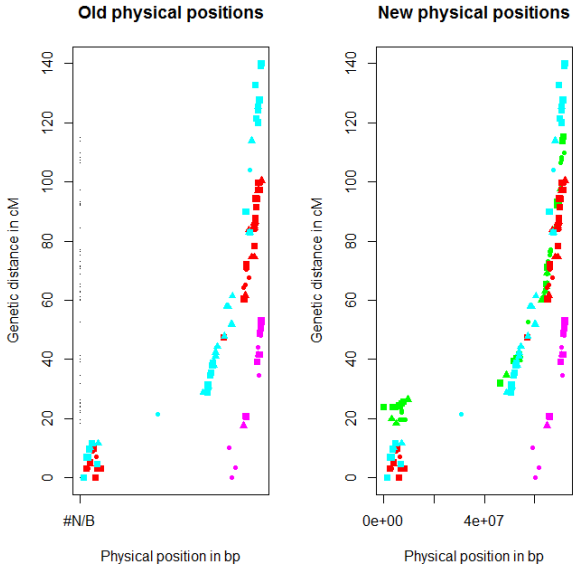

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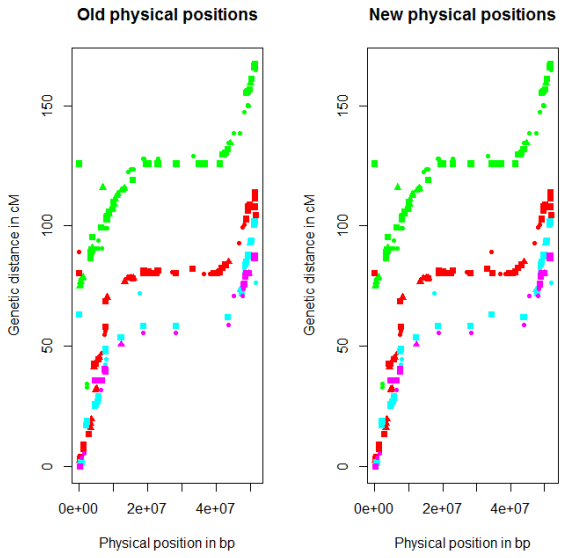
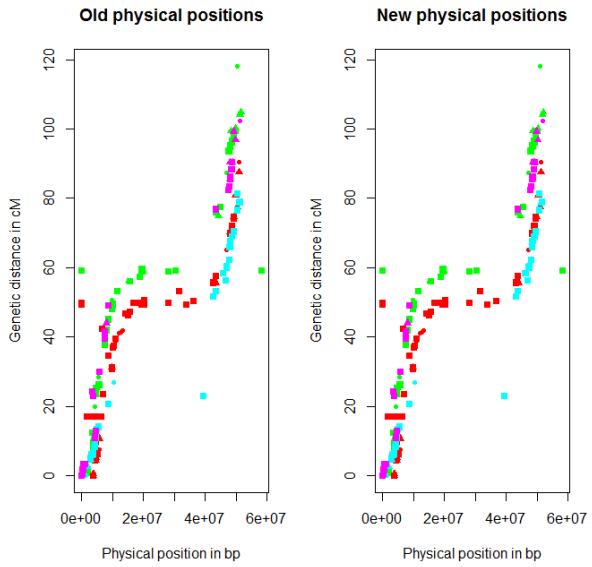
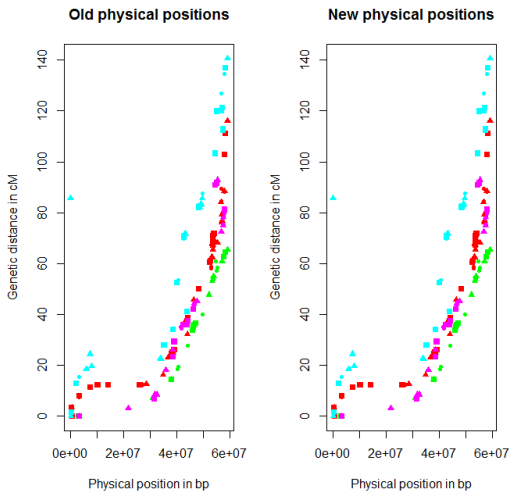


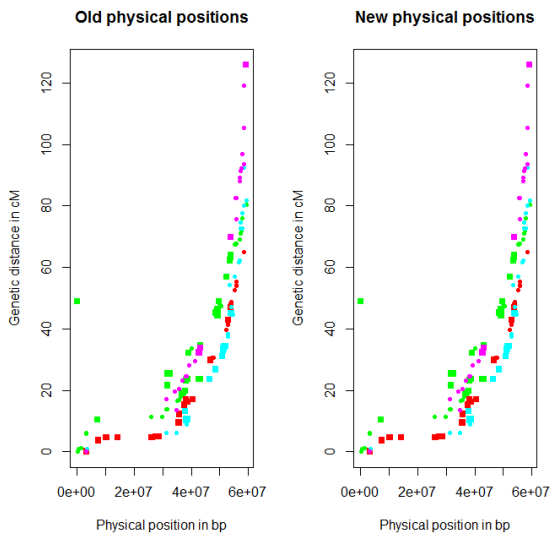
P2 chromosome 5



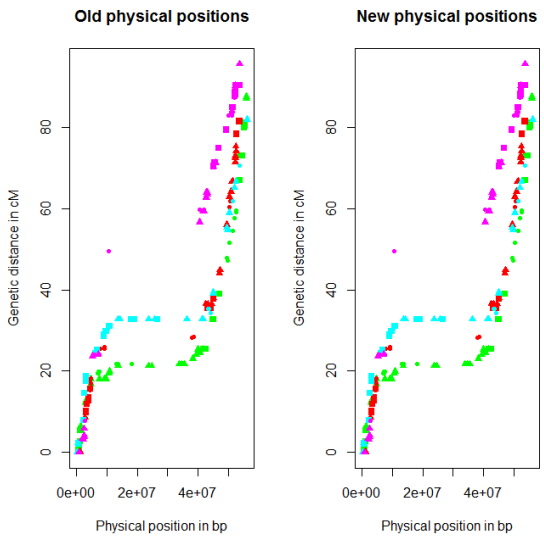
P1 chromosome 6



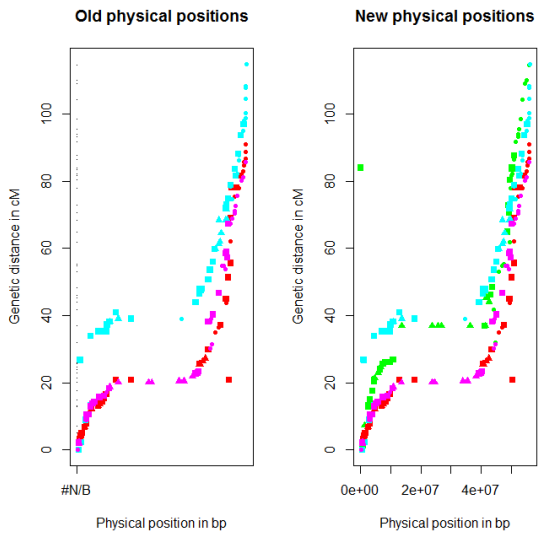
P2 chromosome 6



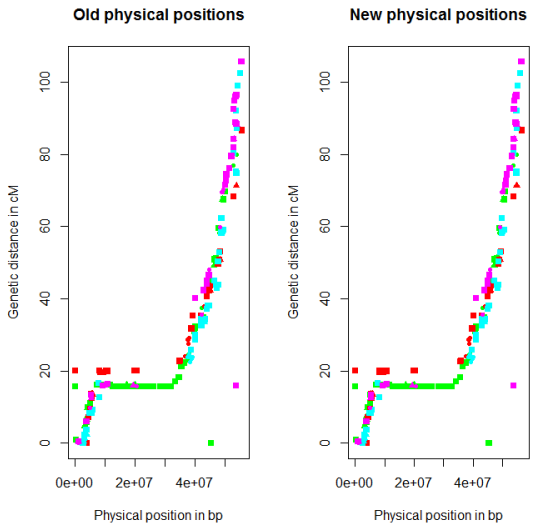
P1 chromosome 7



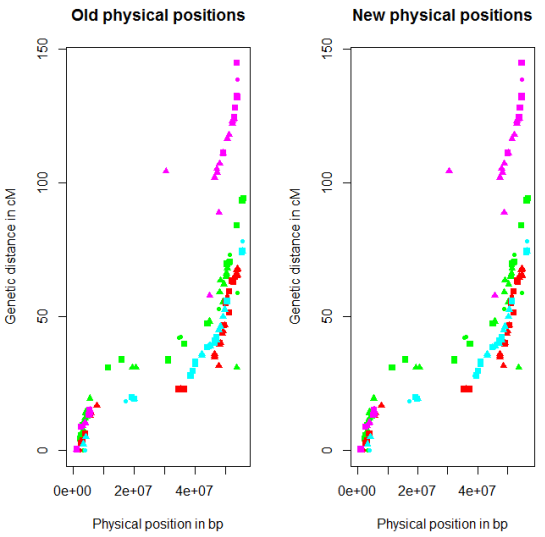
P2 chromosome 7



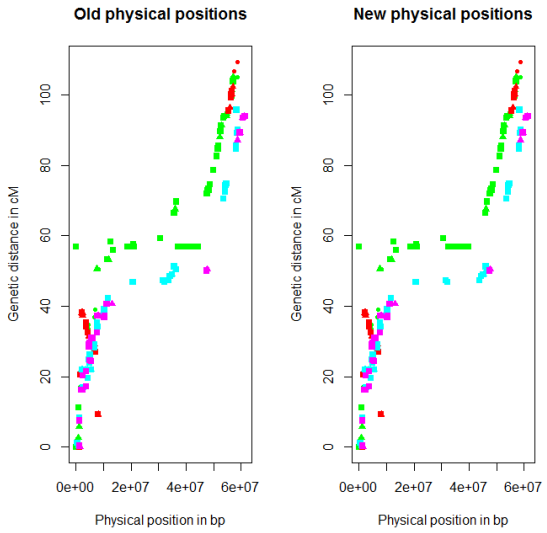
P1 chromosome 8



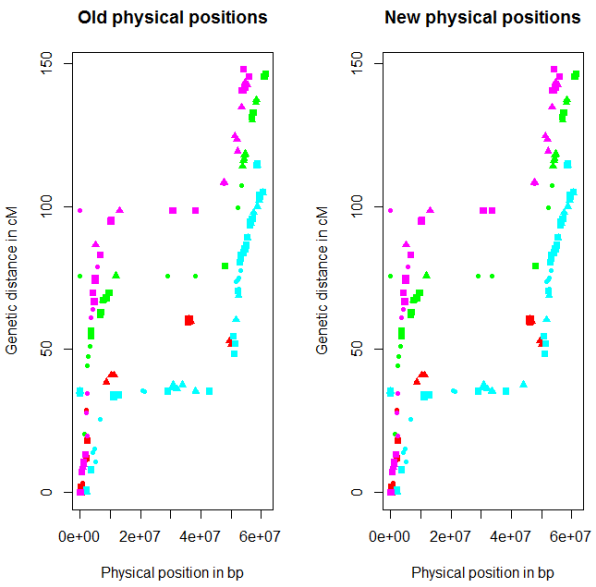
P2 chromosome 8



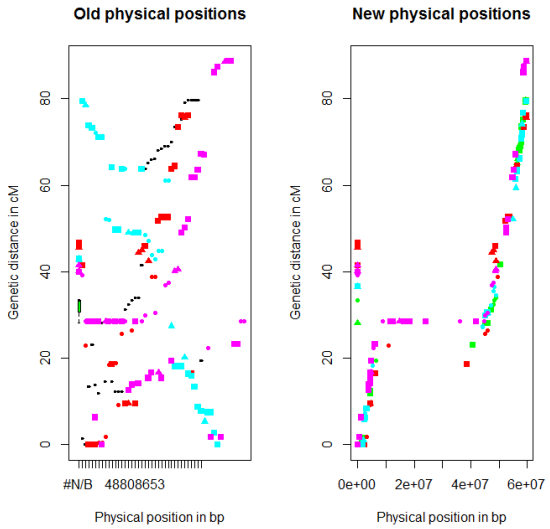
P1 chromosome 9



P2 chromosome 9



P1 chromosome 10



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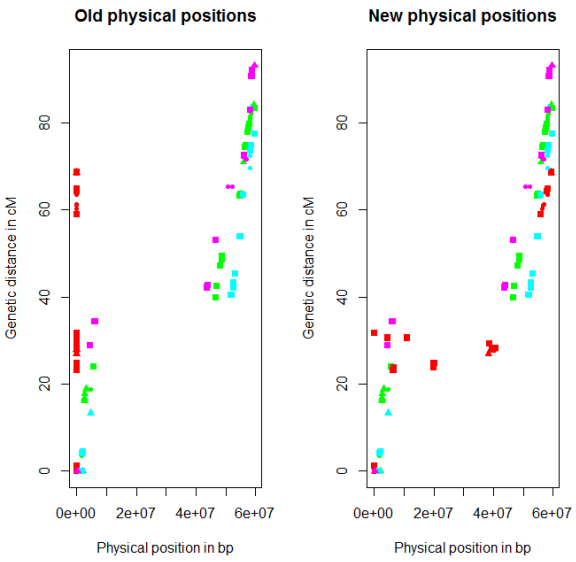
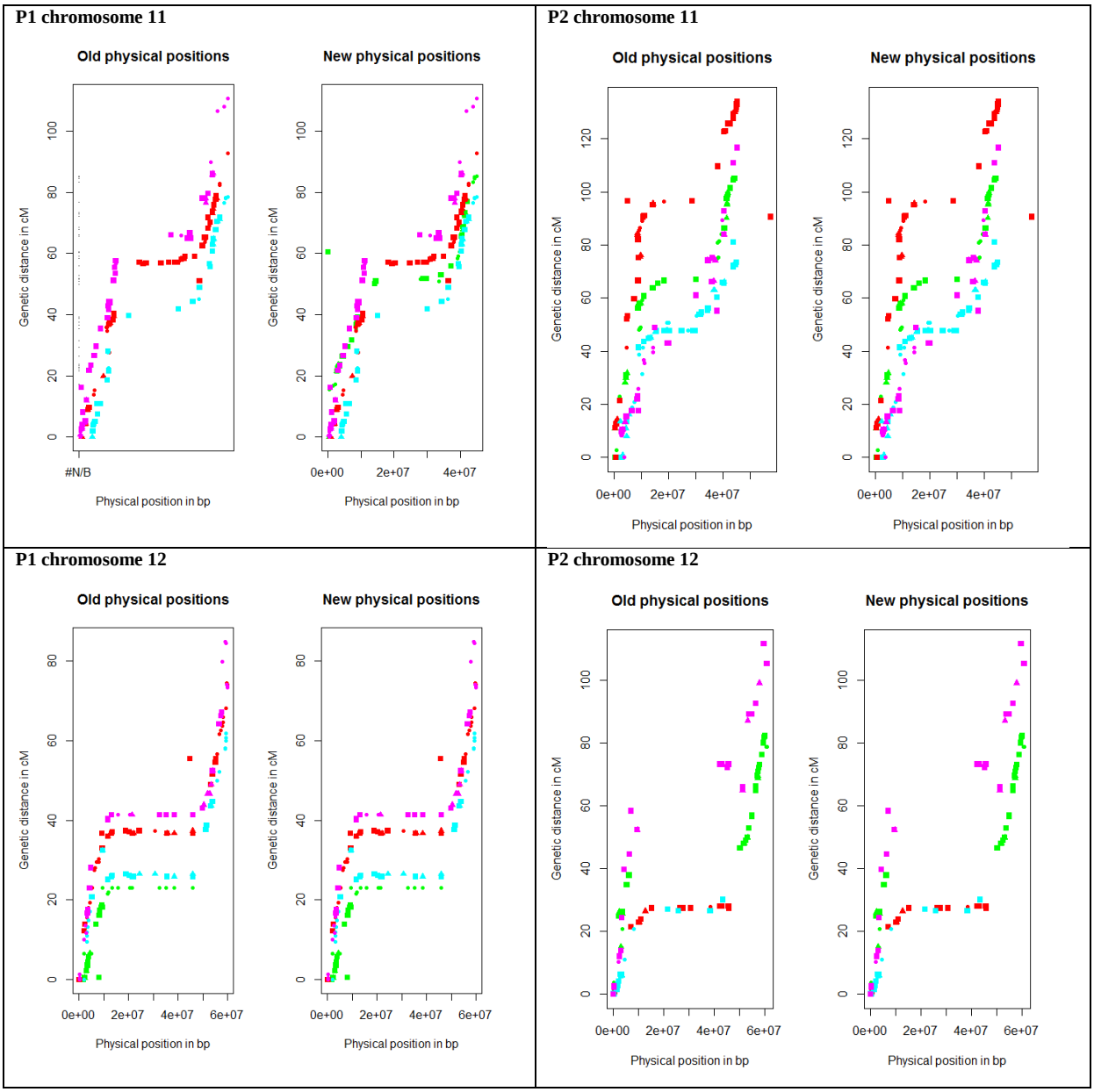
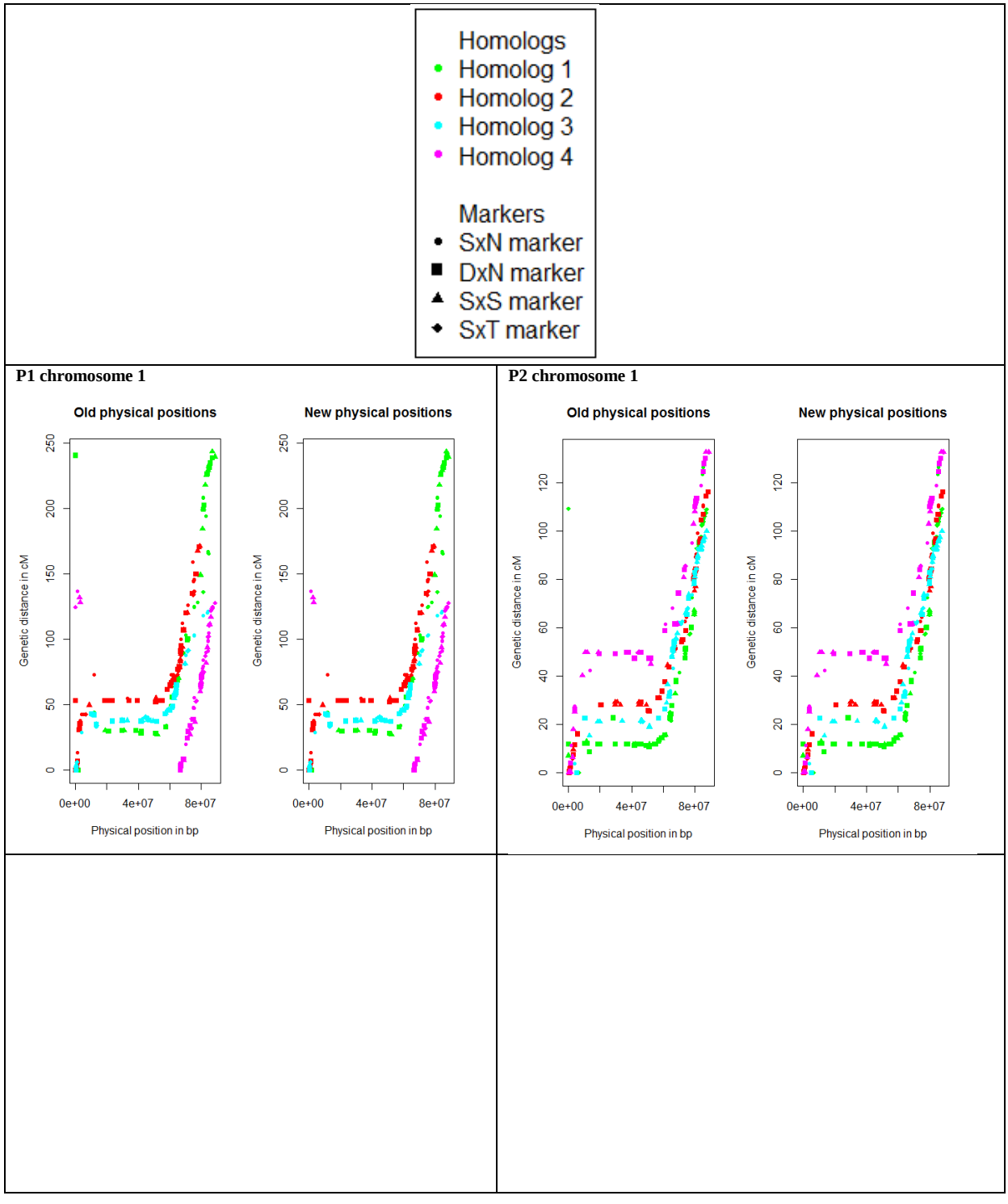



P1 chromosome 11
Old physical positions
New physical positions
Genetic distance in cM
Physical position in bp
#N/B
0e+00
2e+07
4e+07
P2 chromosome 11
Old physical positions
New physical positions
Genetic distance in cM
Physical position in bp
0e+00
2e+07
4e+07
P1 chromosome 12
Old physical positions
New physical positions
Genetic distance in cM
Physical position in bp
0e+00
2e+07
4e+07
6e+07
P2 chromosome 12
Old physical positions
New physical positions
Genetic distance in cM
Physical position in bp
0e+00
2e+07
4e+07
6e+07

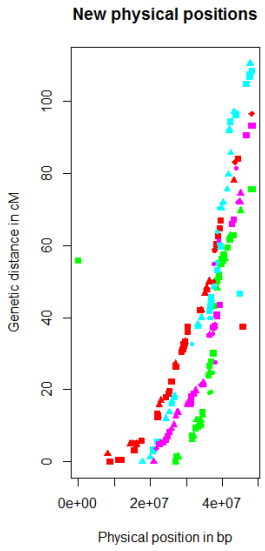
SxT maps

The SxT maps, containing all marker types considered in this thesis, are compared with the physical positions (Figure 30).

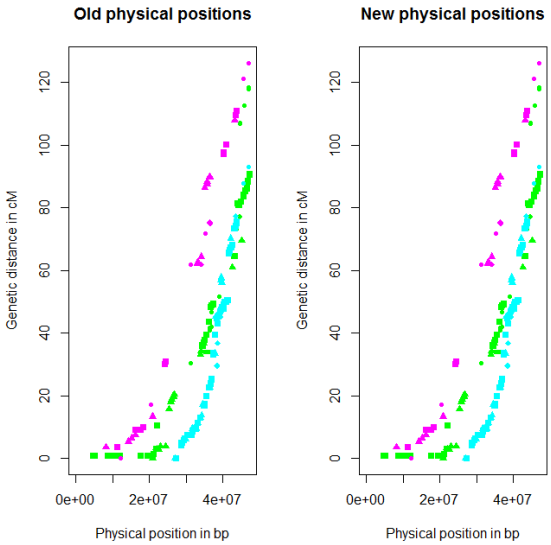
Figure 30. The comparison of the map position of the SxT map with the physical positions. The old and new physical positions are compared with the map. In some cases, the comparison between the map and the old physical positions is wrongfully presented as a vertical line. This means that a non-numerical value is present as physical position.



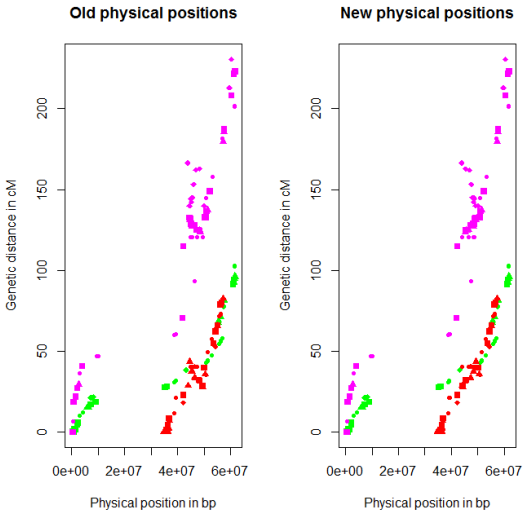
P1 chromosome 2



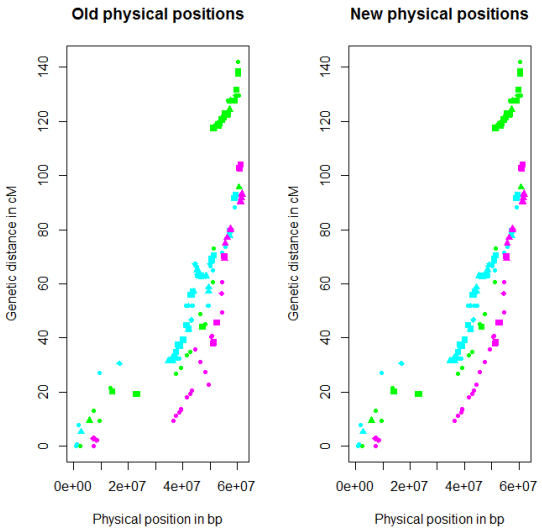
P2 chromosome 2



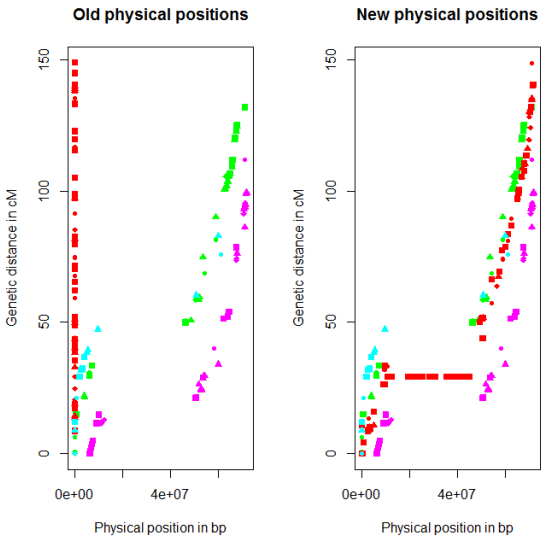
P1 chromosome 3



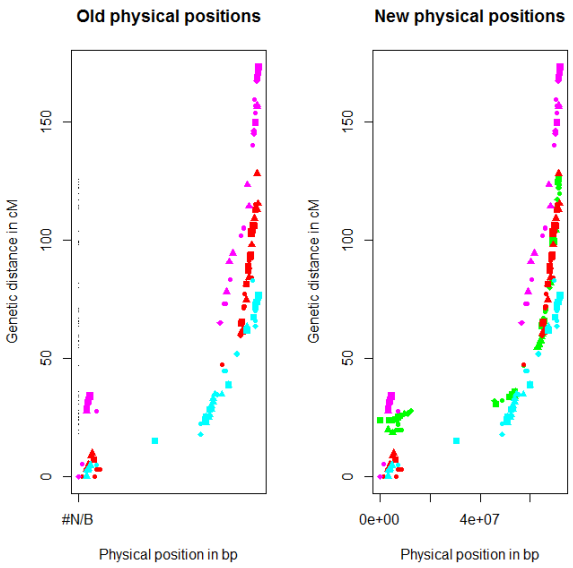
P2 chromosome 3



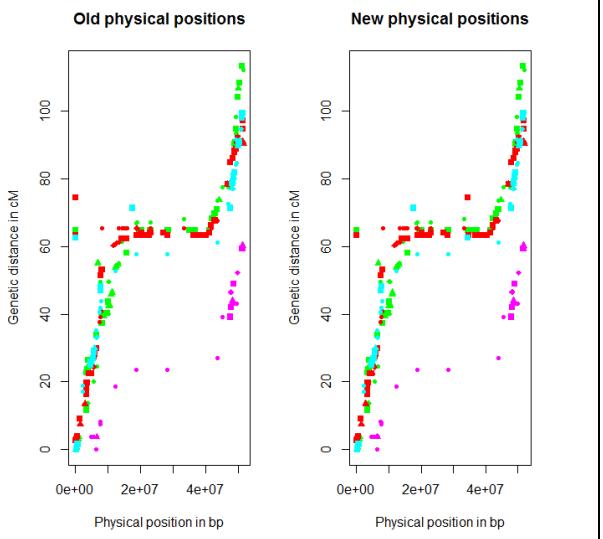
P1 chromosome 4



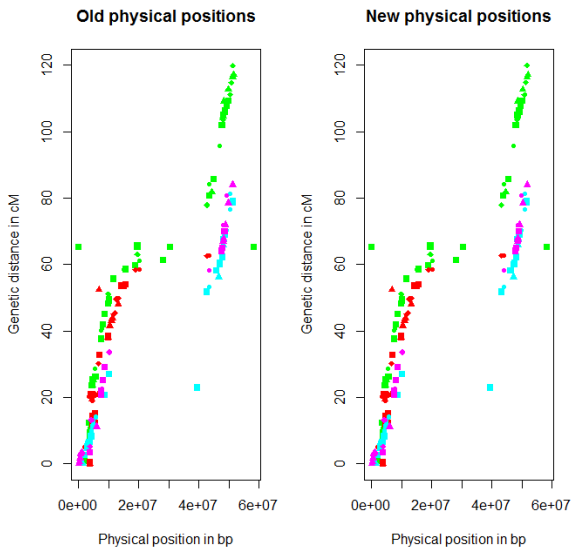
P2 chromosome 4



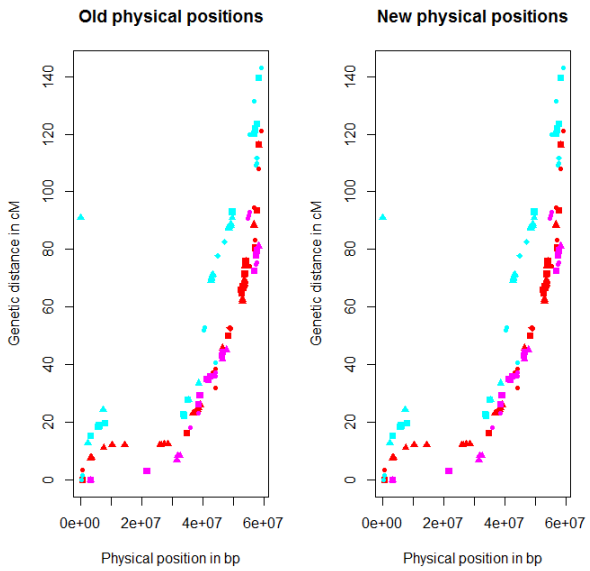
P1 chromosome 5



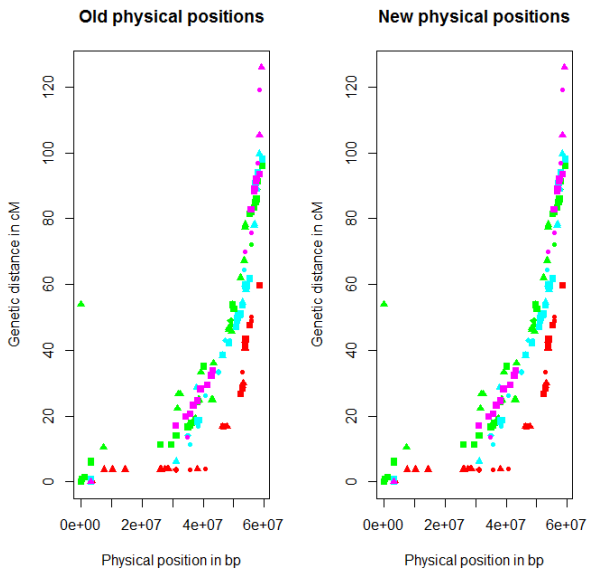
P2 chromosome 5



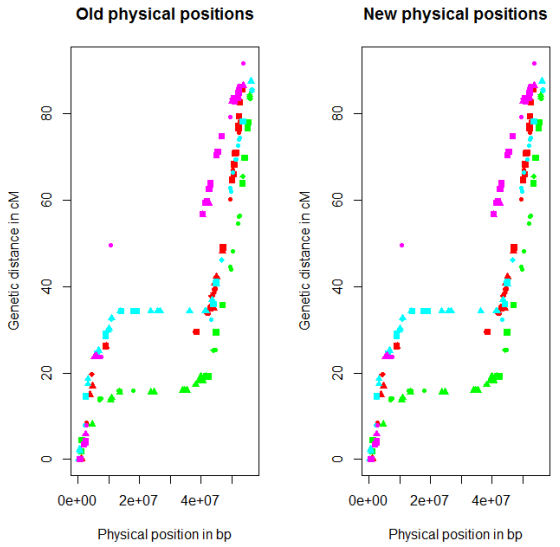
P1 chromosome 6



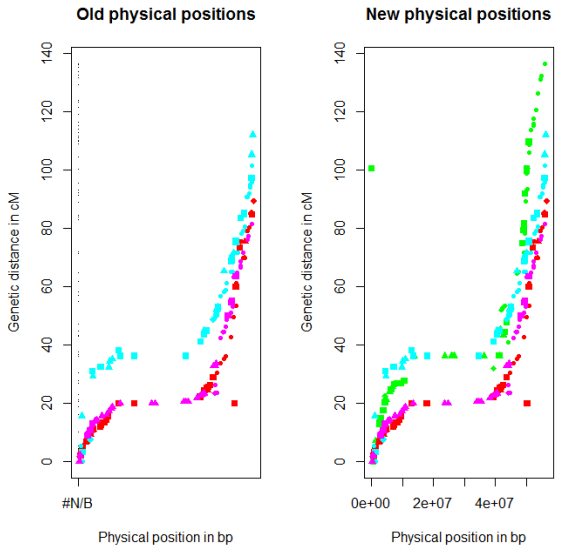
P2 chromosome 6



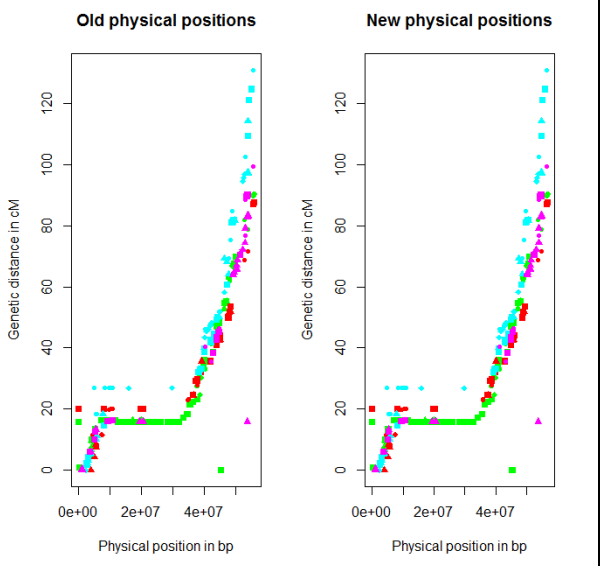
P1 chromosome 7



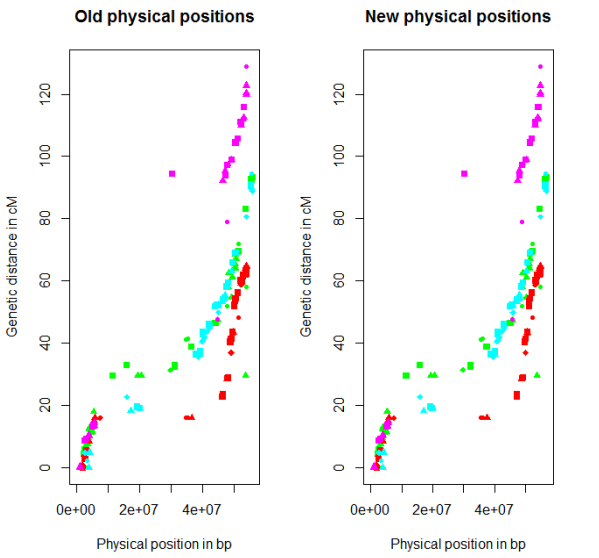
P2 chromosome 7



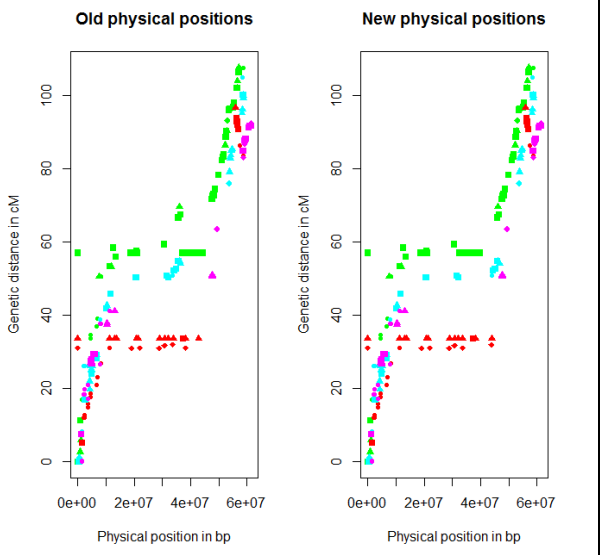
P1 chromosome 8



P2 chromosome 8



P1 chromosome 9



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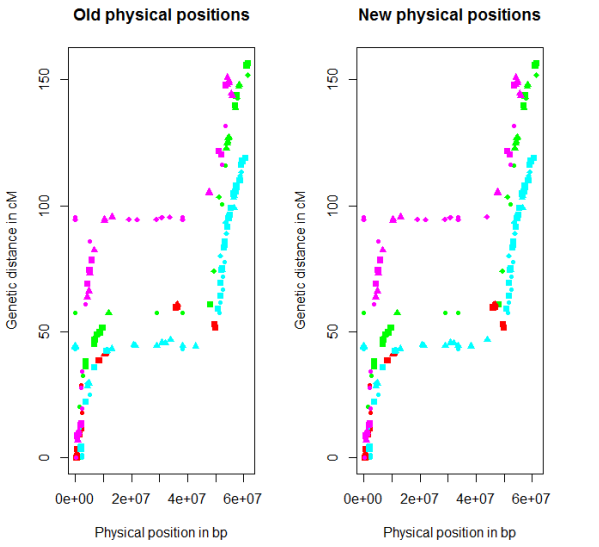

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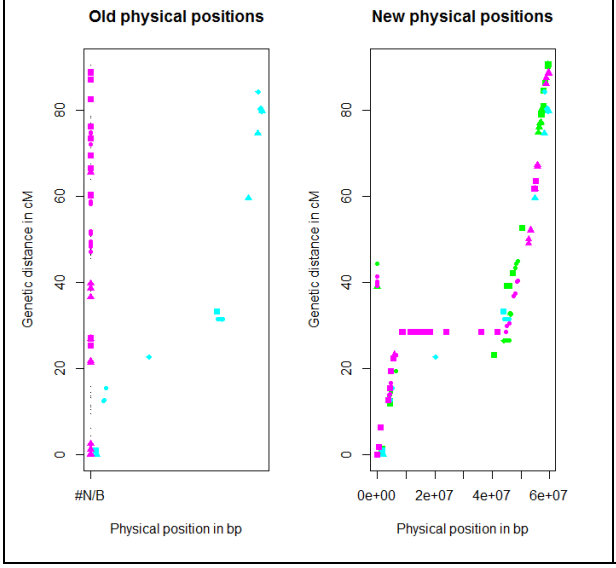
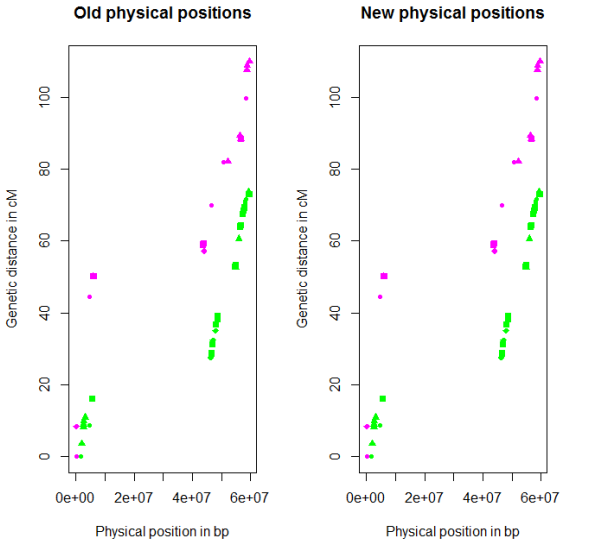
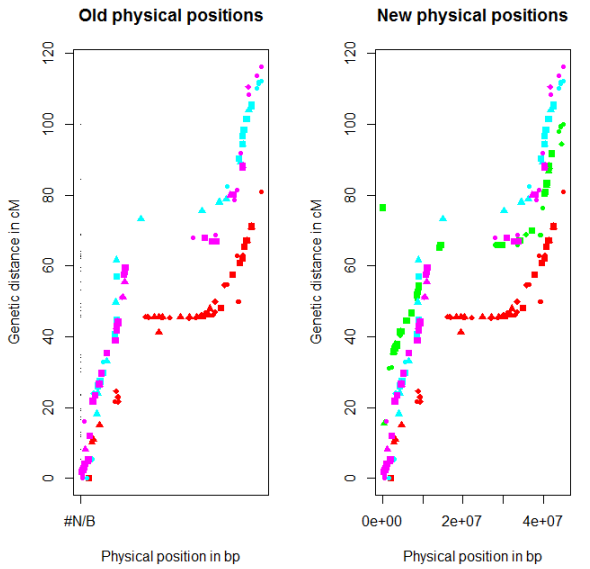


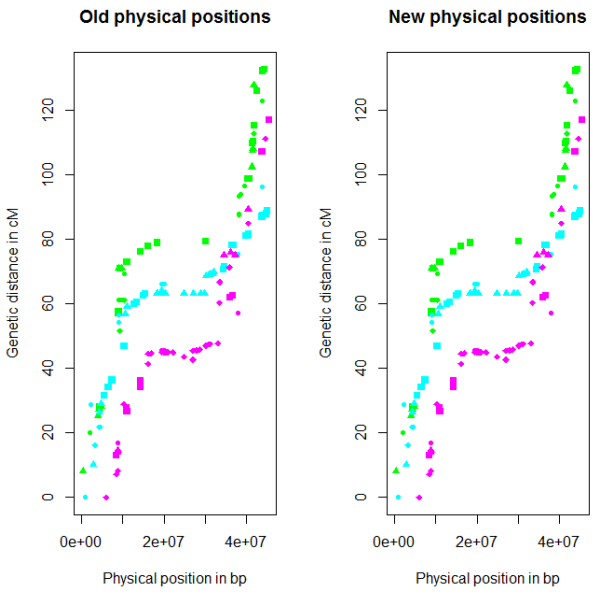
P2 chromosome 10



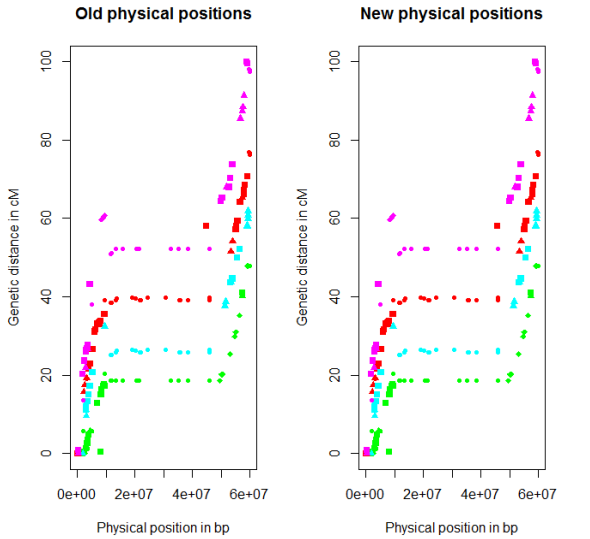
P1 chromosome 11



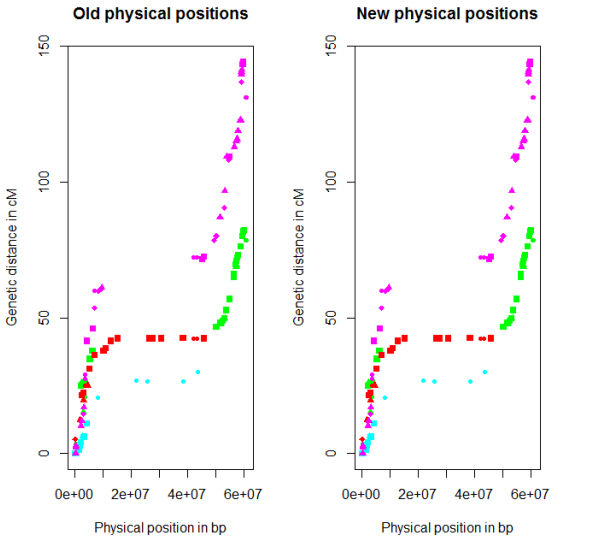
P2 chromosome 11



P1 chromosome 12



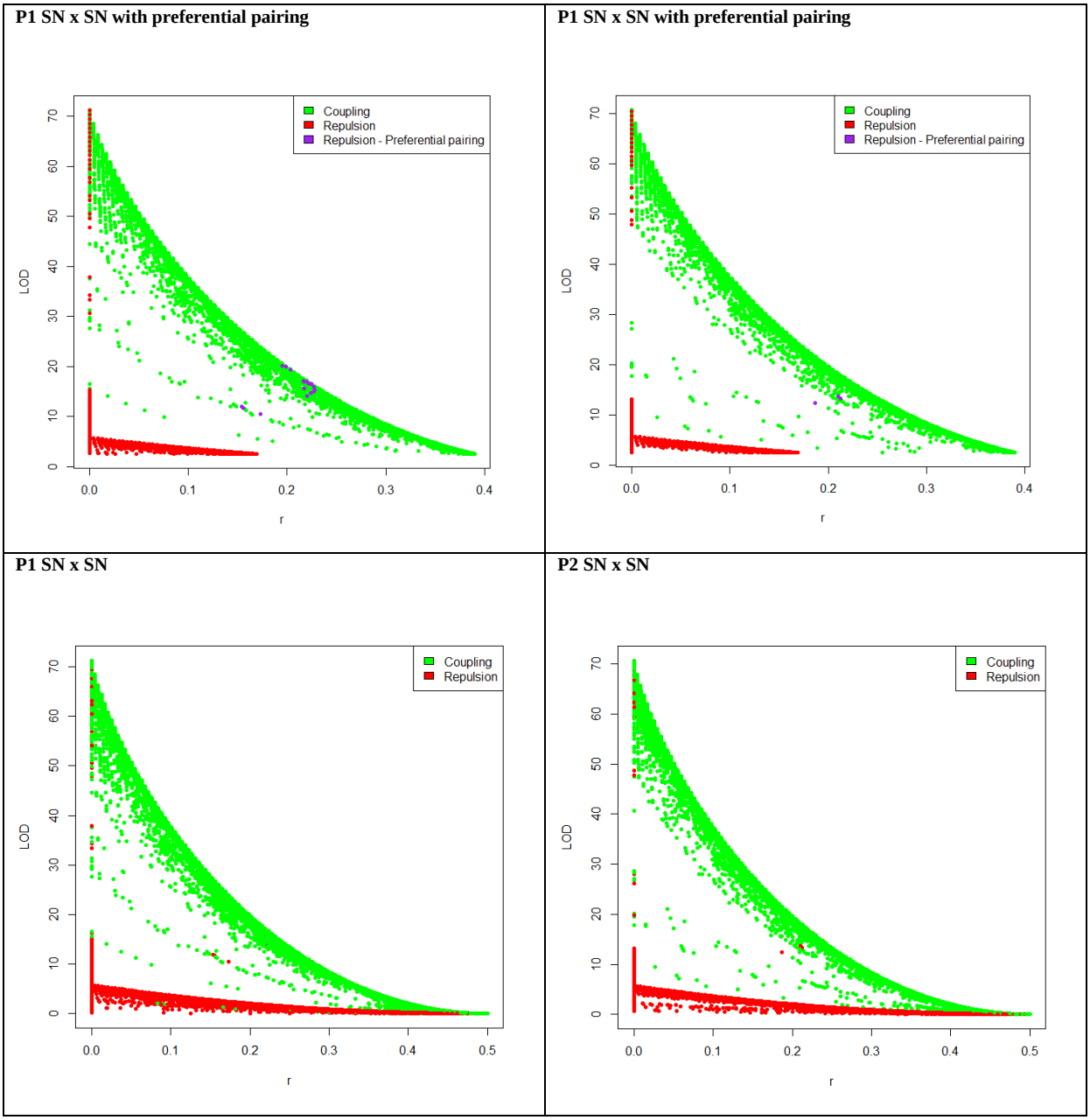
P2 chromosome 12



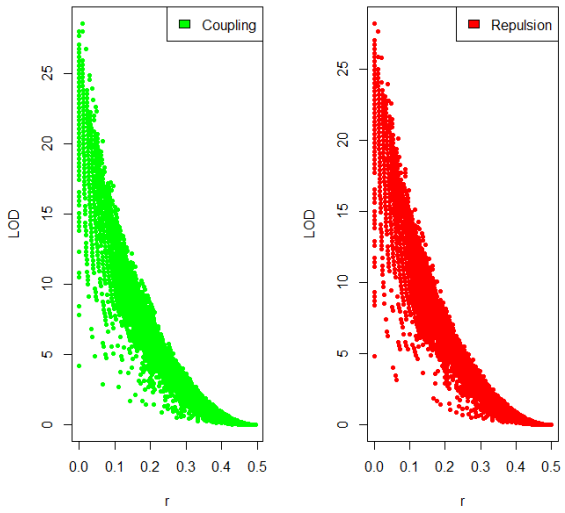
Appendix 7: Relationship between LOD-scores and recombination frequencies

In Chapters 1 to 4, the recombination frequencies and LOD-scores for different marker types and phases are calculated. In Figure 31, the recombination frequencies are plotted against the LOD-scores to give an impression of the information content.

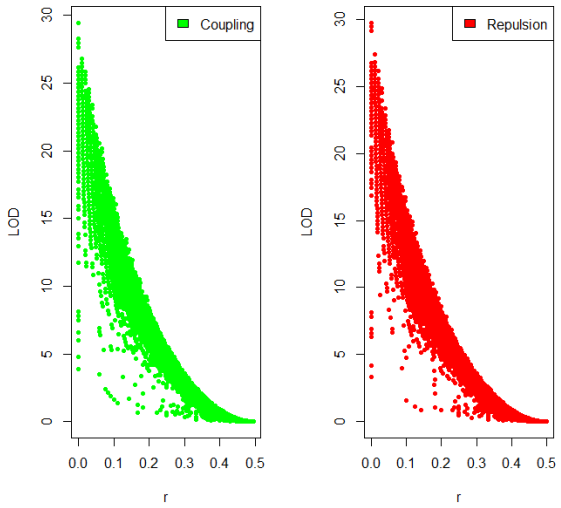
Figure 31. The recombination frequencies of the different marker types and the corresponding LOD-score. Some marker type and phase combination are very informative while some other are not informative at all.



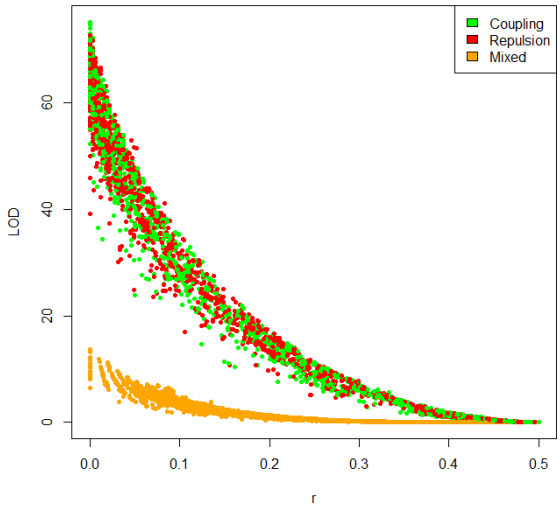
P1 DN x SN



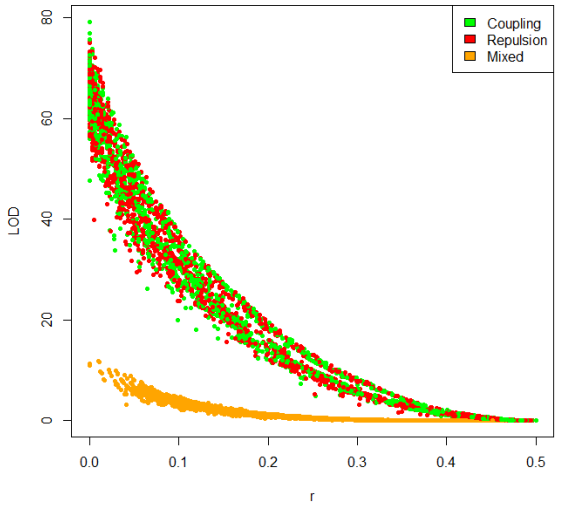
P2 DN x SN



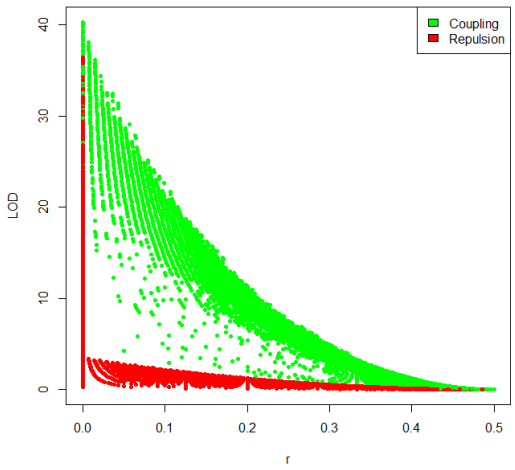
P1 DN x DN



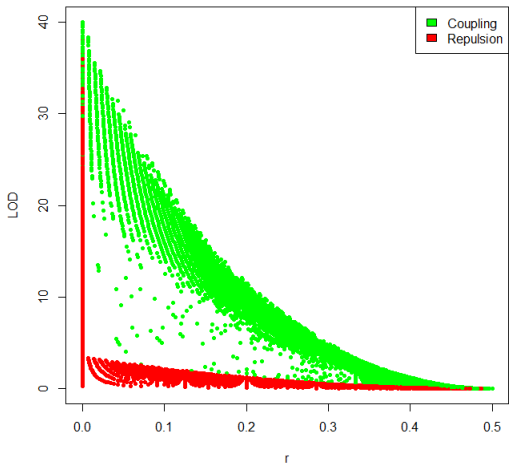
P2 DN x DN



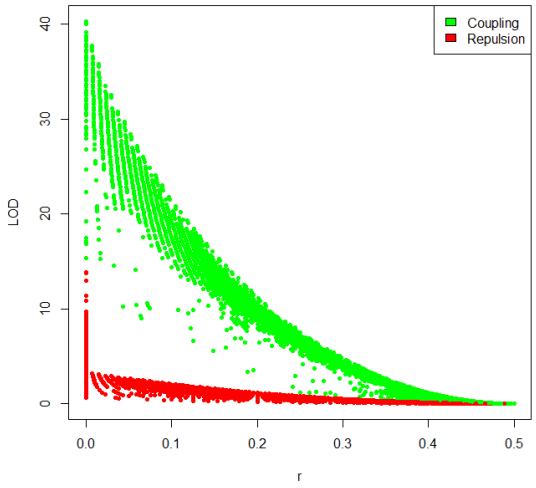
P1 SS x SN



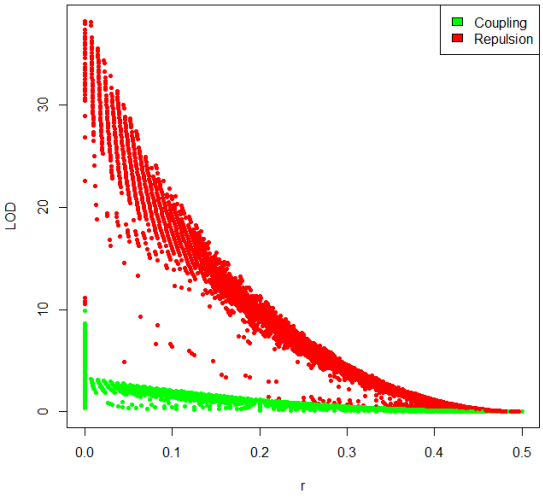
P2 SS x SN



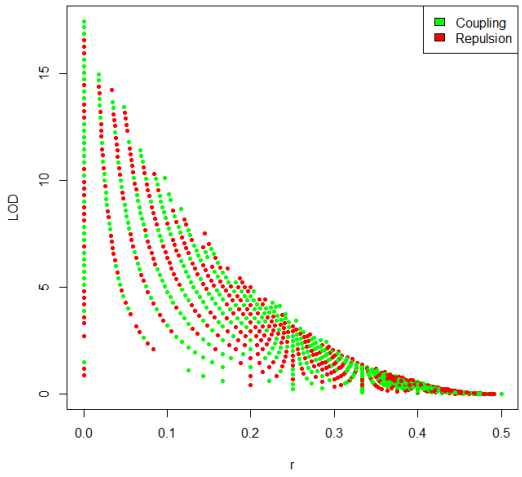
P1 ST X SN



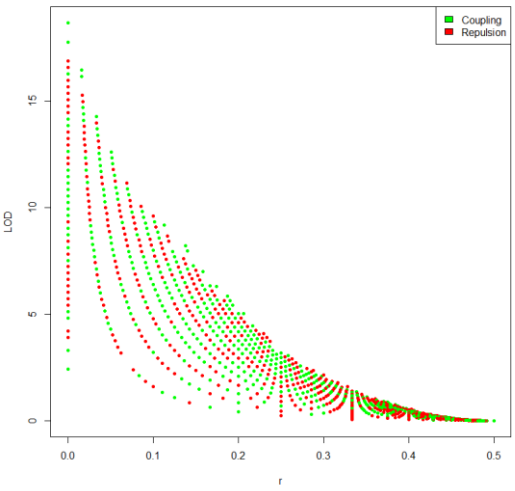
P2 ST x SN



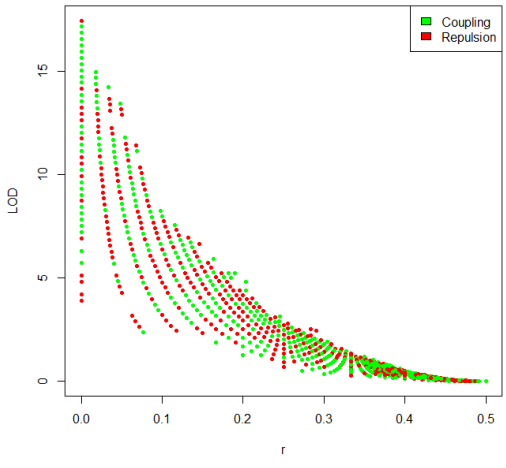
P1 SS x DN



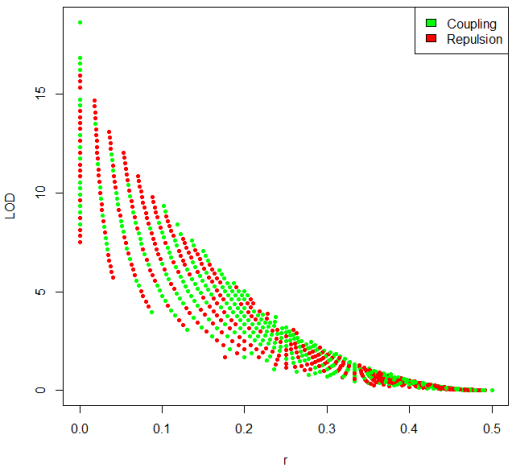
P2 SS x DN



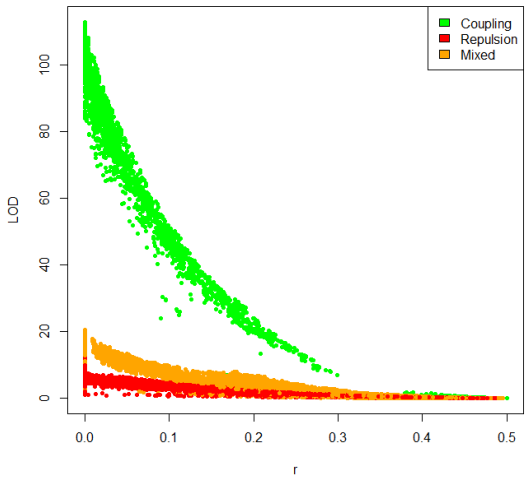
P1 ST x DN



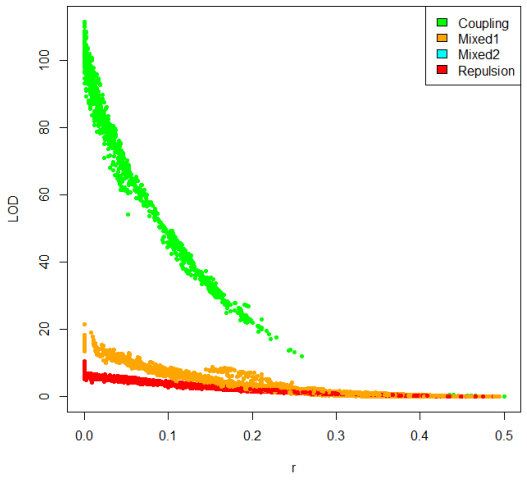
P2 ST x DN



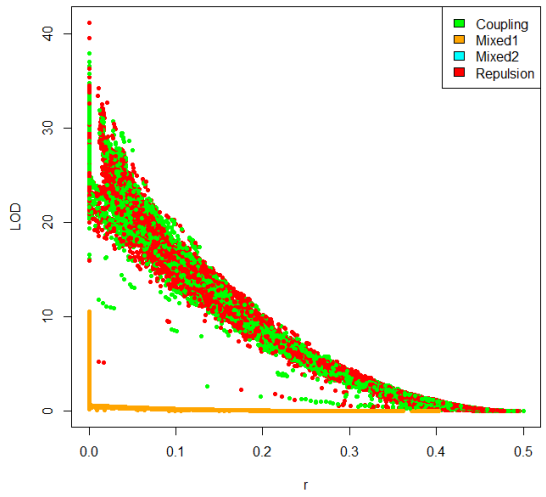
P1 & P2 SS x SS



P1 & P2 ST x ST



P1 & P2 SS x ST



Appendix 8: Removed markers from ordering

During the ordering of markers in Chapter 6, markers were removed by the ordering procedure for different reasons. In Table 18, the markers that were removed are presented. The markers come from the ordering of the same homolog maps that are used in the integration procedure. The reason of removal is shown together with the missing values and the p-value for skewedness.

Table 18. Markers that are removed by the ordering procedure together with some additional statistics. The parent, chromosome, homolog and marker type are shown. The reason of removal is also shown together with the missing values and the p-value for skewedness for each marker.

Marker Name	Parent	Chromosome	Homolog	Marker type	Reason for removal (Jump, Negative distance or Significance)	NA's	Skewedness p-value
PotVar0035883	P1	1	1	DxN	Jump	0	0.252439849
PotVar0036085	P1	1	1	DxN	Jump	0	0.369045461
PotVar0050829	P1	1	1	DxN	Negative distance	6	0.390019539
PotVar0042497	P1	1	1	DxN	Jump	0	0.853655256
PotVar0042350	P1	1	1	DxN	Jump	0	0.853655256
PotVar0029105	P1	1	1	DxN	Jump	0	0.612316282
PotVar0096805	P1	1	2	SxS	Jump	7	0.226059617
PotVar0049626	P1	1	2	DxN	Jump	58	0.002393697
PotVar0061243	P1	1	2	DxN	Jump	1	0.440002629
PotVar0035449	P1	1	2	DxN	Jump	0	0.369045461
PotVar0035721	P1	1	2	DxN	Jump	0	0.211443497
solcap_snp_c2_30957	P1	1	2	DxN	Jump	0	0.399428094
PotVar0006253	P1	1	2	SxN	Jump	76	0.384567151
solcap_snp_c2_49726	P1	1	3	SxT	Negative distance	2	0.446470041
PotVar0095169	P1	1	3	SxT	Negative distance	1	0.737060909
solcap_snp_c2_27894	P1	1	3	SxS	Negative distance	1	0.72775079
PotVar0071925	P1	1	3	SxS	Negative distance	1	0.688746944
PotVar0071945	P1	1	3	SxS	Negative distance	17	0.459657916
solcap_snp_c1_11769	P1	1	3	DxN	Jump	0	0.853655256
PotVar0050459	P1	1	4	SxS	Negative distance	3	0.143679387
PotVar0038673	P1	2	1	SxS	Negative distance	2	0.671747777
solcap_snp_c1_9363	P1	2	1	DxN	Jump	1	0.440002629
solcap_snp_c2_32415	P1	2	1	SxT	Jump	6	0.316842444
PotVar0006989	P1	2	1	DxN	Jump	4	0.87824619
PotVar0038725	P1	2	2	SxT	Negative distance	8	0.738234725
PotVar0094371	P1	2	2	DxN	Jump	2	0.003115777
PotVar0010926	P1	2	2	DxN	Jump	7	0.090030327
PotVar0010550	P1	2	2	DxN	Jump	4	0.091088588

solcap_snp_c1_8113	P1	2	3	SxS	Negative distance	6	0.580834136
solcap_snp_c1_7341	P1	2	3	SxS	Negative distance	5	0.06703193
PotVar0120627	P1	3	1	DxN	Jump	2	0.754337881
PotVar0056918	P1	3	1	DxN	Jump	32	0.193932736
PotVar0121928	P1	3	2	SxN	Jump	17	0.091665418
PotVar0106413	P1	3	2	SxN	Negative distance	2	0.077332376
PotVar0013242	P1	3	2	DxN	Jump	1	0.032902886
PotVar0121927	P1	3	2	SxT	Negative distance	3	0.400704947
PotVar0019184	P1	3	2	SxN	Jump	30	0.108823554
PotVar0019460	P1	3	2	DxN	Jump	6	0.100715603
PotVar0019343	P1	3	2	DxN	Jump	0	0.019145335
PotVar0013592	P1	3	3	DxN	Jump	2	0.928237098
PotVar0019343	P1	3	3	DxN	Jump	0	0.019145335
PotVar0043186	P1	3	4	DxN	Jump	28	0.630951478
PotVar0084554	P1	3	4	DxN	Jump	1	0.07809821
solcap_snp_c2_21590	P1	4	1	SxS	Negative distance	1	0.632783385
solcap_snp_c2_21578	P1	4	1	SxS	Negative distance	3	0.692448531
solcap_snp_c1_6748	P1	4	1	SxS	Negative distance	2	0.89716935
PotVar0101164	P1	4	1	SxN	Negative distance	1	0.896234257
PotVar0101048	P1	4	1	SxN	Negative distance	9	0.506955687
PotVar0076875	P1	4	1	SxN	Negative distance	6	0.552979217
solcap_snp_c2_55090	P1	4	1	SxT	Negative distance	0	0.420173059
solcap_snp_c2_26794	P1	4	1	SxT	Negative distance	1	0.543258784
solcap_snp_c2_26800	P1	4	1	SxT	Negative distance	1	0.593815603
solcap_snp_c2_36957	P1	4	1	SxN	Negative distance	2	0.844572164
solcap_snp_c1_11008	P1	4	1	SxN	Negative distance	2	1
PotVar0026570	P1	4	1	SxN	Negative distance	27	0.240681858
PotVar0076646	P1	4	1	SxS	Negative distance	3	0.024702404
solcap_snp_c1_12564	P1	4	1	DxN	Jump	0	0.829685255
solcap_snp_c1_11391	P1	4	1	DxN	Jump	0	0.712762086
PotVar0071109	P1	4	1	DxN	Negative distance	3	0.911240229
solcap_snp_c1_11722	P1	4	1	DxN	Negative distance	1	0.888123856
solcap_snp_c1_10715	P1	4	1	DxN	Jump	0	0.033841211
solcap_snp_c2_34017	P1	4	2	SxS	Negative distance	5	0.856267532
solcap_snp_c1_12564	P1	4	2	DxN	Jump	0	0.829685255
PotVar0070965	P1	4	2	DxN	Jump	30	0.024651968
solcap_snp_c2_26771	P1	4	3	SxT	Negative distance	4	0.635851839
solcap_snp_c2_48810	P1	4	3	SxT	Negative distance	6	0.835559533
PotVar0071109	P1	4	3	DxN	Jump	3	0.911240229
PotVar0016775	P1	4	4	SxT	Negative distance	5	0.588503495
PotVar0075324	P1	4	4	SxT	Negative distance	7	0.174152124
PotVar0017293	P1	4	4	SxT	Negative distance	9	0.268262453
PotVar0109579	P1	4	4	SxT	Jump	5	0.630522211
solcap_snp_c2_11568	P1	4	4	SxT	Negative distance	1	0.56199002
PotVar0100820	P1	4	4	SxT	Jump	12	0.683861409

PotVar0100941	P1	4	4	SxT	Jump	13	0.642772591
PotVar0107009	P1	4	4	SxT	Jump	5	0.652643567
PotVar0100919	P1	4	4	SxS	Jump	1	0.922647085
PotVar0100767	P1	4	4	SxS	Jump	5	0.890137521
PotVar0106843	P1	4	4	SxS	Jump	0	0.981191782
PotVar0076503	P1	4	4	SxS	Jump	1	0.98736859
PotVar0076511	P1	4	4	SxS	Jump	9	0.647775867
PotVar0076621	P1	4	4	SxS	Jump	2	0.98103324
PotVar0076666	P1	4	4	SxS	Jump	1	0.922647085
solcap_snp_c1_11626	P1	4	4	SxN	Jump	1	0.601860667
solcap_snp_c1_3740	P1	4	4	DxN	Jump	3	0.487751747
solcap_snp_c1_15513	P1	4	4	DxN	Jump	0	0.42552551
solcap_snp_c1_11356	P1	4	4	DxN	Jump	0	0.712762086
PotVar0070856	P1	4	4	DxN	Negative distance	17	0.727470509
solcap_snp_c1_7569	P1	4	4	DxN	Jump	0	0.156047483
PotVar0070965	P1	4	4	DxN	Significance	30	0.024651968
PotVar0075687	P1	4	4	DxN	Jump	7	0.620534601
solcap_snp_c2_23593	P1	4	4	DxN	Negative distance	1	0.49964575
PotVar0034716	P1	5	1	SxN	Negative distance	1	0.03148605
PotVar0034469	P1	5	1	SxN	Negative distance	2	0.026349714
solcap_snp_c2_11685	P1	5	1	DxN	Negative distance	0	0.63000639
solcap_snp_c2_11707	P1	5	1	DxN	Negative distance	0	0.418845499
PotVar0048673	P1	5	1	DxN	Negative distance	24	0.360188865
PotVar0081633	P1	5	3	SxS	Negative distance	2	0.08861942
solcap_snp_c2_50302	P1	5	3	DxN	Negative distance	5	0.593598731
PotVar0123135	P1	5	4	SxS	Negative distance	10	0.140498978
PotVar0081647	P1	5	4	SxT	Negative distance	8	0.532057152
PotVar0048577	P1	5	4	SxN	Jump	36	0.158165345
solcap_snp_c2_33509	P1	5	4	SxS	Jump	8	0.548572033
solcap_snp_c2_23834	P1	5	4	SxS	Jump	0	0.977060455
solcap_snp_c2_24066	P1	6	3	DxN	Jump	13	0.115242775
PotVar0057091	P1	6	4	DxN	Jump	3	1
solcap_snp_c2_9202	P1	6	4	DxN	Jump	0	0.909430492
PotVar0085050	P1	6	4	DxN	Jump	25	0.115826676
PotVar0082855	P1	6	4	DxN	Jump	3	0.056597251
solcap_snp_c2_28212	P1	7	1	DxN	Negative distance	1	0.200065559
PotVar0036843	P1	7	1	SxS	Negative distance	1	0.581367099
PotVar0102524	P1	7	1	SxS	Negative distance	0	0.58147105
solcap_snp_c2_26239	P1	7	1	SxS	Negative distance	0	0.459102853
PotVar0132155	P1	7	1	SxS	Negative distance	22	0.054513749
PotVar0022288	P1	7	1	SxS	Jump	4	0.026663398
solcap_snp_c2_38828	P1	7	1	SxS	Negative distance	5	0.269727031
PotVar0102724	P1	7	1	DxN	Jump	2	0.086110178
solcap_snp_c1_8601	P1	7	2	SxN	Negative distance	21	0.219511208

PotVar0132077	P1	7	2	SxN	Negative distance	0	0.845223367
PotVar0095593	P1	7	2	SxN	Negative distance	1	0.794212476
PotVar0095619	P1	7	2	SxN	Negative distance	5	0.94767273
solcap_snp_c1_16221	P1	7	2	SxN	Negative distance	0	0.696813997
solcap_snp_c2_36838	P1	7	2	SxN	Negative distance	0	0.744901949
PotVar0102362	P1	7	2	SxN	Negative distance	0	0.948117129
PotVar0102547	P1	7	2	SxN	Negative distance	0	0.845223367
solcap_snp_c2_52663	P1	7	2	SxT	Negative distance	6	0.993527531
PotVar0095580	P1	7	2	SxS	Negative distance	1	0.724673625
PotVar0015345	P1	7	3	SxS	Significance	85	0.005946217
solcap_snp_c2_49379	P1	8	1	DxN	Jump	0	0.464951219
solcap_snp_c1_8282	P1	8	3	DxN	Jump	1	0.015741054
PotVar0088739	P1	8	3	SxT	Negative distance	9	0.344455809
solcap_snp_c2_51957	P1	8	3	SxT	Jump	4	0.59365364
PotVar0063333	P1	8	4	DxN	Negative distance	1	0.33265958
PotVar0012337	P1	9	1	DxN	Jump	2	0.773845546
PotVar0012284	P1	9	1	DxN	Jump	16	0.126884299
PotVar0012007	P1	9	1	DxN	Jump	15	0.437052173
solcap_snp_c1_3597	P1	9	1	DxN	Jump	1	0.654601377
PotVar0061732	P1	9	2	SxS	Jump	3	0.17943384
solcap_snp_c2_43241	P1	9	4	SxT	Jump	5	0.40273248
solcap_snp_c2_3063	P1	9	4	DxN	Significance	1	0.476386669
PotVar0123577	P1	10	2	DxN	Jump	7	0.218569295
PotVar0065848	P1	10	2	SxS	Jump	8	0.11794291
solcap_snp_c2_950	P1	10	2	DxN	Jump	0	0.811508223
PotVar0057421	P1	10	3	SxS	Negative distance	4	0.614390559
PotVar0057635	P1	10	3	SxS	Negative distance	4	0.840448381
PotVar0057721	P1	10	3	SxS	Negative distance	25	0.626891918
PotVar0057860	P1	10	3	SxS	Negative distance	4	0.840448381
PotVar0058227	P1	10	3	SxN	Negative distance	2	0.433812405
PotVar0005597	P1	10	3	SxN	Negative distance	1	0.695591422
PotVar0005576	P1	10	3	SxN	Negative distance	1	0.558068429
PotVar0005103	P1	10	3	SxN	Negative distance	2	0.94789635
solcap_snp_c2_40823	P1	10	3	SxN	Negative distance	0	0.516056364
solcap_snp_c2_41394	P1	10	3	SxN	Negative distance	1	0.648726044
solcap_snp_c2_40764	P1	10	3	SxN	Negative distance	0	0.896670248
solcap_snp_c2_45603	P1	10	3	SxT	Negative distance	4	0.660893157
PotVar0132240	P1	10	3	SxT	Negative distance	4	0.745282889
solcap_snp_c1_14236	P1	10	3	SxS	Negative distance	2	0.084566864
PotVar0120165	P1	10	3	SxS	Jump	3	0.596250727
solcap_snp_c2_1263	P1	10	3	SxS	Jump	4	0.563853184
PotVar0104285	P1	10	3	SxS	Jump	4	0.275353495
PotVar0104021	P1	10	3	SxS	Jump	39	0.167314703
PotVar0065380	P1	10	4	SxN	Negative distance	4	0.793351627
solcap_snp_c1_16585	P1	11	2	SxT	Negative distance	10	0.642279779

solcap_snp_c2_4957	P1	11	2	SxT	Negative distance	13	0.741479961
solcap_snp_c1_16586	P1	11	2	SxT	Negative distance	8	0.976268657
PotVar0005899	P1	11	2	SxT	Negative distance	5	0.856267532
solcap_snp_c2_44633	P1	11	2	SxT	Negative distance	9	0.853939666
PotVar0059121	P1	11	2	SxT	Negative distance	6	0.306057378
PotVar0134712	P1	11	2	SxN	Negative distance	0	0.948117129
solcap_snp_c1_14683	P1	11	2	SxN	Negative distance	1	0.896234257
solcap_snp_c2_54586	P1	11	2	SxN	Negative distance	11	0.641575228
solcap_snp_c2_3737	P1	11	2	SxN	Negative distance	2	0.94789635
PotVar0112309	P1	11	2	SxN	Negative distance	5	0.792479885
solcap_snp_c1_4926	P1	11	2	SxN	Negative distance	2	0.55639128
solcap_snp_c1_9183	P1	11	2	SxN	Negative distance	1	0.514276192
solcap_snp_c2_57106	P1	11	2	SxN	Negative distance	0	0.397473921
solcap_snp_c2_56626	P1	11	2	SxN	Negative distance	3	0.600306158
solcap_snp_c2_33905	P1	11	2	SxN	Negative distance	12	0.204163755
PotVar0059873	P1	11	2	SxN	Negative distance	3	0.55639128
solcap_snp_c2_53683	P1	11	2	SxN	Negative distance	5	0.742790582
solcap_snp_c2_12334	P1	11	2	SxN	Negative distance	3	0.512476402
PotVar0058735	P1	11	2	SxN	Negative distance	1	0.514276192
solcap_snp_c2_15340	P1	11	2	SxS	Negative distance	6	0.880112422
solcap_snp_c2_23921	P1	11	2	SxT	Negative distance	7	0.928752451
PotVar0105987	P1	11	2	SxS	Negative distance	3	0.270443437
solcap_snp_c2_54589	P1	11	2	DxN	Negative distance	5	0.093416279
solcap_snp_c2_20948	P1	11	2	SxT	Negative distance	5	0.288985342
PotVar0066299	P1	11	3	DxN	Jump	3	0.574366733
PotVar0064140	P1	11	3	DxN	Jump	4	0.696569307
solcap_snp_c2_18836	P1	12	1	SxS	Negative distance	4	0.379913699
PotVar0030960	P1	12	1	SxS	Negative distance	10	0.006321008
PotVar0107233	P1	12	3	DxN	Jump	8	0.04657954
solcap_snp_c1_13697	P1	12	3	DxN	Jump	4	0.154926128
PotVar0052458	P1	12	3	DxN	Jump	2	0.23682696
PotVar0069011	P1	12	3	DxN	Significance	26	0.79558866
PotVar0098373	P1	12	4	SxS	Jump	6	0.050766455
PotVar0050696	P2	1	1	SxS	Negative distance	2	0.549980564
solcap_snp_c2_9892	P2	1	1	SxS	Negative distance	2	0.722143133
solcap_snp_c2_4896	P2	1	1	SxS	Negative distance	3	0.616987828
PotVar0035753	P2	1	1	SxS	Negative distance	1	0.805653367
PotVar0035852	P2	1	1	SxS	Negative distance	2	0.786293197
PotVar0036054	P2	1	1	SxS	Negative distance	1	0.778800783
solcap_snp_c1_15123	P2	1	1	DxN	Jump	0	0.42552551
PotVar0061044	P2	1	1	DxN	Jump	0	0.333503718
PotVar0050201	P2	1	1	DxN	Jump	2	0.165650962
solcap_snp_c2_27894	P2	1	1	SxS	Negative distance	1	0.72775079
PotVar0045420	P2	1	1	DxN	Jump	14	0.003808089

PotVar0071966	P2	1	1	SxT	Jump	1	0.574023613
PotVar0071853	P2	1	1	SxS	Jump	2	0.547645193
PotVar0029356	P2	1	2	DxN	Jump	37	0.560598677
solcap_snp_c1_2519	P2	1	3	SxS	Negative distance	3	0.345037365
PotVar0042445	P2	1	3	SxS	Negative distance	2	0.417083814
PotVar0041272	P2	1	3	SxS	Negative distance	2	0.260068945
solcap_snp_c1_3895	P2	1	3	SxS	Negative distance	1	0.043658559
PotVar0006268	P2	1	3	SxS	Negative distance	7	0.107481689
PotVar0029221	P2	1	3	SxS	Negative distance	2	0.88578892
solcap_snp_c2_20502	P2	1	3	SxT	Negative distance	0	0.028706465
PotVar0041226	P2	1	3	DxN	Negative distance	0	0.993690873
PotVar0006051	P2	1	3	DxN	Negative distance	17	0.695934314
PotVar0044821	P2	1	4	SxT	Negative distance	1	0.954459402
solcap_snp_c2_17539	P2	1	4	DxN	Jump	3	0.253651279
PotVar0050306	P2	1	4	DxN	Significance	1	0.125396923
PotVar0050855	P2	1	4	DxN	Jump	4	0.330096878
PotVar0060676	P2	1	4	DxN	Significance	1	0.407690993
PotVar0126809	P2	1	4	DxN	Jump	0	0.152628741
PotVar0036238	P2	1	4	DxN	Jump	31	0.413837641
PotVar0041660	P2	1	4	DxN	Negative distance	0	0.944629941
solcap_snp_c2_14274	P2	1	4	DxN	Jump	1	0.958512303
PotVar0120130	P2	1	4	SxT	Jump	12	0.750761941
PotVar0071945	P2	1	4	SxS	Jump	17	0.459657916
PotVar0009857	P2	2	1	SxT	Jump	8	0.688415675
solcap_snp_c2_27271	P2	2	1	DxN	Jump	2	0.065025308
solcap_snp_c2_17415	P2	2	1	DxN	Jump	33	0.004665095
PotVar0094352	P2	2	2	SxN	Jump	0	0.152838641
PotVar0094561	P2	2	2	SxN	Jump	2	0.089661905
PotVar0088857	P2	2	2	SxS	Jump	5	0.181427972
PotVar0009867	P2	2	2	SxS	Jump	16	0.300785628
solcap_snp_c1_8113	P2	2	2	SxS	Jump	6	0.580834136
PotVar0124339	P2	2	2	SxN	Jump	0	0.051100537
PotVar0002139	P2	2	2	DxN	Jump	5	0.633245845
PotVar0001573	P2	2	2	DxN	Jump	1	0.290170054
PotVar0001694	P2	2	2	DxN	Jump	1	0.230823554
PotVar0117579	P2	2	2	SxN	Jump	2	0.067544047
solcap_snp_c2_53818	P2	2	2	SxN	Jump	0	0.091031106
PotVar0029477	P2	2	2	SxN	Jump	0	0.091031106
solcap_snp_c1_12354	P2	2	2	SxS	Jump	2	0.125089799
PotVar0123873	P2	2	2	SxS	Jump	1	0.153030406
solcap_snp_c2_42059	P2	2	2	SxS	Jump	3	0.100774312
solcap_snp_c1_11553	P2	2	2	SxS	Jump	16	0.036849804
solcap_snp_c2_47765	P2	2	2	SxN	Jump	2	0.361135437
solcap_snp_c1_868	P2	2	2	SxN	Jump	2	0.433812405
solcap_snp_c2_41884	P2	2	2	SxN	Jump	1	0.397473921

solcap_snp_c2_41874	P2	2	2	SxN	Jump	25	0.010875333
solcap_snp_c2_32237	P2	2	2	SxN	Jump	1	0.397473921
PotVar0109750	P2	2	2	SxN	Jump	8	0.290350496
solcap_snp_c2_45311	P2	2	2	SxS	Jump	0	0.019145335
PotVar0089282	P2	2	2	SxN	Jump	61	0.001914064
solcap_snp_c2_55863	P2	2	2	SxS	Jump	4	0.808603695
solcap_snp_c2_805	P2	2	2	DxN	Jump	7	0.129718144
PotVar0116077	P2	2	3	SxS	Jump	2	0.53157292
PotVar0046789	P2	2	3	SxS	Negative distance	5	0.720661163
solcap_snp_c1_16540	P2	2	3	SxS	Negative distance	3	0.704387005
solcap_snp_c1_10493	P2	2	3	SxT	Jump	6	0.911126445
PotVar0119058	P2	2	3	SxT	Jump	6	0.835559533
PotVar0009178	P2	2	3	SxS	Jump	7	0.320097246
solcap_snp_c2_41963	P2	2	3	SxS	Jump	32	0.123055236
PotVar0109718	P2	2	3	SxN	Jump	1	0.948117129
solcap_snp_c2_27271	P2	2	3	DxN	Jump	2	0.065025308
solcap_snp_c2_735	P2	2	3	DxN	Jump	1	0.346690775
solcap_snp_c2_32467	P2	2	3	SxT	Significance	8	0.170951473
solcap_snp_c1_2350	P2	2	3	SxT	Significance	11	0.072199758
solcap_snp_c2_805	P2	2	3	DxN	Jump	7	0.129718144
PotVar0010377	P2	2	4	DxN	Negative distance	4	0.561438399
solcap_snp_c2_9497	P2	3	1	SxN	Negative distance	36	0.39737829
PotVar0013867	P2	3	1	SxT	Negative distance	6	0.590979455
PotVar0013866	P2	3	1	SxT	Negative distance	5	0.588503495
PotVar0021187	P2	3	1	SxT	Negative distance	6	0.357672138
PotVar0113388	P2	3	1	DxN	Negative distance	0	0.087448183
solcap_snp_c2_46605	P2	3	1	DxN	Negative distance	0	0.062725492
PotVar0129499	P2	3	1	DxN	Negative distance	1	0.233034726
PotVar0095322	P2	3	1	DxN	Negative distance	0	0.309112301
PotVar0094840	P2	3	1	DxN	Negative distance	4	0.224330427
PotVar0021338	P2	3	1	SxN	Jump	22	0.495333072
solcap_snp_c1_15839	P2	3	1	DxN	Significance	0	0.965788776
PotVar0019272	P2	3	1	DxN	Negative distance	0	0.993690873
solcap_snp_c1_5388	P2	3	1	DxN	Significance	0	0.895154013
solcap_snp_c1_15783	P2	3	1	DxN	Significance	1	0.899485628
solcap_snp_c2_17218	P2	3	1	DxN	Significance	0	0.965788776
PotVar0084678	P2	3	1	DxN	Significance	2	0.882027614
solcap_snp_c2_36231	P2	3	1	DxN	Significance	2	0.663932715
PotVar0068047	P2	3	2	SxN	Jump	1	0.397473921
PotVar0070350	P2	3	2	SxN	Jump	1	0.268427312
solcap_snp_c2_37991	P2	3	2	SxN	Jump	4	1
PotVar0095449	P2	3	2	SxN	Jump	0	0.795062658
PotVar0094878	P2	3	2	SxN	Jump	0	0.896670248
PotVar0085735	P2	3	2	SxN	Jump	2	0.896234257

solcap_snp_c1_167	P2	3	2	SxN	Jump	2	0.794212476
PotVar0056335	P2	3	2	SxN	Jump	1	0.216078094
PotVar0055974	P2	3	2	SxN	Jump	1	0.328866863
solcap_snp_c2_1835	P2	3	2	SxN	Jump	5	0.554694997
PotVar0027440	P2	3	2	SxN	Jump	1	0.474044299
solcap_snp_c2_57258	P2	3	2	SxN	Jump	2	0.601860667
PotVar0030069	P2	3	2	SxN	Jump	2	0.361135437
PotVar0121236	P2	3	2	SxN	Jump	3	0.472161104
PotVar0013408	P2	3	2	SxN	Jump	3	0.55639128
PotVar0013895	P2	3	2	SxN	Jump	4	0.512476402
PotVar0014057	P2	3	2	SxN	Jump	3	0.266389411
PotVar0014208	P2	3	2	SxN	Jump	4	0.359081609
solcap_snp_c2_1579	P2	3	2	SxS	Jump	9	0.003006383
solcap_snp_c2_20259	P2	3	2	SxS	Jump	1	0.571596456
solcap_snp_c2_1722	P2	3	2	DxN	Jump	0	0.447625887
PotVar0055776	P2	3	2	DxN	Jump	0	0.541222911
PotVar0030088	P2	3	2	DxN	Jump	1	0.830787398
solcap_snp_c2_18271	P2	3	2	DxN	Jump	2	0.663932715
solcap_snp_c2_35553	P2	3	2	DxN	Jump	1	0.970774554
solcap_snp_c2_5286	P2	3	2	DxN	Jump	1	0.305306015
solcap_snp_c1_1909	P2	3	2	DxN	Jump	91	0.01564609
PotVar0021136	P2	3	2	DxN	Jump	0	0.211443497
solcap_snp_c1_15839	P2	3	2	DxN	Jump	0	0.965788776
PotVar0019272	P2	3	2	DxN	Jump	0	0.993690873
PotVar0019302	P2	3	2	DxN	Jump	1	0.992612171
solcap_snp_c1_5388	P2	3	2	DxN	Jump	0	0.895154013
solcap_snp_c1_15783	P2	3	2	DxN	Jump	1	0.899485628
solcap_snp_c2_17218	P2	3	2	DxN	Jump	0	0.965788776
PotVar0084678	P2	3	2	DxN	Jump	2	0.882027614
solcap_snp_c2_36231	P2	3	2	DxN	Jump	2	0.663932715
PotVar0120484	P2	3	3	SxT	Jump	20	0.58457724
solcap_snp_c1_6332	P2	3	3	SxS	Negative distance	27	0.045480292
solcap_snp_c1_9292	P2	3	3	SxS	Negative distance	1	0.703494715
PotVar0094922	P2	3	3	SxS	Negative distance	1	0.805653367
PotVar0029778	P2	3	3	SxS	Negative distance	5	0.953692684
PotVar0121499	P2	3	3	SxN	Negative distance	3	0.844572164
PotVar0014077	P2	3	3	SxN	Negative distance	2	0.601860667
solcap_snp_c2_5263	P2	3	3	SxN	Negative distance	2	0.794212476
solcap_snp_c2_26402	P2	3	3	DxN	Jump	4	0.714739663
PotVar0029727	P2	3	4	SxN	Negative distance	2	0.117256565
solcap_snp_c1_5794	P2	3	4	SxN	Negative distance	1	0.171499463
solcap_snp_c1_7111	P2	3	4	SxN	Negative distance	3	0.042479994
PotVar0121403	P2	3	4	SxN	Negative distance	9	0.097575937
solcap_snp_c1_151	P2	3	4	SxN	Negative distance	3	0.101991434
solcap_snp_c2_616	P2	3	4	SxN	Negative distance	2	0.151099073

PotVar0021118	P2	3	4	SxN	Negative distance	3	0.214123258
PotVar0021255	P2	3	4	DxN	Jump	0	0.001766761
PotVar0020884	P2	3	4	DxN	Jump	0	0.008069851
PotVar0021083	P2	3	4	DxN	Jump	6	0.053996764
solcap_snp_c2_18268	P2	3	4	SxS	Negative distance	5	0.6843332
solcap_snp_c2_18271	P2	3	4	DxN	Jump	2	0.663932715
PotVar0055776	P2	3	4	DxN	Jump	0	0.541222911
solcap_snp_c2_16722	P2	4	1	SxS	Negative distance	0	0.745836445
PotVar0000514	P2	4	2	SxT	Negative distance	3	0.423596317
PotVar0017609	P2	4	2	SxS	Jump	9	0.367879441
solcap_snp_c1_3461	P2	4	2	SxS	Jump	6	0.432720897
PotVar0058240	P2	4	2	SxN	Negative distance	100	0.016432262
PotVar0075700	P2	4	3	DxN	Jump	62	0.004086771
solcap_snp_c2_55793	P2	4	3	DxN	Jump	2	0.120006093
PotVar0000759	P2	4	3	DxN	Jump	1	0.04464066
solcap_snp_c1_8330	P2	4	3	DxN	Jump	14	0.00145046
PotVar0118472	P2	4	3	DxN	Jump	13	0.411316266
solcap_snp_c2_11490	P2	4	3	DxN	Jump	7	0.426486778
solcap_snp_c2_39322	P2	4	3	DxN	Jump	19	0.005871679
solcap_snp_c2_36993	P2	4	4	SxT	Jump	8	0.85266491
solcap_snp_c2_36941	P2	4	4	SxS	Negative distance	2	0.226960628
PotVar0034970	P2	5	1	SxT	Negative distance	6	0.658527552
PotVar0081707	P2	5	4	SxT	Negative distance	3	0.220287776
solcap_snp_c2_42451	P2	5	4	SxT	Negative distance	3	0.357037475
PotVar0117367	P2	5	4	DxN	Negative distance	1	0.677889363
PotVar0117324	P2	5	4	DxN	Jump	0	0.788721679
PotVar0129937	P2	5	4	DxN	Jump	1	0.762474327
PotVar0080320	P2	5	4	DxN	Negative distance	1	0.598869322
PotVar0080026	P2	5	4	DxN	Jump	0	0.706027376
PotVar0080800	P2	5	4	DxN	Jump	6	0.653557557
solcap_snp_c2_11747	P2	5	4	DxN	Jump	14	0.539780918
solcap_snp_c1_1126	P2	5	4	SxN	Negative distance	3	0.214123258
solcap_snp_c2_51765	P2	6	1	DxN	Jump	1	0.360167369
PotVar0040162	P2	6	1	DxN	Jump	3	0.273932982
PotVar0086012	P2	6	2	SxN	Negative distance	1	0.268427312
PotVar0069582	P2	6	2	SxT	Negative distance	2	0.208443948
PotVar0104586	P2	6	2	SxN	Negative distance	1	0.845223367
solcap_snp_c2_43080	P2	6	2	SxN	Negative distance	18	0.176407874
PotVar0090367	P2	6	2	SxN	Negative distance	2	1
solcap_snp_c1_3125	P2	6	3	SxT	Negative distance	8	0.993471188
solcap_snp_c2_56590	P2	6	3	DxN	Jump	0	0.231766399
solcap_snp_c2_37358	P2	6	3	DxN	Jump	2	0.278688788
solcap_snp_c2_37329	P2	6	3	DxN	Jump	1	0.258801243
solcap_snp_c1_16128	P2	6	3	SxS	Jump	5	0.034070944

PotVar0065903	P2	6	3	DxN	Jump	5	0.091918455
PotVar0015345	P2	7	1	SxS	Significance	85	0.005946217
PotVar0102371	P2	7	2	SxS	Negative distance	6	0.769584314
PotVar0134970	P2	7	2	DxN	Jump	1	0.264622988
PotVar0093025	P2	7	3	SxS	Negative distance	3	0.614356754
solcap_snp_c1_2404	P2	7	4	SxT	Negative distance	3	0.535833595
solcap_snp_c2_33488	P2	7	4	SxS	Negative distance	1	0.63547036
PotVar0093776	P2	7	4	SxS	Negative distance	2	0.61694295
PotVar0093742	P2	7	4	DxN	Jump	2	0.514328241
PotVar0102773	P2	7	4	DxN	Jump	35	0.336516226
PotVar0047739	P2	7	4	DxN	Jump	0	0.895154013
PotVar0103342	P2	8	1	SxT	Negative distance	2	0.049681251
solcap_snp_c2_28433	P2	8	1	DxN	Jump	0	0.567533389
solcap_snp_c2_47905	P2	8	2	SxS	Negative distance	25	0.066073922
PotVar0124889	P2	8	2	DxN	Significance	70	0.016103116
solcap_snp_c1_10384	P2	8	4	SxT	Negative distance	1	0.593815603
solcap_snp_c1_8297	P2	8	4	SxT	Negative distance	2	0.540698413
PotVar0011929	P2	9	1	DxN	Negative distance	2	0.215891627
solcap_snp_c2_46431	P2	9	2	SxN	Negative distance	2	0.240256334
solcap_snp_c2_46427	P2	9	2	SxN	Negative distance	0	0.43575911
PotVar0132972	P2	9	2	SxN	Negative distance	0	0.43575911
PotVar0034273	P2	9	2	SxN	Negative distance	6	0.292450194
solcap_snp_c1_4248	P2	9	2	SxN	Negative distance	0	0.516056364
solcap_snp_c1_4282	P2	9	2	SxN	Negative distance	2	0.361135437
solcap_snp_c1_1000	P2	9	2	SxS	Negative distance	4	0.68397882
PotVar0012446	P2	9	2	DxN	Negative distance	4	0.255978725
PotVar0101835	P2	9	2	SxN	Negative distance	2	0.601860667
PotVar0103657	P2	9	2	SxN	Negative distance	2	0.695591422
PotVar0103791	P2	9	2	SxN	Negative distance	5	0.94767273
PotVar0103920	P2	9	2	SxN	Negative distance	1	0.648726044
PotVar0103891	P2	9	2	SxN	Negative distance	1	0.744901949
PotVar0107741	P2	9	2	SxN	Negative distance	1	0.744901949
PotVar0107499	P2	9	2	SxN	Negative distance	2	0.514276192
solcap_snp_c2_42964	P2	9	2	SxT	Significance	7	0.061341152
solcap_snp_c1_16414	P2	9	2	SxT	Significance	5	0.052656504
PotVar0131150	P2	9	2	DxN	Negative distance	0	0.464951219
PotVar0054644	P2	9	2	DxN	Negative distance	1	0.388712511
PotVar0012077	P2	9	2	DxN	Jump	6	0.148697066
PotVar0012114	P2	9	2	DxN	Negative distance	13	0.028147056
PotVar0011657	P2	9	2	DxN	Negative distance	71	0.030933869
solcap_snp_c2_4196	P2	9	2	DxN	Negative distance	3	0.937908799
solcap_snp_c1_975	P2	9	2	DxN	Negative distance	14	0.008309476
solcap_snp_c2_3323	P2	9	2	DxN	Negative distance	5	0.340416229
PotVar0130658	P2	9	2	DxN	Negative distance	1	0.268861387
solcap_snp_c1_1053	P2	9	2	DxN	Negative distance	1	0.300493094

PotVar0103876	P2	9	3	SxT	Jump	4	0.234922912
PotVar0097335	P2	9	3	SxT	Jump	7	0.403049598
PotVar0101947	P2	9	3	DxN	Jump	23	0.094437873
PotVar0105170	P2	9	3	SxS	Jump	7	0.703157823
PotVar0105349	P2	9	3	SxS	Jump	7	0.679120621
solcap_snp_c2_3949	P2	9	4	SxS	Negative distance	8	0.31367789
solcap_snp_c2_3323	P2	9	4	DxN	Jump	5	0.340416229
PotVar0130658	P2	9	4	DxN	Jump	1	0.268861387
PotVar0065848	P2	10	2	SxS	Jump	8	0.11794291
solcap_snp_c2_56515	P2	10	2	DxN	Significance	2	0.754337881
solcap_snp_c2_27827	P2	10	2	DxN	Significance	9	0.041821609
solcap_snp_c1_307	P2	10	4	DxN	Significance	0	0.132789868
PotVar0105750	P2	11	1	SxS	Negative distance	25	0.242902697
PotVar0063968	P2	11	1	SxN	Jump	8	0.354916224
PotVar0067438	P2	11	3	SxS	Negative distance	7	0.264362296
PotVar0067013	P2	11	3	SxT	Negative distance	4	0.103050905
solcap_snp_c2_20948	P2	11	3	SxT	Negative distance	5	0.288985342
PotVar0064771	P2	11	3	DxN	Jump	4	0.002240943
PotVar0064519	P2	11	3	DxN	Jump	24	0.016479571
solcap_snp_c2_50977	P2	11	4	SxS	Jump	3	0.216554175
PotVar0130698	P2	11	4	SxS	Jump	9	0.164864463
PotVar0047372	P2	11	4	SxS	Jump	3	0.576210605
PotVar0058600	P2	11	4	SxS	Jump	14	0.12456101
PotVar0105566	P2	11	4	SxN	Jump	1	0.558068429
PotVar0106057	P2	11	4	SxN	Jump	3	0.55639128
solcap_snp_c2_6256	P2	11	4	SxN	Jump	1	0.474044299
PotVar0067017	P2	11	4	SxN	Jump	1	0.216078094
PotVar0110432	P2	11	4	SxN	Jump	10	0.001389865
PotVar0067764	P2	11	4	SxN	Jump	21	0.117389103
solcap_snp_c1_2162	P2	11	4	SxN	Jump	0	0.298647087
PotVar0112755	P2	11	4	DxN	Jump	3	0.340642044
PotVar0066337	P2	11	4	DxN	Jump	4	0.689875153
PotVar0064787	P2	11	4	DxN	Jump	16	0.069117612
PotVar0064771	P2	11	4	DxN	Jump	4	0.002240943
PotVar0064519	P2	11	4	DxN	Jump	24	0.016479571
PotVar0008553	P2	11	4	DxN	Negative distance	6	0.916070147
solcap_snp_c2_18788	P2	12	4	SxS	Negative distance	0	0.155226615
solcap_snp_c2_24595	P2	12	4	DxN	Jump	1	0.476386669
PotVar0098059	P2	12	4	DxN	Negative distance	1	0.377752164

Appendix 9: The integrated map or the final orders

In Chapter 7, the individual homolog maps were integrated. The map positions of all the markers on the integrated map are shown in Table 19.

Table 19. Map position in cM of all the markers on the integrated map. Every chromosome has a sub-table with its own markers and map positions.

Chromosome 1	
Name	cM
PotVar0120126	0
PotVar0120075	0.43
PotVar0119913	0.43
PotVar0119973	0.43
PotVar0044821	2.31
PotVar0044815	2.31
PotVar0071852	2.58
solcap_snp_c2_21099	3.62
PotVar0120088	5.83
PotVar0119912	6.26
solcap_snp_c1_6674	6.26
solcap_snp_c2_6906	6.53
PotVar0072072	6.53
PotVar0119989	6.68
PotVar0119975	6.68
solcap_snp_c2_21234	7.11
PotVar0071853	7.72
PotVar0120034	8.23
PotVar0120004	8.66
PotVar0119813	8.66
solcap_snp_c1_10930	9.03
solcap_snp_c2_36658	9.03
solcap_snp_c2_36660	9.46
PotVar0071925	9.46
PotVar0120070	9.46
PotVar0044985	9.55
PotVar0044829	9.55
PotVar0072052	9.55
PotVar0071924	9.95
PotVar0072063	10.81
PotVar0071966	12.01
PotVar0072033	12.14
PotVar0044840	12.14
PotVar0072076	12.9
PotVar0071846	13.69
solcap_snp_c2_6683	15.08
solcap_snp_c2_6713	17.44
solcap_snp_c2_21247	18.09
PotVar0044864	18.82
PotVar0044823	18.84
solcap_snp_c2_21227	20.13
solcap_snp_c2_21233	20.13
PotVar0045000	20.13
PotVar0045260	26.02
PotVar0045340	26.02
PotVar0045502	26.02
PotVar0045662	26.02
PotVar0045167	27.03
PotVar0045459	27.03
PotVar0045210	28.48
PotVar0045404	28.48
PotVar0045339	28.48
PotVar0045505	28.48
PotVar0045145	28.48
solcap_snp_c1_6114	28.61
solcap_snp_c2_51800	33.68
solcap_snp_c2_55012	33.78
PotVar0114875	33.78
solcap_snp_c1_13296	34.02
solcap_snp_c2_48051	34.11
solcap_snp_c2_27918	34.12
PotVar0045460	34.61
PotVar0122300	37.63
PotVar0045420	37.8
solcap_snp_c2_52705	41.04
solcap_snp_c2_2332	41.49
solcap_snp_c2_53521	43.13
solcap_snp_c2_43984	43.13
solcap_snp_c1_12937	43.13
solcap_snp_c2_43973	43.13
solcap_snp_c2_686	43.44
PotVar0102233	43.44
solcap_snp_c2_54303	44.48
solcap_snp_c2_54306	44.48
PotVar0088430	44.48
solcap_snp_c2_45395	44.48
solcap_snp_c2_53763	44.48
PotVar0100708	44.48
solcap_snp_c1_5477	44.48
solcap_snp_c2_2873	44.48
solcap_snp_c2_55618	44.48
PotVar0071270	44.48
PotVar0014900	44.48
PotVar0102229	44.8
solcap_snp_c1_14649	44.8
PotVar0102234	44.96
PotVar0102148	45.53
PotVar0109024	45.53
solcap_snp_c2_694	45.53
solcap_snp_c2_49719	45.53
solcap_snp_c1_12152	45.91
PotVar0088385	46.12
PotVar0095087	46.12
PotVar0095116	46.12
PotVar0122548	46.12
solcap_snp_c1_15612	46.12
solcap_snp_c1_15853	46.12
solcap_snp_c1_16423	46.12
solcap_snp_c1_16690	46.12
solcap_snp_c1_6795	46.12
solcap_snp_c2_27681	46.12
solcap_snp_c2_2871	46.12
PotVar0122472	46.12
PotVar0132283	46.12
PotVar0132289	46.12
PotVar0132309	46.12

solcap_snp_c1_15855	46.12
solcap_snp_c1_16425	46.12
solcap_snp_c1_8535	46.12
solcap_snp_c2_2874	46.12
solcap_snp_c2_32111	46.12
solcap_snp_c2_55113	46.12
solcap_snp_c2_55621	46.12
solcap_snp_c2_56843	46.12
solcap_snp_c2_54307	46.12
PotVar0000042	46.46
solcap_snp_c1_12938	46.9
solcap_snp_c2_43970	46.9
PotVar0102174	46.96
solcap_snp_c2_35601	47.39
PotVar0102161	48.16
solcap_snp_c2_49722	48.16
solcap_snp_c2_41438	48.16
solcap_snp_c2_49724	48.16
solcap_snp_c2_49726	48.16
PotVar0118576	48.71
PotVar0102189	48.81
PotVar0102258	48.81
solcap_snp_c2_49732	48.81
solcap_snp_c1_14648	49.16
solcap_snp_c1_8362	49.16
PotVar0028605	49.16
PotVar0100622	49.16
PotVar0102235	49.18
solcap_snp_c2_2653	49.18
PotVar0114310	49.18
PotVar0037326	49.6
PotVar0122454	49.6
PotVar0000062	49.6
PotVar0122549	49.6
PotVar0095159	49.6
solcap_snp_c2_40112	49.6
PotVar0071533	49.6
PotVar0124795	49.81
solcap_snp_c2_35518	49.81
PotVar0088355	50.16
PotVar0122473	50.16
PotVar0088290	50.16
PotVar0122550	50.48
PotVar0014240	50.48

solcap_snp_c2_24677	50.48
PotVar0122547	50.48
PotVar0122493	50.48
PotVar0081107	50.48
solcap_snp_c1_14248	50.48
PotVar0081102	50.48
PotVar0132314	50.48
solcap_snp_c2_45625	50.51
solcap_snp_c2_45626	50.51
solcap_snp_c2_45627	50.51
PotVar0071625	50.51
PotVar0071645	50.51
solcap_snp_c2_56842	50.74
solcap_snp_c2_35532	50.74
solcap_snp_c2_40131	50.74
PotVar0095162	50.74
solcap_snp_c1_16169	50.74
PotVar0006081	50.74
solcap_snp_c2_48549	50.74
solcap_snp_c2_45623	50.74
solcap_snp_c2_57284	50.74
solcap_snp_c1_15521	50.74
PotVar0088357	50.74
solcap_snp_c2_35220	50.74
PotVar0095169	50.74
solcap_snp_c2_27682	50.74
PotVar0095184	50.74
PotVar0132333	50.74
solcap_snp_c2_27677	50.74
PotVar0000406	50.74
solcap_snp_c1_9378	50.97
solcap_snp_c1_14249	50.97
PotVar0100717	51.02
PotVar0100729	51.02
PotVar0114353	51.02
PotVar0100762	51.02
solcap_snp_c1_12858	51.37
solcap_snp_c2_45621	51.37
PotVar0018983	51.37
PotVar0006104	51.54
PotVar0018985	52.22
PotVar0018968	52.22
PotVar0071624	52.22
PotVar0071575	52.22

PotVar0018933	52.22
solcap_snp_c1_14219	52.22
PotVar0018848	52.22
solcap_snp_c2_38406	52.4
PotVar0049628	52.4
PotVar0018685	52.57
PotVar0049426	52.83
PotVar0049351	52.83
PotVar0049273	52.83
PotVar0049427	52.83
solcap_snp_c1_14633	53.11
PotVar0049291	53.26
PotVar0018833	53.58
PotVar0132267	53.59
PotVar0095172	53.59
solcap_snp_c2_35503	54.02
PotVar0018687	54.02
solcap_snp_c2_41339	54.11
solcap_snp_c2_35536	54.45
solcap_snp_c1_13430	54.45
PotVar0018694	54.45
solcap_snp_c2_35537	54.45
solcap_snp_c2_2591	54.45
PotVar0018693	54.45
PotVar0006125	54.45
PotVar0018832	54.5
PotVar0049174	54.54
solcap_snp_c1_12131	54.54
PotVar0018996	54.56
PotVar0071554	54.56
PotVar0049691	55.75
PotVar0049692	55.75
PotVar0049754	56.17
PotVar0049777	56.17
PotVar0006142	56.57
PotVar0049542	57.03
solcap_snp_c2_38404	57.03
PotVar0049593	57.03
solcap_snp_c2_56359	57.4
solcap_snp_c1_16515	57.4
solcap_snp_c2_45622	57.4
PotVar0005994	58.2
PotVar0005918	59.67
PotVar0049567	60

PotVar0049564	60
solcap_snp_c2_20798	60
solcap_snp_c2_13671	60
solcap_snp_c2_20799	60.63
PotVar0049594	60.85
PotVar0033081	61.11
PotVar0032877	61.11
PotVar0014615	61.11
PotVar0033046	61.64
PotVar0126047	62.21
PotVar0072127	62.38
PotVar0072239	62.38
PotVar0072439	62.38
PotVar0072169	62.38
PotVar0072448	62.38
PotVar0126146	62.49
solcap_snp_c1_4415	62.62
PotVar0032910	63.05
PotVar0032928	63.05
PotVar0049199	63.34
PotVar0049037	63.34
solcap_snp_c2_32367	63.34
PotVar0049005	63.34
PotVar0126052	63.34
PotVar0126035	63.34
solcap_snp_c1_13686	63.34
solcap_snp_c2_40954	63.34
PotVar0033086	63.34
solcap_snp_c2_13751	63.48
PotVar0126039	63.51
PotVar0032879	63.51
PotVar0033013	63.51
PotVar0032875	63.51
PotVar0033007	63.51
PotVar0032984	63.51
PotVar0032987	64.42
PotVar0032926	64.42
PotVar0032887	64.44
PotVar0032906	64.44
PotVar0033135	64.71
PotVar0049099	65.89
solcap_snp_c2_41336	65.89
solcap_snp_c2_13650	67.86
solcap_snp_c1_4757	69.19
PotVar0033411	69.61
PotVar0033735	69.61
PotVar0033208	69.61
solcap_snp_c2_14470	69.61
PotVar0033409	69.61
solcap_snp_c1_4744	69.61
solcap_snp_c2_14491	69.61
solcap_snp_c2_14492	69.61
PotVar0033907	69.61
solcap_snp_c1_4706	69.61
solcap_snp_c2_14489	69.61
solcap_snp_c2_14580	69.61
solcap_snp_c1_4752	69.61
solcap_snp_c2_14589	69.61
PotVar0129842	69.61
PotVar0129827	69.61
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solcap_snp_c1_5150	69.61
solcap_snp_c2_14623	69.61
PotVar0098682	69.61
PotVar0098595	69.61
PotVar0098794	69.61
PotVar0098709	69.61
PotVar0098530	69.61
PotVar0098422	69.61
PotVar0098430	69.61
solcap_snp_c2_20521	69.61
PotVar0072262	69.61
PotVar0072139	69.61
PotVar0043708	69.61
PotVar0098727	69.61
PotVar0129853	69.61
solcap_snp_c1_4745	69.61
PotVar0129817	69.61
solcap_snp_c2_20569	69.61
PotVar0098524	69.61
solcap_snp_c2_20522	69.61
solcap_snp_c2_20501	69.61
solcap_snp_c2_20513	69.61
solcap_snp_c1_6501	69.61
PotVar0006051	69.61
solcap_snp_c2_20506	70.04
PotVar0098389	70.04
PotVar0098497	70.04
solcap_snp_c2_20517	70.04
solcap_snp_c2_20530	70.04
solcap_snp_c2_52492	70.04
solcap_snp_c2_52484	70.04
PotVar0072157	70.04
PotVar0072133	70.04
solcap_snp_c2_20507	70.04
PotVar0098421	70.04
PotVar0072434	70.04
solcap_snp_c2_20508	70.39
PotVar0098536	70.39
PotVar0043650	70.39
solcap_snp_c2_12216	72.63
solcap_snp_c2_31821	73.5
PotVar0072441	74.52
PotVar0043665	74.6
PotVar0072433	74.95
PotVar0072443	74.95
PotVar0043513	75.42
PotVar0043404	75.42
PotVar0043821	75.52
PotVar0043814	75.52
solcap_snp_c2_13758	75.52
PotVar0043559	75.85
PotVar0041585	77.11
solcap_snp_c1_11769	78.46
PotVar0043296	78.52
solcap_snp_c2_17539	78.52
solcap_snp_c2_17537	79.62
PotVar0043484	79.62
PotVar0043426	79.62
solcap_snp_c2_17529	79.62
PotVar0043347	79.62
PotVar0043570	79.62
solcap_snp_c2_14274	81.22
PotVar0041660	82.85
solcap_snp_c1_3895	83.41
PotVar0006158	83.41
solcap_snp_c1_5653	83.41
PotVar0041488	84.24
solcap_snp_c1_5656	86.08
solcap_snp_c2_17191	86.08
PotVar0041226	86.26
PotVar0041271	86.26
PotVar0041241	86.26
PotVar0041233	86.26
PotVar0041397	87.96

PotVar0041586	87.96
PotVar0041366	87.96
PotVar0041674	88.39
PotVar0006246	88.49
PotVar0006265	89.3
PotVar0006356	89.36
PotVar0006243	90.02
PotVar0006198	90.31
solcap_snp_c1_3852	90.9
solcap_snp_c1_3851	90.9
solcap_snp_c2_17192	91.99
solcap_snp_c1_3853	92.08
solcap_snp_c1_3854	92.08
solcap_snp_c2_12215	92.08
PotVar0041919	93.73
PotVar0042300	93.73
PotVar0006395	94.12
PotVar0028758	94.18
solcap_snp_c2_2506	94.39
PotVar0041859	94.48
PotVar0041901	94.48
solcap_snp_c1_5295	94.48
PotVar0042036	94.48
PotVar0041272	95.13
PotVar0041319	95.13
PotVar0041415	95.13
PotVar0041439	95.13
solcap_snp_c1_4604	95.13
PotVar0041571	95.13
PotVar0041593	95.13
PotVar0006384	95.13
PotVar0041677	95.23
PotVar0042489	96.75
PotVar0029118	96.79
PotVar0042709	97.19
PotVar0006430	97.21
solcap_snp_c1_601	97.22
solcap_snp_c1_4617	98.76
solcap_snp_c1_573	101.13
solcap_snp_c2_2291	101.13
PotVar0110247	101.13
PotVar0042358	101.65
PotVar0042350	101.65
PotVar0049903	102.27

PotVar0049914	102.27
PotVar0096681	102.28
solcap_snp_c1_2531	102.28
solcap_snp_c2_7242	102.28
PotVar0049988	102.28
solcap_snp_c1_2458	102.28
PotVar0050015	102.28
PotVar0042756	102.29
PotVar0042497	102.29
PotVar0049886	102.71
solcap_snp_c1_5267	102.71
solcap_snp_c1_5281	102.71
solcap_snp_c2_16425	102.71
solcap_snp_c2_16424	102.71
PotVar0042710	102.71
PotVar0028699	102.71
PotVar0028811	102.71
PotVar0110417	102.71
PotVar0041748	102.71
PotVar0041770	102.71
PotVar0041837	102.71
PotVar0041852	102.71
PotVar0042445	102.71
PotVar0042723	102.71
PotVar0042153	102.71
PotVar0029382	102.71
PotVar0041686	103.96
PotVar0096706	107.05
solcap_snp_c1_2519	107.05
PotVar0049919	107.05
PotVar0049790	107.84
PotVar0029356	108.47
PotVar0050459	108.82
PotVar0049792	109.36
PotVar0050056	110.23
PotVar0050009	110.23
PotVar0049974	110.23
PotVar0050140	110.67
PotVar0050116	110.67
PotVar0050638	111.1
PotVar0050484	111.1
PotVar0050052	111.8
PotVar0049948	111.8
PotVar0096787	112.05

PotVar0096778	112.05
PotVar0029221	112.67
PotVar0049906	112.93
PotVar0049853	113.37
PotVar0049929	113.37
solcap_snp_c2_5078	113.48
PotVar0050201	113.48
PotVar0061252	113.48
PotVar0050061	114.28
solcap_snp_c2_7059	114.71
solcap_snp_c2_7056	114.71
PotVar0050349	115.15
PotVar0050406	115.15
PotVar0050409	115.15
PotVar0050432	115.15
solcap_snp_c1_1838	115.15
solcap_snp_c1_1847	115.15
PotVar0050120	115.15
PotVar0050133	115.15
PotVar0050207	115.15
PotVar0050245	115.15
PotVar0050453	115.15
PotVar0050599	115.15
PotVar0050401	115.15
solcap_snp_c2_7007	115.4
PotVar0096805	115.98
PotVar0050806	116.04
solcap_snp_c2_9988	116.04
PotVar0050814	116.04
PotVar0050773	116.04
PotVar0061225	116.11
PotVar0061136	116.11
PotVar0061187	116.11
PotVar0096770	116.2
PotVar0096798	116.2
PotVar0061224	117.14
PotVar0061106	117.14
PotVar0061243	117.14
PotVar0060673	117.81
PotVar0060854	118.66
PotVar0060695	118.88
PotVar0035449	119.37
PotVar0035721	120.62
PotVar0050306	121.17

solcap_snp_c2_6990	121.32
PotVar0050855	122.13
PotVar0049982	122.69
PotVar0050316	122.69
PotVar0050601	122.69
solcap_snp_c2_5076	122.69
PotVar0050824	122.69
PotVar0050864	122.69
solcap_snp_c2_9925	122.69
PotVar0060988	122.98
PotVar0060952	123.19
PotVar0061206	124.3
PotVar0050829	124.3
PotVar0035136	124.3
solcap_snp_c1_1645	124.51
PotVar0061197	124.63
PotVar0061119	124.63
PotVar0061100	124.63
PotVar0061268	124.63
PotVar0050696	124.63
solcap_snp_c2_4799	125.43
solcap_snp_c2_4860	125.43
solcap_snp_c1_1638	125.43
PotVar0035248	127.96
PotVar0061043	127.96
solcap_snp_c2_9892	127.96
PotVar0060753	127.96
PotVar0060667	127.96
PotVar0060678	127.96
PotVar0035605	127.96
PotVar0035780	127.96
solcap_snp_c2_4896	127.96
solcap_snp_c2_4910	127.96
PotVar0035238	127.96
solcap_snp_c2_4906	127.96
PotVar0035451	127.96
solcap_snp_c2_4709	127.96
PotVar0035693	127.96
solcap_snp_c2_4707	127.96
PotVar0035883	127.96
PotVar0035470	127.96
PotVar0035850	127.96
solcap_snp_c2_34546	127.96
solcap_snp_c2_34547	127.96
PotVar0035955	127.96
solcap_snp_c2_24	127.96
PotVar0126918	127.96
PotVar0126768	127.96
PotVar0127072	127.96
solcap_snp_c2_46448	127.96
solcap_snp_c2_14709	127.96
solcap_snp_c2_14708	127.96
solcap_snp_c2_14841	127.96
solcap_snp_c2_37816	127.96
PotVar0099836	127.96
PotVar0122409	127.96
PotVar0036058	127.96
solcap_snp_c2_34478	127.96
solcap_snp_c1_1737	127.96
solcap_snp_c2_4614	127.96
PotVar0035543	127.96
PotVar0035301	127.96
PotVar0060740	127.96
PotVar0060676	127.96
PotVar0035697	127.96
solcap_snp_c2_36571	127.96
PotVar0035595	127.96
PotVar0126676	127.96
PotVar0126593	127.96
PotVar0036150	127.96
PotVar0036238	127.96
PotVar0126809	127.96
PotVar0099900	127.96
PotVar0061044	127.96
solcap_snp_c1_15123	127.96
PotVar0035546	127.96
PotVar0035378	128.74
solcap_snp_c2_30963	129.73
PotVar0036191	129.75
PotVar0036085	129.75
PotVar0126645	130.23
PotVar0126891	130.23
PotVar0126574	130.23
PotVar0126772	130.23
PotVar0127026	130.46
PotVar0035753	131.29
PotVar0124628	131.56
PotVar0035852	131.72
PotVar0036149	133.4
PotVar0126587	133.4
PotVar0126685	133.6
PotVar0099829	134.05
PotVar0126769	134.29
PotVar0036054	134.72
PotVar0127038	134.72
solcap_snp_c2_49917	136.9
solcap_snp_c2_49911	136.9
PotVar0124515	136.9
PotVar0124464	136.9
PotVar0124552	136.92
solcap_snp_c2_49906	136.92
PotVar0124463	136.92
PotVar0099321	139.11
PotVar0099426	139.11
PotVar0099782	140.78
PotVar0099756	140.78
solcap_snp_c2_30961	141.7
solcap_snp_c2_30958	141.7
solcap_snp_c2_30956	141.7
solcap_snp_c2_30955	141.7
PotVar0122386	141.7
PotVar0122388	141.7
solcap_snp_c2_31041	141.7
PotVar0122414	141.7
PotVar0122353	141.7
PotVar0122423	141.7
PotVar0099652	141.7
PotVar0099578	141.7
solcap_snp_c1_9401	141.7

Chromosome 2	
Name	cM
solcap_snp_c2_41124	0
solcap_snp_c2_735	0
solcap_snp_c2_55863	1.11
PotVar0075207	1.36
solcap_snp_c2_730	1.8
PotVar0109627	1.8
PotVar0039162	2.94

PotVar0039524	2.94
PotVar0039293	3.39
PotVar0039273	3.39
PotVar0039503	3.39
solcap_snp_c2_4505	3.57
PotVar0109716	3.57
solcap_snp_c2_30952	3.6
solcap_snp_c2_41879	3.6
PotVar0032158	4.23
PotVar0039416	4.23
solcap_snp_c1_15873	4.23
solcap_snp_c2_17424	4.23
solcap_snp_c2_30164	4.23
solcap_snp_c2_785	4.23
PotVar0032441	4.23
PotVar0032521	4.23
PotVar0039373	4.23
PotVar0039384	4.23
PotVar0054564	4.23
PotVar0075203	4.23
PotVar0099232	4.23
solcap_snp_c1_4792	4.23
solcap_snp_c2_17427	4.23
PotVar0054547	4.23
solcap_snp_c2_40336	4.67
solcap_snp_c2_16347	5.39
PotVar0038914	5.58
PotVar0039112	5.58
solcap_snp_c2_16362	6.48
solcap_snp_c2_30926	7.36
solcap_snp_c2_30914	7.36
solcap_snp_c2_30929	7.36
PotVar0054490	8.21
PotVar0054559	8.21
PotVar0054438	9
PotVar0054546	9
solcap_snp_c2_30915	9
solcap_snp_c2_47096	9
solcap_snp_c1_15973	9.87
PotVar0039456	13.38
PotVar0039219	13.38
solcap_snp_c2_17415	13.38
PotVar0039036	14.73
PotVar0039005	17.17

PotVar0039021	17.17
solcap_snp_c1_11344	17.17
solcap_snp_c2_32400	17.17
solcap_snp_c2_32415	17.17
PotVar0039004	17.17
PotVar0039094	17.17
PotVar0039050	17.6
solcap_snp_c2_32425	18.14
solcap_snp_c2_37248	18.57
solcap_snp_c2_39705	18.57
PotVar0029524	19.43
solcap_snp_c2_32406	20.28
solcap_snp_c2_52630	20.28
PotVar0029505	21.18
solcap_snp_c2_50889	21.41
PotVar0117650	21.57
solcap_snp_c2_21717	21.57
PotVar0117640	21.57
solcap_snp_c2_21721	21.57
PotVar0029506	22.32
PotVar0088857	22.49
solcap_snp_c2_21746	23.18
PotVar0089300	23.58
PotVar0117601	24.04
PotVar0029531	25.09
PotVar0029568	25.95
solcap_snp_c2_45323	25.97
solcap_snp_c1_12305	25.97
PotVar0089006	26.66
solcap_snp_c1_12330	26.96
solcap_snp_c2_41963	26.96
PotVar0039003	28.08
PotVar0062655	29.99
PotVar0124338	30.79
PotVar0124219	30.79
solcap_snp_c2_45319	30.79
PotVar0124142	30.79
PotVar0124128	30.79
PotVar0124165	30.79
solcap_snp_c2_48239	30.86
solcap_snp_c1_5091	30.86
solcap_snp_c1_9363	31.57
solcap_snp_c2_45311	31.57
PotVar0062569	31.72

PotVar0062136	32.17
PotVar0062180	32.17
PotVar0062276	32.17
solcap_snp_c2_51113	32.17
PotVar0062231	32.17
PotVar0062385	32.17
solcap_snp_c2_51115	32.17
PotVar0117656	33.35
PotVar0062628	34.78
PotVar0088875	35.58
solcap_snp_c2_48194	35.64
PotVar0089071	36.23
PotVar0062568	36.5
PotVar0062484	36.94
PotVar0062566	36.94
PotVar0089083	37.32
PotVar0062335	37.38
PotVar0089235	37.54
PotVar0089338	37.54
PotVar0089350	37.54
PotVar0062308	37.81
PotVar0062079	37.81
PotVar0062004	37.81
PotVar0062472	37.81
PotVar0062277	37.81
PotVar0062114	37.81
PotVar0062077	37.81
PotVar0062142	37.81
solcap_snp_c1_9356	37.98
PotVar0082241	39.02
PotVar0082281	39.02
PotVar0094274	39.02
PotVar0094547	39.02
PotVar0082429	39.02
PotVar0082458	39.02
PotVar0094234	39.02
PotVar0082531	39.02
PotVar0094604	40.22
PotVar0082552	40.44
PotVar0082313	41.8
PotVar0082438	41.8
PotVar0125072	41.8
solcap_snp_c2_45307	42.16
PotVar0124264	42.16

solcap_snp_c1_12320	43.46
solcap_snp_c1_12354	43.46
PotVar0123873	43.46
PotVar0123826	43.46
solcap_snp_c2_42059	43.46
solcap_snp_c1_11553	43.46
PotVar0124100	43.46
PotVar0038032	46.48
PotVar0038002	46.48
PotVar0082442	48.11
PotVar0094414	48.32
PotVar0094582	48.32
PotVar0082550	48.32
PotVar0094224	49.13
PotVar0094537	49.13
PotVar0094171	49.13
PotVar0094115	49.14
PotVar0094276	49.14
PotVar0082332	49.14
PotVar0094218	49.14
PotVar0111837	49.25
solcap_snp_c1_13233	49.25
PotVar0082226	49.94
PotVar0082166	49.94
solcap_snp_c2_23192	50.38
solcap_snp_c2_41495	50.69
PotVar0094383	50.69
PotVar0094361	51.11
PotVar0131484	51.42
solcap_snp_c2_51986	51.84
PotVar0111702	52
PotVar0111704	52
solcap_snp_c1_13887	52
PotVar0131512	52
solcap_snp_c2_39175	52
PotVar0038035	52.27
PotVar0038033	52.27
PotVar0094371	52.36
PotVar0038345	56.12
PotVar0038256	56.12
solcap_snp_c2_44768	57.13
PotVar0120925	57.13
PotVar0120894	57.13
PotVar0120885	57.13
PotVar0038096	57.13
PotVar0038136	57.13
solcap_snp_c1_12257	57.13
PotVar0120910	57.13
solcap_snp_c1_12287	57.13
PotVar0094229	57.13
PotVar0038755	57.13
PotVar0128369	57.13
PotVar0045713	57.13
solcap_snp_c2_17937	57.13
solcap_snp_c2_17935	57.13
solcap_snp_c2_17921	57.13
PotVar0045967	57.13
PotVar0131510	57.13
PotVar0120737	57.13
PotVar0037994	57.13
solcap_snp_c2_33108	57.14
solcap_snp_c1_4192	57.61
PotVar0038674	57.79
PotVar0119003	57.79
PotVar0120697	57.82
PotVar0038855	57.92
PotVar0038592	57.92
PotVar0038830	57.92
PotVar0038662	57.92
PotVar0038423	57.96
PotVar0038425	57.96
PotVar0038389	57.96
PotVar0038395	58.4
PotVar0038427	58.4
PotVar0038759	58.4
PotVar0038673	58.83
PotVar0038624	58.83
solcap_snp_c2_17914	59.59
PotVar0046773	59.6
solcap_snp_c1_12264	59.6
PotVar0038876	59.69
PotVar0038880	59.69
PotVar0038859	59.69
PotVar0128492	61.03
PotVar0046016	61.39
PotVar0128490	61.43
solcap_snp_c2_40167	61.59
PotVar0046427	62.3
PotVar0046364	62.73
PotVar0046249	62.94
PotVar0046234	63.28
PotVar0046114	63.28
PotVar0046535	63.6
PotVar0046724	63.6
PotVar0046900	63.6
PotVar0046141	63.61
PotVar0045853	63.69
PotVar0046115	63.69
PotVar0045730	63.69
PotVar0046193	63.69
PotVar0046194	63.69
PotVar0045695	63.69
PotVar0046418	63.94
PotVar0045784	63.95
PotVar0045938	63.95
PotVar0046722	64.03
PotVar0046608	64.03
PotVar0046903	64.03
PotVar0046065	64.6
PotVar0046178	64.6
PotVar0046109	64.6
solcap_snp_c2_17930	64.6
PotVar0045735	64.6
PotVar0046179	64.6
PotVar0046292	64.6
solcap_snp_c2_17809	64.63
solcap_snp_c1_16172	64.82
solcap_snp_c2_17858	64.82
PotVar0046789	64.9
PotVar0046968	64.9
PotVar0047042	65.33
PotVar0045734	65.56
PotVar0045743	65.56
solcap_snp_c2_17926	65.56
PotVar0045952	65.56
PotVar0045976	65.72
PotVar0046782	65.97
PotVar0047112	65.97
PotVar0046549	65.97
PotVar0046936	65.97
PotVar0046605	65.97
solcap_snp_c2_42265	66.2
PotVar0046575	67.04
PotVar0046916	67.04
PotVar0046640	67.04

solcap_snp_c2_40635	67.86
PotVar0046637	68.73
PotVar0115838	69.24
PotVar0046422	70.3
PotVar0046462	70.3
PotVar0046419	70.3
PotVar0010943	70.4
PotVar0115882	70.4
PotVar0115831	70.41
PotVar0047107	70.72
PotVar0046902	70.72
PotVar0047075	70.72
PotVar0010676	70.84
solcap_snp_c1_10494	70.84
PotVar0115923	70.84
solcap_snp_c1_12373	70.84
solcap_snp_c2_42169	71.15
PotVar0116077	71.95
PotVar0119034	72.05
solcap_snp_c1_10492	72.05
PotVar0038744	72.62
PotVar0118971	72.97
PotVar0010377	73.59
PotVar0128434	73.7
PotVar0010082	74.21
PotVar0128389	74.35
PotVar0010835	74.67
PotVar0010677	74.67
PotVar0010948	74.67
PotVar0010076	74.72
solcap_snp_c2_25766	75.15
PotVar0010550	75.15
PotVar0010106	75.15
PotVar0010664	75.66
solcap_snp_c2_42132	75.66
PotVar0119004	75.66
PotVar0010618	75.66
PotVar0010869	75.66
PotVar0010684	75.66
PotVar0010629	75.66
PotVar0010133	75.66
solcap_snp_c1_15481	75.66
PotVar0010851	75.66
PotVar0010535	75.66

solcap_snp_c2_53034	75.66
PotVar0010668	75.66
PotVar0045674	75.89
PotVar0115971	76.1
PotVar0115988	76.1
PotVar0119013	76.1
solcap_snp_c2_53033	76.1
solcap_snp_c2_17925	76.1
solcap_snp_c1_10493	76.1
PotVar0118945	76.1
PotVar0119053	76.1
PotVar0119058	76.1
PotVar0010928	76.1
PotVar0010874	76.1
PotVar0010934	76.1
PotVar0010735	76.1
PotVar0010547	76.1
PotVar0010400	76.1
PotVar0010195	76.1
PotVar0010303	76.1
PotVar0010331	76.1
PotVar0010351	76.1
PotVar0010350	76.1
PotVar0010145	76.1
PotVar0010080	76.1
PotVar0010072	76.1
PotVar0009928	76.1
PotVar0009943	76.1
PotVar0009802	76.1
PotVar0009955	76.1
PotVar0009408	76.1
PotVar0009568	76.1
PotVar0009279	76.1
PotVar0009159	76.1
solcap_snp_c1_7957	76.1
PotVar0090166	76.1
solcap_snp_c2_7559	76.1
PotVar0010183	76.25
PotVar0010353	76.47
PotVar0010345	76.47
solcap_snp_c2_42133	76.47
PotVar0010270	76.47
PotVar0010926	76.48
PotVar0115953	76.49

PotVar0115816	76.49
PotVar0010703	76.49
solcap_snp_c2_40610	76.49
PotVar0010678	76.49
PotVar0010401	77.67
PotVar0010077	78.43
PotVar0010033	79.55
D_locus_(DFR)_A_LG02	80.43
D_locus_(DFR)_C_LG02	80.43
D_locus_(DFR)_E_LG02	80.43
D_locus_(DFR)_G_LG02	80.43
D_locus_(DFR)_H_LG02	80.43
PotVar0009951	80.43
PotVar0009747	80.43
solcap_snp_c1_7964	80.43
PotVar0009505	80.43
PotVar0009466	80.43
PotVar0009844	80.43
PotVar0009827	80.43
PotVar0009483	80.43
D_locus_(DFR)_D_LG02	80.43
solcap_snp_c2_25044	80.86
PotVar0010007	80.86
PotVar0010024	81.38
PotVar0009282	82.17
PotVar0009178	82.17
PotVar0009171	82.17
PotVar0090084	82.79
PotVar0090045	82.79
PotVar0090077	82.79
solcap_snp_c1_7342	82.92
solcap_snp_c2_22894	82.92
solcap_snp_c1_7341	82.92
PotVar0010500	82.94
PotVar0009548	82.94
PotVar0009474	82.94
PotVar0009867	82.94
PotVar0009567	82.94
PotVar0009857	82.94
PotVar0090139	82.94
PotVar0009673	83.18
PotVar0009808	83.18
PotVar0009651	83.18
PotVar0009460	83.63

PotVar0009411	83.63
PotVar0089984	83.65
solcap_snp_c1_2656	83.65
solcap_snp_c2_7631	83.94
solcap_snp_c1_15746	84.52
PotVar0118927	85.39
solcap_snp_c2_7423	86.17
solcap_snp_c2_7424	86.17
solcap_snp_c2_7501	86.26
PotVar0006700	86.56
PotVar0006735	86.56
PotVar0090074	87.09
solcap_snp_c1_2641	87.09
solcap_snp_c1_16540	87.09
PotVar0118925	87.42
solcap_snp_c2_7422	87.5
PotVar0006761	87.5
PotVar0089995	88.41
PotVar0006851	88.71
PotVar0006826	88.71
solcap_snp_c1_2574	88.86
PotVar0006863	89.47
PotVar0006684	89.47
PotVar0006870	90.69
PotVar0006747	90.69
solcap_snp_c1_16542	90.86
PotVar0006913	91.57
PotVar0006934	91.57
PotVar0007012	92.45
PotVar0007054	92.45
PotVar0007051	92.45
PotVar0007146	92.8
PotVar0007182	92.8
PotVar0007178	92.88
PotVar0001581	93.2
PotVar0001799	94.34
PotVar0006916	94.69
PotVar0006948	94.69
PotVar0001571	94.69
PotVar0006681	94.69
PotVar0006947	96.25
PotVar0006881	96.33
PotVar0007040	97.63
PotVar0003459	97.99
PotVar0003645	97.99

solcap_snp_c2_43350	99.71
PotVar0001550	99.92
PotVar0001625	99.92
solcap_snp_c2_27268	99.92
solcap_snp_c2_27372	99.92
PotVar0001686	99.92
solcap_snp_c2_43408	99.92
solcap_snp_c1_4860	99.92
PotVar0002114	99.92
PotVar0002440	99.92
PotVar0002607	99.92
PotVar0002530	99.92
PotVar0002800	99.92
solcap_snp_c1_10593	99.92
PotVar0001694	99.92
PotVar0001573	99.92
solcap_snp_c1_12771	99.93
PotVar0002139	100.04
solcap_snp_c1_5931	100.23
PotVar0003452	100.23
PotVar0001749	100.36
PotVar0001789	100.36
PotVar0001921	100.36
solcap_snp_c1_12509	100.36
solcap_snp_c2_42570	100.36
PotVar0001704	100.36
PotVar0006989	100.36
PotVar0002132	102.08
PotVar0002188	102.08
PotVar0002196	102.08
solcap_snp_c1_7871	102.08
solcap_snp_c2_15066	102.08
solcap_snp_c2_15067	102.08
PotVar0002627	102.47
PotVar0002507	102.47
PotVar0002438	102.56
PotVar0002461	102.56
PotVar0002481	102.56
solcap_snp_c2_24869	102.56
PotVar0002433	102.56
PotVar0002715	103
PotVar0002556	103
PotVar0002594	103
PotVar0002504	103
PotVar0002736	103.8

PotVar0002934	104.24
PotVar0002940	104.24
PotVar0002954	104.24
PotVar0003017	104.24
PotVar0003379	104.67
PotVar0003253	105.1
solcap_snp_c2_47199	105.53
solcap_snp_c2_47200	105.85
PotVar0003529	105.95
PotVar0003444	106.47
PotVar0003791	106.47
PotVar0003792	106.47
PotVar0003627	106.47
PotVar0002770	107.07
PotVar0002772	107.07
PotVar0002892	107.51
solcap_snp_c2_47196	107.51
solcap_snp_c2_47201	107.51
solcap_snp_c2_47163	107.51
solcap_snp_c1_11459	107.95
PotVar0002976	107.95
PotVar0002948	107.95
PotVar0003078	107.95
PotVar0003105	107.95
PotVar0003151	107.95
PotVar0003427	107.95
PotVar0003313	107.95
PotVar0003054	107.95
solcap_snp_c1_5908	107.95
solcap_snp_c2_35689	107.95
solcap_snp_c2_35693	107.95
solcap_snp_c2_35694	107.95
PotVar0002935	107.95
PotVar0003004	107.95
PotVar0003084	107.95
PotVar0003442	107.95
PotVar0003462	107.95
PotVar0003546	107.95
solcap_snp_c1_5909	107.95
solcap_snp_c1_5924	107.95
solcap_snp_c2_35691	107.95
solcap_snp_c2_35695	107.95
solcap_snp_c2_35698	107.95
solcap_snp_c2_35701	107.95
solcap_snp_c2_35702	107.95

PotVar0003761	107.95

solcap_snp_c2_15047	108.06

PotVar0002908	118.9

Chromosome 3	
Name	cM
PotVar0084575	0
PotVar0084566	0
solcap_snp_c1_12825	0
solcap_snp_c2_52806	0
solcap_snp_c2_52813	0
PotVar0084741	0
solcap_snp_c2_54290	0.05
solcap_snp_c2_54286	0.05
PotVar0019336	2.23
PotVar0019456	4.71
PotVar0019201	4.71
PotVar0084666	4.85
PotVar0084730	4.85
PotVar0084556	5.28
PotVar0084554	5.38
solcap_snp_c2_52815	6.52
solcap_snp_c1_15782	6.52
solcap_snp_c2_51389	6.52
PotVar0019302	8.35
PotVar0019259	9.19
solcap_snp_c2_17279	10.5
PotVar0019680	10.7
solcap_snp_c1_13059	11.59
PotVar0019460	12.78
PotVar0021474	14.33
solcap_snp_c1_1914	14.33
solcap_snp_c2_5269	14.33
PotVar0055456	14.33
solcap_snp_c1_8969	14.33
solcap_snp_c2_29441	14.33
solcap_snp_c2_5289	14.33
solcap_snp_c2_5292	14.33
solcap_snp_c2_57638	14.33
PotVar0021479	14.33
PotVar0019554	15.05
solcap_snp_c1_13052	15.05
PotVar0021288	15.23
solcap_snp_c1_7144	15.23
solcap_snp_c2_14424	15.23
solcap_snp_c2_5736	15.23
PotVar0085038	16.22
PotVar0106434	16.22
PotVar0106457	16.22
PotVar0121921	16.22
PotVar0121932	16.22
PotVar0132195	16.22
PotVar0132206	16.22
solcap_snp_c1_3347	16.22
solcap_snp_c2_10088	16.22
solcap_snp_c2_11269	16.22
solcap_snp_c2_35563	16.22
solcap_snp_c2_37411	16.22
PotVar0085563	16.22
PotVar0085679	16.22
PotVar0106337	16.22
PotVar0106377	16.22
solcap_snp_c1_16052	16.22
solcap_snp_c1_16382	16.22
solcap_snp_c2_37431	16.22
solcap_snp_c2_41163	16.22
solcap_snp_c2_41178	16.22
solcap_snp_c2_10087	16.22
solcap_snp_c2_50636	17.75
solcap_snp_c2_50635	17.75
solcap_snp_c2_54530	17.75
solcap_snp_c2_53606	17.97
PotVar0021457	19.74
PotVar0121927	21.08
PotVar0113278	21.11
PotVar0021445	21.53
solcap_snp_c1_12751	21.98
PotVar0085575	21.98
PotVar0085799	21.98
PotVar0131468	21.98
PotVar0094670	21.98
solcap_snp_c2_43182	21.98
PotVar0094679	21.98
PotVar0129473	22.48
PotVar0129536	22.48
solcap_snp_c2_5286	23.75
solcap_snp_c2_54674	24.22
solcap_snp_c2_5300	24.44
solcap_snp_c1_1918	24.87
solcap_snp_c2_5226	24.87
solcap_snp_c1_15204	27.22
solcap_snp_c2_5732	27.22
solcap_snp_c1_3662	27.63
PotVar0026680	27.63
PotVar0106352	28.59
PotVar0094787	28.64
PotVar0085747	29.52
PotVar0094713	29.52
PotVar0085802	29.52
PotVar0085581	29.72
solcap_snp_c2_35553	29.88
PotVar0131462	30.18
solcap_snp_c2_35354	30.18
PotVar0094922	30.39
solcap_snp_c1_9292	30.81
PotVar0085797	31.03
PotVar0085748	31.03
PotVar0094840	31.54
PotVar0094886	32.55
PotVar0094925	32.55
solcap_snp_c2_30730	32.55
PotVar0094857	32.55
solcap_snp_c1_9268	32.59
PotVar0095450	33.25
solcap_snp_c2_36469	33.52
PotVar0095271	33.52
solcap_snp_c2_49970	33.52
solcap_snp_c2_48378	33.59
PotVar0129579	33.59
solcap_snp_c2_52495	35.1
solcap_snp_c1_4814	35.1
PotVar0095473	35.1
solcap_snp_c1_7139	35.1
PotVar0129442	35.1
PotVar0129720	35.1
solcap_snp_c2_48362	35.1
solcap_snp_c2_48363	35.1

solcap_snp_c2_48381	35.1
PotVar0095451	35.1
solcap_snp_c2_38068	35.1
solcap_snp_c2_48390	35.1
solcap_snp_c1_14316	35.1
PotVar0129474	35.1
PotVar0129705	35.1
solcap_snp_c1_11350	35.1
solcap_snp_c2_48368	35.1
solcap_snp_c1_16679	35.65
solcap_snp_c2_37989	35.65
PotVar0095322	36.34
solcap_snp_c2_49976	36.78
solcap_snp_c2_55729	36.78
solcap_snp_c2_48359	37.3
PotVar0129499	37.61
PotVar0068140	39.7
PotVar0068122	39.7
PotVar0068152	39.7
PotVar0115488	39.82
PotVar0115519	39.82
PotVar0115783	39.82
solcap_snp_c2_42312	39.82
PotVar0115449	39.82
solcap_snp_c2_38047	40.37
PotVar0068173	40.64
PotVar0115703	41.28
PotVar0115750	41.28
PotVar0115775	41.28
PotVar0115570	41.28
PotVar0068141	41.72
solcap_snp_c2_46592	41.78
solcap_snp_c1_7882	41.99
solcap_snp_c2_24983	41.99
solcap_snp_c2_45699	42
PotVar0068033	43.25
solcap_snp_c2_46605	44.46
PotVar0067935	44.59
PotVar0113388	46.63
PotVar0068174	46.82
solcap_snp_c2_42306	47.28
solcap_snp_c2_57349	48.19
PotVar0068133	48.5
PotVar0070260	48.82
PotVar0055399	48.82
PotVar0120627	48.82
PotVar0129496	49.95
solcap_snp_c2_48385	49.95
solcap_snp_c1_13847	50.98
PotVar0056918	51.16
PotVar0068149	51.47
PotVar0068134	51.9
PotVar0042853	52.27
PotVar0042845	52.27
solcap_snp_c2_13825	52.51
PotVar0113509	53.12
PotVar0055361	53.31
solcap_snp_c2_55465	54.04
solcap_snp_c1_9161	54.04
solcap_snp_c2_46603	54.04
PotVar0070258	55.42
PotVar0070245	55.42
PotVar0070248	55.42
PotVar0043163	57.09
solcap_snp_c1_6869	59.66
PotVar0070335	59.7
PotVar0055353	60.94
PotVar0055210	60.94
PotVar0055234	60.94
PotVar0055248	60.94
PotVar0055339	60.94
PotVar0055105	60.94
PotVar0055756	61.85
solcap_snp_c1_6864	62.27
PotVar0055556	62.28
PotVar0055722	62.28
solcap_snp_c2_1567	64.39
PotVar0056354	64.69
PotVar0070281	66.7
PotVar0113506	66.85
PotVar0113511	66.85
PotVar0113398	66.85
PotVar0070299	66.85
solcap_snp_c2_20347	66.85
PotVar0056884	67.09
PotVar0121873	68.09
PotVar0120554	68.09
PotVar0120452	68.09
PotVar0043186	68.09
solcap_snp_c2_57865	68.09
solcap_snp_c2_17552	68.09
PotVar0043196	68.09
solcap_snp_c2_25560	69.05
PotVar0055403	69.48
solcap_snp_c2_14017	69.51
PotVar0027434	69.51
PotVar0113472	69.9
solcap_snp_c2_55276	69.92
PotVar0055120	70.35
PotVar0070334	71.12
solcap_snp_c1_6332	71.12
solcap_snp_c2_54785	71.21
PotVar0043187	71.21
PotVar0055394	71.21
solcap_snp_c1_8069	71.21
solcap_snp_c2_55279	71.21
solcap_snp_c2_55284	71.21
solcap_snp_c2_55285	71.21
PotVar0042968	71.21
PotVar0042948	71.21
solcap_snp_c1_9025	71.21
PotVar0043256	71.21
solcap_snp_c2_29678	71.21
PotVar0043210	71.21
PotVar0056507	72.08
PotVar0056231	72.08
solcap_snp_c2_55283	72.09
PotVar0055003	72.09
PotVar0055362	72.09
PotVar0054961	72.09
PotVar0042852	72.09
PotVar0055831	72.5
PotVar0042846	72.52
PotVar0054986	72.52
PotVar0055130	72.52
solcap_snp_c2_57860	72.52
PotVar0055205	72.52
PotVar0056253	72.69
solcap_snp_c2_1579	72.69
solcap_snp_c1_3637	72.95
PotVar0042829	72.95
PotVar0043145	72.96
PotVar0043197	72.96
PotVar0043007	72.96
solcap_snp_c1_3638	73.4

PotVar0042906	73.4
PotVar0043199	73.4
PotVar0043211	73.4
PotVar0030088	73.6
PotVar0120608	74.26
PotVar0120301	74.26
PotVar0120444	74.26
PotVar0120279	74.26
PotVar0120480	74.26
PotVar0121744	74.26
PotVar0120489	74.26
PotVar0055916	74.26
solcap_snp_c2_1722	74.26
PotVar0120478	74.26
PotVar0120613	74.26
PotVar0120283	74.26
PotVar0121756	74.26
PotVar0121761	74.26
PotVar0121805	74.26
solcap_snp_c2_20176	74.26
PotVar0043245	74.26
PotVar0120252	74.26
PotVar0120600	74.26
solcap_snp_c2_55072	74.26
PotVar0120595	74.26
PotVar0120488	74.26
PotVar0055692	74.69
PotVar0056242	76.31
PotVar0120531	76.31
PotVar0120487	76.31
PotVar0120416	76.31
PotVar0120323	76.31
PotVar0121869	76.31
solcap_snp_c2_20113	76.31
solcap_snp_c2_20097	76.31
PotVar0120242	76.31
PotVar0120555	76.31
solcap_snp_c2_20175	76.74
solcap_snp_c2_1688	76.84
PotVar0056881	77.03
PotVar0121803	77.03
PotVar0070435	77.16
PotVar0056835	77.16
PotVar0055694	77.17
PotVar0056297	77.59
solcap_snp_c2_1556	77.59
PotVar0056380	77.59
PotVar0056911	77.93
PotVar0070449	77.93
PotVar0070532	77.93
PotVar0056921	77.93
PotVar0056200	79.17
PotVar0056554	79.17
PotVar0056273	79.17
PotVar0056042	79.39
PotVar0056453	79.39
solcap_snp_c2_20259	79.46
PotVar0056506	79.85
PotVar0056116	79.85
PotVar0056464	79.85
PotVar0014120	79.88
PotVar0027609	80.5
solcap_snp_c1_7096	80.5
PotVar0029778	80.5
PotVar0029786	80.5
PotVar0029784	80.5
PotVar0029844	80.5
PotVar0055583	81.23
solcap_snp_c2_18268	82.01
PotVar0030288	82.01
PotVar0055978	82.32
PotVar0055885	82.32
PotVar0055804	82.32
PotVar0055999	82.32
PotVar0055755	82.32
PotVar0056019	82.32
solcap_snp_c2_1720	82.32
solcap_snp_c2_1718	83.28
solcap_snp_c1_7112	84.5
PotVar0029965	84.5
solcap_snp_c1_4509	85.19
solcap_snp_c2_22466	86.65
PotVar0122174	87.73
solcap_snp_c2_1724	88.68
solcap_snp_c2_17631	88.68
PotVar0020948	88.68
solcap_snp_c2_14064	88.68
solcap_snp_c1_4542	88.68
PotVar0055603	88.68
solcap_snp_c2_1725	88.68
PotVar0055568	88.68
PotVar0030875	88.89
PotVar0121169	89
solcap_snp_c2_14155	89.47
solcap_snp_c2_57263	89.56
PotVar0027485	89.56
PotVar0121351	89.63
PotVar0013242	89.63
solcap_snp_c1_16234	90
PotVar0029733	90.43
PotVar0029816	90.43
PotVar0029766	90.43
PotVar0030743	91.07
PotVar0021019	91.16
PotVar0020971	91.59
PotVar0030033	91.76
PotVar0029865	91.76
PotVar0030066	91.76
solcap_snp_c1_7115	91.76
PotVar0029968	91.76
PotVar0030874	91.88
PotVar0030504	92.64
PotVar0030330	92.64
PotVar0030456	93.22
solcap_snp_c1_5951	93.22
solcap_snp_c2_18308	93.22
PotVar0121328	93.51
PotVar0121124	93.51
PotVar0013238	93.96
PotVar0013245	93.96
PotVar0030909	93.96
PotVar0121530	93.96
solcap_snp_c1_8203	93.96
PotVar0121399	93.96
solcap_snp_c1_8194	93.96
solcap_snp_c2_18428	93.96
PotVar0121402	93.96
PotVar0014009	94.18
PotVar0013943	94.18
PotVar0121139	94.96
solcap_snp_c1_111	95.51
PotVar0013322	96.26

PotVar0030768	96.53
PotVar0121290	98.49
PotVar0013592	98.49
PotVar0013766	98.49
PotVar0013866	98.49
PotVar0013867	98.49
PotVar0013496	98.55
PotVar0013434	98.76
PotVar0013544	98.76
PotVar0013533	98.76
PotVar0013345	98.76
PotVar0013816	98.76
PotVar0014106	98.76
solcap_snp_c2_26402	98.76
PotVar0014097	98.76
PotVar0014107	98.76
PotVar0013845	98.76
PotVar0014087	98.76
PotVar0014196	98.76
PotVar0014192	98.76
PotVar0021255	100.74
PotVar0021251	100.74
PotVar0021083	100.74
PotVar0020884	100.74

PotVar0014217	100.74
solcap_snp_c2_578	100.74
PotVar0014025	100.93
PotVar0013510	101.37
solcap_snp_c2_326	101.37
PotVar0013907	101.84
PotVar0021209	102.7
PotVar0021026	108.7
PotVar0021098	108.7
PotVar0021166	108.7
PotVar0021182	109.59
PotVar0020803	110.42
PotVar0020656	110.85
PotVar0020782	111.7
PotVar0020802	111.92
PotVar0020426	111.96
PotVar0020507	112.39
PotVar0020213	113.24
PotVar0021136	113.34
PotVar0019945	114.48
PotVar0019908	114.48
PotVar0019861	114.48
PotVar0019800	114.48
solcap_snp_c2_37121	114.48

PotVar0020074	114.73
solcap_snp_c2_37139	114.95
PotVar0020457	114.95
PotVar0020402	114.95
PotVar0021131	121.05
PotVar0020249	123.73
PotVar0020227	123.73
PotVar0020451	123.73
PotVar0020808	123.82
PotVar0020653	123.82
PotVar0020171	124.17
PotVar0020716	124.25
solcap_snp_c2_9531	124.25
PotVar0020079	125.04
PotVar0019703	125.48
PotVar0019900	125.48
PotVar0019827	125.48
PotVar0019773	125.48
PotVar0020037	125.48
PotVar0020552	125.57
PotVar0020485	125.57
PotVar0020566	125.57
PotVar0020413	125.57

Chromosome 4	
Name	cM
solcap_snp_c1_11030	0
solcap_snp_c2_36955	0
solcap_snp_c2_36993	0.67
PotVar0026619	2.44
solcap_snp_c2_36951	6.23
solcap_snp_c2_23611	6.48
solcap_snp_c1_7570	6.48
solcap_snp_c1_7571	6.48
solcap_snp_c2_54463	10.97
solcap_snp_c2_29872	10.99
PotVar0076761	10.99
PotVar0076759	10.99
PotVar0076872	10.99
solcap_snp_c2_36941	14.95
solcap_snp_c2_23596	15
solcap_snp_c1_7574	18.15
solcap_snp_c2_31719	21.4

PotVar0106844	21.4
solcap_snp_c1_7569	27.51
solcap_snp_c2_39322	27.63
solcap_snp_c2_29850	28.49
solcap_snp_c2_29851	28.49
PotVar0076654	28.92
solcap_snp_c1_13626	29.35
PotVar0076557	29.35
PotVar0076616	29.35
solcap_snp_c2_31688	29.35
solcap_snp_c2_21915	29.35
R2_E_LG04	29.35
solcap_snp_c2_11564	29.35
solcap_snp_c2_48871	29.35
PotVar0039597	29.35
PotVar0076646	29.35
PotVar0106655	30.21
PotVar0106745	30.21
PotVar0076666	30.45

PotVar0076621	30.45
PotVar0106922	30.66
solcap_snp_c1_9546	30.66
PotVar0106917	30.66
PotVar0106871	30.66
solcap_snp_c2_31732	30.66
PotVar0106851	30.66
PotVar0127847	30.66
solcap_snp_c2_11432	30.66
solcap_snp_c2_11435	30.66
PotVar0076873	30.66
PotVar0076511	31.03
PotVar0076503	31.25
PotVar0106843	31.68
PotVar0100848	31.87
PotVar0101108	31.87
PotVar0076554	31.87
PotVar0100790	31.87
PotVar0101074	31.87

PotVar0106727	31.87
PotVar0106974	31.87
R2_D_LG04	31.87
PotVar0100916	31.87
PotVar0076901	31.91
PotVar0109580	32.23
PotVar0109408	32.31
PotVar0109406	32.31
PotVar0100767	33
PotVar0127735	33.17
PotVar0127894	33.21
PotVar0100919	33.21
solcap_snp_c2_11490	33.21
PotVar0076636	33.21
solcap_snp_c2_39624	33.63
solcap_snp_c2_21858	34.35
solcap_snp_c1_13859	35.42
PotVar0076517	35.84
PotVar0106874	36.28
PotVar0106780	36.76
PotVar0076874	38.05
PotVar0100934	38.19
solcap_snp_c1_3722	38.46
PotVar0076628	38.48
PotVar0100792	38.72
PotVar0109404	39.19
solcap_snp_c1_3740	39.93
solcap_snp_c2_11534	40.05
solcap_snp_c2_11488	41.34
PotVar0127881	42.31
PotVar0127732	42.62
PotVar0106766	42.93
PotVar0007646	43.24
solcap_snp_c2_48864	43.91
PotVar0101281	44.62
solcap_snp_c1_8341	44.77
solcap_snp_c2_26814	44.77
solcap_snp_c2_26791	44.77
solcap_snp_c2_51637	45.51
solcap_snp_c1_16079	45.72
solcap_snp_c2_16720	46.28
solcap_snp_c2_38729	47.89
solcap_snp_c2_56253	47.89
solcap_snp_c2_14930	47.89
solcap_snp_c2_56052	47.89
solcap_snp_c1_11406	47.89
solcap_snp_c2_38243	47.89
PotVar0008082	47.89
PotVar0008075	47.89
solcap_snp_c2_18221	47.89
PotVar0073568	47.89
PotVar0073629	47.89
PotVar0014872	47.89
PotVar0014738	47.89
solcap_snp_c1_13125	47.89
solcap_snp_c2_26884	47.89
solcap_snp_c2_47244	47.89
solcap_snp_c1_14038	47.89
solcap_snp_c1_6127	47.89
solcap_snp_c2_54090	47.89
solcap_snp_c2_51176	47.89
solcap_snp_c2_51549	47.89
solcap_snp_c1_15085	47.89
PotVar0121064	47.89
solcap_snp_c2_56254	47.89
solcap_snp_c2_56255	47.89
solcap_snp_c2_56256	47.89
solcap_snp_c1_16261	47.89
solcap_snp_c2_18225	47.89
solcap_snp_c2_18223	47.89
solcap_snp_c2_39961	47.89
PotVar0073731	47.89
PotVar0073743	47.89
solcap_snp_c1_9839	47.89
solcap_snp_c1_12887	47.89
PotVar0007768	47.89
PotVar0007750	47.89
solcap_snp_c1_6157	47.89
PotVar0007732	47.89
PotVar0014770	47.89
solcap_snp_c2_19422	47.89
solcap_snp_c1_13124	47.89
solcap_snp_c1_6126	47.89
solcap_snp_c1_10941	47.89
solcap_snp_c2_14924	47.89
solcap_snp_c2_53248	47.89
PotVar0007761	47.89
solcap_snp_c2_26780	50.67
solcap_snp_c2_26801	50.67
solcap_snp_c2_26779	50.67
solcap_snp_c2_26842	50.67
solcap_snp_c2_31403	50.67
solcap_snp_c1_8353	50.67
solcap_snp_c2_26796	53.52
solcap_snp_c2_26793	53.52
solcap_snp_c2_26795	53.52
solcap_snp_c1_16643	53.52
solcap_snp_c2_26794	53.52
solcap_snp_c2_26800	53.52
PotVar0091972	53.74
PotVar0092188	54.17
solcap_snp_c2_51560	55.04
PotVar0121097	55.04
solcap_snp_c2_44601	56.75
solcap_snp_c2_56758	57.65
PotVar0009086	58.63
solcap_snp_c1_3310	59.44
solcap_snp_c2_16722	59.44
PotVar0076076	59.59
solcap_snp_c2_16712	60.96
solcap_snp_c2_55090	60.96
solcap_snp_c2_55711	62.58
solcap_snp_c2_55710	62.58
solcap_snp_c2_39856	63.03
PotVar0076174	63.03
PotVar0076126	63.03
PotVar0076291	63.46
solcap_snp_c1_15530	65.72
PotVar0076127	66.5
PotVar0076251	66.57
solcap_snp_c1_13396	67
PotVar0076322	67
solcap_snp_c1_16534	67.01
PotVar0076141	67.43
solcap_snp_c2_54533	67.43
PotVar0076084	67.43
PotVar0076175	67.43
PotVar0076311	67.43
solcap_snp_c1_11791	67.43
PotVar0076312	67.43
solcap_snp_c1_6033	67.43
solcap_snp_c2_58078	68.29

solcap_snp_c1_15982	68.29
solcap_snp_c2_48694	70.71
PotVar0074748	70.71
solcap_snp_c2_48693	70.71
solcap_snp_c2_48691	70.71
solcap_snp_c2_1499	70.71
solcap_snp_c2_53566	71.36
solcap_snp_c1_6905	71.55
PotVar0130958	71.69
PotVar0074876	72.91
PotVar0133113	74.18
solcap_snp_c2_45035	74.27
PotVar0075104	74.27
PotVar0074959	74.27
solcap_snp_c1_16625	75.13
solcap_snp_c1_12945	75.13
solcap_snp_c2_54887	75.13
PotVar0074809	75.13
PotVar0075042	75.13
solcap_snp_c2_45040	75.13
PotVar0075008	75.13
PotVar0075013	75.13
PotVar0075056	75.13
PotVar0074712	75.13
solcap_snp_c2_48810	75.13
PotVar0116182	76.43
PotVar0116232	76.43
PotVar0116335	76.43
PotVar0116179	76.43
PotVar0100515	77.19
solcap_snp_c1_11758	79.05
solcap_snp_c2_55849	79.58
solcap_snp_c2_36059	79.91
solcap_snp_c2_55854	79.91
solcap_snp_c2_36027	79.91
PotVar0116492	79.91
PotVar0100544	80.79
PotVar0084388	80.79
solcap_snp_c2_51234	80.89
solcap_snp_c2_51232	80.89
solcap_snp_c1_11391	82.18
solcap_snp_c2_34948	83.26
PotVar0084331	83.26
solcap_snp_c1_10750	83.26
PotVar0116499	83.26

PotVar0084519	83.26
solcap_snp_c2_38116	83.39
solcap_snp_c1_11356	83.39
solcap_snp_c2_48290	85.92
solcap_snp_c2_52884	87.58
solcap_snp_c2_36060	88.27
PotVar0118472	88.27
PotVar0100536	89.01
PotVar0070877	89.04
PotVar0071120	89.94
PotVar0071127	89.94
solcap_snp_c2_39342	90.8
PotVar0070856	91.82
PotVar0099137	92.36
PotVar0099182	92.36
PotVar0000820	92.54
PotVar0098992	92.57
PotVar0071025	98.88
PotVar0070881	98.88
solcap_snp_c2_32543	98.88
solcap_snp_c2_32550	98.88
PotVar0000459	99.07
solcap_snp_c2_50004	99.1
solcap_snp_c2_39453	100.18
PotVar0000812	100.28
PotVar0000774	100.28
PotVar0000759	100.28
PotVar0113773	101.78
solcap_snp_c2_43748	101.78
PotVar0113891	101.78
PotVar0113797	101.78
solcap_snp_c1_11639	102.02
PotVar0087115	103.2
PotVar0087136	103.2
solcap_snp_c1_8330	103.2
solcap_snp_c2_55784	103.55
solcap_snp_c2_55774	103.55
solcap_snp_c2_55793	103.55
solcap_snp_c2_39463	103.76
PotVar0000732	103.76
PotVar0000760	103.76
solcap_snp_c1_6749	104.61
PotVar0000474	104.61
PotVar0000512	104.61
solcap_snp_c2_21590	104.61

PotVar0000615	104.61
solcap_snp_c1_6748	104.61
solcap_snp_c2_21578	104.61
PotVar0000800	104.61
PotVar0000495	104.61
PotVar0000460	104.61
solcap_snp_c2_26675	104.61
PotVar0000484	104.61
PotVar0000619	104.82
PotVar0000579	104.82
PotVar0000481	104.82
PotVar0000514	104.82
solcap_snp_c2_26758	105.93
solcap_snp_c1_8328	105.93
PotVar0000542	105.93
solcap_snp_c2_26731	105.93
PotVar0123717	106.78
solcap_snp_c2_55791	107.22
PotVar0087118	107.41
PotVar0123633	108.78
solcap_snp_c2_55777	108.78
PotVar0123624	108.78
PotVar0087222	109.15
PotVar0087243	109.76
PotVar0087323	109.76
PotVar0087064	109.76
PotVar0087312	110.02
PotVar0015560	110.93
PotVar0015617	110.93
PotVar0015713	110.93
PotVar0015711	110.93
PotVar0015907	111.8
PotVar0015743	111.8
PotVar0111404	112.39
PotVar0111409	112.39
PotVar0075291	112.39
PotVar0075409	112.39
solcap_snp_c2_34812	112.39
PotVar0087234	112.39
PotVar0075324	112.39
PotVar0076006	112.39
PotVar0016524	113.21
PotVar0016743	113.21
PotVar0017079	113.21
PotVar0017285	113.21

solcap_snp_c2_10798	113.21
PotVar0016521	113.21
PotVar0075251	114.33
PotVar0075236	114.33
PotVar0075516	114.6
PotVar0075331	114.78
PotVar0017413	115.1
PotVar0017380	115.1
PotVar0017497	115.97
PotVar0017942	115.97
PotVar0017463	115.97
PotVar0111515	116.45
PotVar0111414	116.45
solcap_snp_c1_13172	117.58
PotVar0111537	118.47
solcap_snp_c2_52205	120.85
PotVar0075295	121.63
solcap_snp_c1_4140	122.39
solcap_snp_c1_10424	123.16
solcap_snp_c2_34876	123.16
solcap_snp_c1_9614	123.16
solcap_snp_c1_9613	123.16
PotVar0111553	123.16
solcap_snp_c1_9619	123.16
PotVar0075793	123.16
PotVar0076032	123.16
PotVar0075888	123.16
PotVar0130793	123.16
PotVar0130846	123.16
solcap_snp_c2_12959	123.16
PotVar0130835	123.16
solcap_snp_c1_10435	123.16
PotVar0075293	123.16
PotVar0075407	123.16
solcap_snp_c2_34873	123.16
PotVar0075700	123.16
solcap_snp_c1_13085	123.16
solcap_snp_c1_13077	123.16
solcap_snp_c2_12954	123.16
solcap_snp_c1_4178	123.16
PotVar0130789	123.16
solcap_snp_c2_52196	123.16
PotVar0111367	123.16
PotVar0111470	123.16
solcap_snp_c2_32099	123.16
solcap_snp_c2_52203	123.16
solcap_snp_c1_15237	123.16
solcap_snp_c2_12947	123.26
PotVar0075590	123.6
solcap_snp_c2_12956	123.7
solcap_snp_c2_12957	123.7
solcap_snp_c2_12953	123.7
solcap_snp_c2_12958	123.7
PotVar0130885	123.7
solcap_snp_c2_12924	123.87
PotVar0015039	124.2
solcap_snp_c2_12936	124.69
solcap_snp_c2_34019	127.27
solcap_snp_c2_35970	127.27
PotVar0015370	127.27
solcap_snp_c2_12937	127.71
solcap_snp_c2_12921	128.57
solcap_snp_c2_12930	128.57
PotVar0015456	128.93
PotVar0015535	128.93
solcap_snp_c1_4175	129
solcap_snp_c1_4162	129
solcap_snp_c1_4172	129
PotVar0015063	129.43
PotVar0015087	129.43
PotVar0015108	129.43
PotVar0015043	129.43
PotVar0016703	130.24
solcap_snp_c1_4109	130.29
PotVar0016173	130.71
solcap_snp_c1_10670	130.72
solcap_snp_c1_10668	130.72
PotVar0015174	131.15
PotVar0015207	131.15
solcap_snp_c1_10196	131.15
PotVar0015145	131.15
PotVar0015152	131.58
PotVar0015291	131.58
solcap_snp_c1_10178	134.33
solcap_snp_c2_34017	134.33
PotVar0015639	134.89
PotVar0016414	137.39
solcap_snp_c1_3545	137.64
PotVar0015848	137.64
PotVar0015898	137.64
solcap_snp_c2_35959	137.64
PotVar0016394	138.04
PotVar0016316	138.04
solcap_snp_c1_10667	138.04
PotVar0015940	138.04
PotVar0015998	138.04
solcap_snp_c2_35995	138.04
solcap_snp_c1_10713	138.04
PotVar0016706	138.04
PotVar0016270	138.04
PotVar0016172	138.04
PotVar0017157	138.04
PotVar0016800	138.04
PotVar0016863	138.04
PotVar0017188	138.04
PotVar0016906	138.04
PotVar0016819	138.04
solcap_snp_c2_10614	138.04
PotVar0017371	138.04
solcap_snp_c1_10202	138.04
solcap_snp_c2_10693	138.04
PotVar0016775	138.04
PotVar0016403	138.04
PotVar0016397	138.04
PotVar0017149	138.04
PotVar0017260	138.04
solcap_snp_c2_10690	138.04
PotVar0016968	138.04
PotVar0017276	138.04
PotVar0017024	138.04
PotVar0015513	138.04
PotVar0015583	138.04
PotVar0015728	138.04
PotVar0015864	138.04
solcap_snp_c1_10679	138.04
PotVar0015588	138.04
PotVar0015597	138.04
solcap_snp_c2_35958	138.04
solcap_snp_c1_10677	138.04
PotVar0015899	138.04
PotVar0015433	138.04
PotVar0015419	138.04

PotVar0017710	138.48
solcap_snp_c1_3462	138.48
PotVar0017842	138.48
solcap_snp_c1_3461	138.48
PotVar0017609	138.7
PotVar0017293	138.97
solcap_snp_c1_3522	138.97
PotVar0017171	138.97

PotVar0017084	139.42
PotVar0017411	141.24
solcap_snp_c1_3497	141.24
solcap_snp_c2_10615	141.68
PotVar0017377	141.68
solcap_snp_c2_10612	142.45
PotVar0017372	142.45
PotVar0017726	142.91

PotVar0017806	142.91
PotVar0017501	142.91
PotVar0017828	142.91
solcap_snp_c2_10567	142.91
PotVar0017868	143.43
PotVar0017895	143.87
PotVar0017531	143.87
PotVar0016416	151.26

Chromosome 5	
Name	cM
PotVar0048675	0
PotVar0048610	0
PotVar0048582	0
PotVar0048835	0
PotVar0048790	0
solcap_snp_c2_23735	0
PotVar0048467	0
PotVar0048925	0
solcap_snp_c2_23834	0
solcap_snp_c2_33509	0.86
solcap_snp_c2_33532	0.86
solcap_snp_c2_52070	0.86
PotVar0114697	1.29
PotVar0114766	1.29
solcap_snp_c2_11758	1.29
solcap_snp_c2_11605	1.29
PotVar0048155	1.54
PotVar0048673	3.32
solcap_snp_c1_7632	5.95
PotVar0048854	6.38
PotVar0025938	6.47
PotVar0025923	6.47
PotVar0048301	7.26
PotVar0048303	7.26
PotVar0025983	7.61
PotVar0025773	7.61
PotVar0025592	8.14
PotVar0025762	8.56
PotVar0025753	9.42
PotVar0026021	10.85
PotVar0025449	10.85
PotVar0025320	12.28
PotVar0025959	12.28

solcap_snp_c2_23803	13.71
solcap_snp_c2_33518	13.94
PotVar0048921	14.25
solcap_snp_c1_10042	15.22
solcap_snp_c2_33517	15.22
PotVar0048229	15.37
PotVar0114686	16.44
PotVar0114705	16.44
solcap_snp_c2_23831	16.67
solcap_snp_c2_23828	16.88
PotVar0048171	16.88
PotVar0048114	17.1
PotVar0024773	17.1
PotVar0025052	17.1
PotVar0025609	17.1
PotVar0025348	17.1
PotVar0026049	17.1
solcap_snp_c2_11707	17.16
PotVar0024686	18.5
PotVar0024709	18.5
PotVar0024728	18.5
solcap_snp_c2_11685	18.75
PotVar0024528	19.61
PotVar0025140	19.8
PotVar0024602	19.82
PotVar0024611	19.82
PotVar0026091	19.84
PotVar0026113	19.84
PotVar0026057	20.08
PotVar0024744	20.33
PotVar0024936	21.26
PotVar0024781	21.26
PotVar0025065	21.26
PotVar0025139	21.26
PotVar0025527	21.72

PotVar0025740	21.72
PotVar0025764	21.72
PotVar0025780	21.72
solcap_snp_c2_11924	21.72
PotVar0026051	21.72
PotVar0025053	22.45
PotVar0024816	22.45
PotVar0026317	23.46
PotVar0078044	23.48
PotVar0078215	23.48
PotVar0078683	23.48
PotVar0078882	23.48
PotVar0079450	23.48
PotVar0079612	23.48
solcap_snp_c2_22959	23.48
PotVar0077849	23.48
PotVar0078927	23.48
PotVar0079086	23.48
PotVar0079250	23.48
PotVar0079251	23.48
PotVar0079591	23.48
PotVar0079570	23.48
PotVar0025179	24.21
PotVar0079948	25.01
PotVar0025350	25.97
PotVar0079378	25.97
PotVar0080850	25.97
PotVar0080789	25.97
PotVar0130000	25.97
PotVar0080275	25.97
PotVar0117065	25.97
PotVar0117352	25.97
solcap_snp_c1_14840	25.97
PotVar0117419	25.97
PotVar0089832	25.97

PotVar0079940	25.97
PotVar0079782	25.97
PotVar0080614	25.97
PotVar0080670	25.97
PotVar0080048	25.97
PotVar0080122	25.97
PotVar0080575	25.97
PotVar0080883	25.97
PotVar0089637	26.91
PotVar0089842	26.91
PotVar0117221	26.91
PotVar0089709	26.91
PotVar0078469	28.08
PotVar0078533	28.08
PotVar0078025	28.08
PotVar0026274	28.59
PotVar0026316	28.59
PotVar0079955	28.59
solcap_snp_c2_50302	28.59
PotVar0078411	28.59
PotVar0078439	28.59
PotVar0079038	28.59
PotVar0079085	28.59
PotVar0079110	28.59
PotVar0079157	28.59
PotVar0079489	28.59
PotVar0079577	28.59
PotVar0079585	28.59
PotVar0079877	28.59
PotVar0026238	28.59
PotVar0078060	28.59
PotVar0079430	28.59
PotVar0078520	28.59
PotVar0078561	28.59
PotVar0079406	28.59
PotVar0079428	28.59
PotVar0079652	28.59
PotVar0078045	28.59
PotVar0078769	28.59
PotVar0079027	28.59
PotVar0079081	28.59
PotVar0079374	28.59
PotVar0079376	28.59
PotVar0026556	28.59

PotVar0079653	28.59
PotVar0080867	28.59
PotVar0078609	28.59
PotVar0117366	28.59
solcap_snp_c2_51478	28.59
PotVar0117354	28.59
PotVar0089662	28.59
PotVar0089604	28.59
solcap_snp_c2_38193	28.59
PotVar0079737	28.59
solcap_snp_c2_38163	28.89
PotVar0080026	29.54
PotVar0080320	29.85
PotVar0080800	30.5
PotVar0117437	31.02
PotVar0025360	31.02
PotVar0025579	31.02
solcap_snp_c1_3795	31.02
solcap_snp_c2_11923	31.02
PotVar0079966	31.02
PotVar0080476	31.02
PotVar0117192	31.02
solcap_snp_c2_38167	31.02
PotVar0025607	31.02
solcap_snp_c2_47284	31.02
PotVar0116903	31.02
PotVar0025980	31.02
PotVar0025599	31.02
PotVar0078229	31.02
PotVar0078648	31.02
PotVar0078670	31.02
PotVar0078972	31.02
PotVar0079124	31.02
PotVar0078022	31.02
PotVar0080027	31.02
PotVar0079860	31.02
PotVar0080686	31.02
PotVar0116897	31.02
PotVar0079901	31.02
PotVar0080213	31.02
PotVar0080365	31.02
PotVar0080570	31.02
PotVar0117073	31.02
PotVar0117095	31.02

solcap_snp_c2_22995	31.02
PotVar0079820	31.02
PotVar0117047	31.02
PotVar0117275	31.02
PotVar0117190	31.02
PotVar0080004	31.02
PotVar0117280	31.02
PotVar0129937	31.16
PotVar0117324	31.79
PotVar0117438	32.1
PotVar0117367	32.1
PotVar0026053	32.87
PotVar0025817	32.87
PotVar0089374	33.42
solcap_snp_c2_52084	33.42
solcap_snp_c2_11747	33.42
PotVar0026355	33.42
PotVar0078379	33.42
PotVar0079403	33.42
PotVar0079611	33.42
PotVar0026425	33.42
PotVar0077822	33.42
PotVar0078126	33.42
PotVar0079063	33.42
PotVar0079368	33.42
PotVar0026211	33.42
PotVar0083808	34.84
PotVar0083817	35.94
solcap_snp_c2_45517	36.35
PotVar0084178	37.24
PotVar0083684	37.34
PotVar0084089	37.69
PotVar0084163	37.98
solcap_snp_c2_37719	37.98
PotVar0085303	38.44
PotVar0125832	38.45
solcap_snp_c1_11267	39.53
PotVar0084164	39.53
PotVar0125947	39.53
solcap_snp_c2_55452	39.88
PotVar0089376	40.26
PotVar0125819	40.45
PotVar0047235	40.74
PotVar0085501	41.53

PotVar0084190	42.7
PotVar0085312	43.68
PotVar0085401	43.68
PotVar0085405	43.68
PotVar0085531	43.68
PotVar0085459	43.68
PotVar0125830	43.81
solcap_snp_c2_37692	43.99
PotVar0014494	44.47
PotVar0014510	44.47
PotVar0014440	44.47
PotVar0091638	44.62
PotVar0091918	44.62
PotVar0091929	44.62
PotVar0091364	44.62
PotVar0014380	44.9
PotVar0090934	44.91
solcap_snp_c2_56464	45.33
PotVar0014357	45.33
PotVar0091038	45.48
solcap_snp_c2_53298	45.55
solcap_snp_c2_53306	45.55
solcap_snp_c2_53307	45.55
PotVar0109994	45.55
PotVar0085259	45.78
PotVar0085257	45.78
PotVar0091177	45.91
PotVar0001033	46.34
PotVar0084120	46.42
solcap_snp_c2_38748	46.47
solcap_snp_c2_54725	46.47
PotVar0104925	46.47
PotVar0104911	46.47
solcap_snp_c2_49286	46.47
PotVar0104871	46.47
solcap_snp_c1_15292	46.76
PotVar0083923	46.76
PotVar0084086	46.76
PotVar0091259	46.76
PotVar0091740	46.76
PotVar0091619	47.11
PotVar0091465	47.11
PotVar0091464	47.11
PotVar0091432	47.11
PotVar0091575	47.11

PotVar0091625	47.56
PotVar0091668	47.56
PotVar0134951	47.58
solcap_snp_c2_49385	47.58
PotVar0001247	47.58
PotVar0001272	47.58
PotVar0001295	47.58
PotVar0001317	47.58
PotVar0001451	47.58
solcap_snp_c1_15192	47.58
solcap_snp_c1_15690	47.58
PotVar0001495	47.58
PotVar0001507	47.58
PotVar0001074	47.58
solcap_snp_c2_50226	47.58
solcap_snp_c2_47967	47.58
solcap_snp_c2_48587	47.58
solcap_snp_c2_57245	47.58
PotVar0001227	47.58
solcap_snp_c2_15722	47.58
solcap_snp_c2_52397	47.58
PotVar0001360	47.58
solcap_snp_c1_14645	47.66
PotVar0091229	47.66
solcap_snp_c1_11078	48.23
PotVar0090998	48.23
PotVar0091176	48.23
solcap_snp_c2_32854	48.23
PotVar0091126	48.23
PotVar0014571	48.23
solcap_snp_c2_43663	48.23
PotVar0083756	48.23
PotVar0090986	48.23
PotVar0001530	48.23
PotVar0000967	48.23
solcap_snp_c2_52053	48.23
solcap_snp_c2_40089	48.23
solcap_snp_c1_11868	48.23
PotVar0001438	48.23
solcap_snp_c2_49666	48.23
PotVar0125811	48.23
PotVar0001271	48.23
PotVar0014379	49.77
PotVar0014299	50.2
PotVar0001415	50.31

PotVar0024151	50.31
PotVar0084430	50.31
PotVar0001283	50.31
PotVar0024137	50.31
PotVar0084432	50.31
PotVar0001195	50.31
solcap_snp_c2_54598	50.63
PotVar0001310	50.76
PotVar0109880	51.06
PotVar0055481	51.06
PotVar0104798	51.06
solcap_snp_c2_44034	51.06
solcap_snp_c2_54741	52
PotVar0014475	52.13
PotVar0104886	52.31
solcap_snp_c2_48821	54.35
PotVar0123241	54.35
PotVar0123263	54.35
PotVar0001525	54.35
PotVar0001067	54.35
PotVar0001163	54.35
solcap_snp_c2_54576	54.35
solcap_snp_c2_48422	54.35
PotVar0001318	54.35
solcap_snp_c2_52058	54.35
solcap_snp_c2_38365	54.35
solcap_snp_c2_38364	54.35
solcap_snp_c2_40092	54.35
PotVar0001147	54.35
solcap_snp_c2_51980	54.91
PotVar0104796	55.01
solcap_snp_c2_54743	55.01
solcap_snp_c2_54742	55.01
solcap_snp_c1_12966	55.43
PotVar0104857	55.86
PotVar0104802	55.86
PotVar0001239	56.3
solcap_snp_c1_5058	56.43
PotVar0001513	56.74
PotVar0001214	56.74
solcap_snp_c2_38252	57.67
solcap_snp_c2_47405	57.77
solcap_snp_c2_5214	57.77
solcap_snp_c2_5006	57.77
solcap_snp_c2_5003	57.77

solcap_snp_c2_5217	57.77
solcap_snp_c1_1802	57.87
PotVar0001290	58.09
PotVar0001324	58.09
solcap_snp_c2_48820	58.09
solcap_snp_c2_52056	58.09
PotVar0001270	58.09
PotVar0018043	58.09
solcap_snp_c2_52055	58.09
PotVar0001413	58.09
PotVar0014413	58.54
solcap_snp_c1_14700	58.57
PotVar0134955	58.57
solcap_snp_c2_44073	58.57
PotVar0001015	58.57
solcap_snp_c2_47389	58.74
solcap_snp_c2_47390	58.74
solcap_snp_c2_50231	59.04
PotVar0001436	59.14
PotVar0106493	59.19
solcap_snp_c2_5150	59.19
PotVar0106489	60.07
PotVar0106504	60.07
solcap_snp_c2_5154	60.07
PotVar0106500	60.07
PotVar0033995	61.23
PotVar0018022	61.77
PotVar0034046	63.07
PotVar0106514	63.07
solcap_snp_c2_15676	63.47
PotVar0001127	63.47
PotVar0034048	65.9
PotVar0034098	65.9
solcap_snp_c1_15965	66.84
PotVar0033952	66.93
PotVar0123233	68.14
PotVar0123271	68.69
PotVar0106516	69.56
PotVar0033946	69.66
solcap_snp_c2_40775	69.66
PotVar0106494	69.66
PotVar0033999	70
solcap_snp_c1_1875	70
PotVar0106501	70

PotVar0034096	71.73
PotVar0034089	71.73
solcap_snp_c1_12414	72.69
solcap_snp_c2_42374	72.69
solcap_snp_c2_49653	73.74
PotVar0126177	75.52
PotVar0081337	75.64
solcap_snp_c2_49116	75.95
PotVar0081577	76.52
PotVar0081379	76.97
PotVar0007814	76.97
PotVar0081513	77.7
solcap_snp_c2_49128	78.3
solcap_snp_c1_11996	78.95
PotVar0081356	79.05
PotVar0081357	79.06
PotVar0123209	79.32
solcap_snp_c1_12439	79.56
PotVar0081571	79.56
PotVar0081369	79.56
solcap_snp_c2_10338	79.56
solcap_snp_c2_10341	79.56
PotVar0081647	79.56
PotVar0081633	79.56
PotVar0081749	79.56
PotVar0082012	79.56
PotVar0082125	79.56
PotVar0123108	80.03
PotVar0123086	80.46
PotVar0081707	81.34
PotVar0081723	81.34
PotVar0081615	81.34
PotVar0081622	81.34
PotVar0122968	81.34
PotVar0123135	81.34
PotVar0128000	81.76
solcap_snp_c2_10287	81.85
PotVar0081678	82.8
PotVar0081681	82.8
PotVar0081987	82.9
PotVar0082001	82.9
PotVar0081821	82.9
PotVar0082011	82.9
PotVar0082064	82.9

PotVar0081993	82.9
PotVar0082095	82.9
PotVar0082074	82.9
PotVar0082079	83.24
PotVar0082142	83.24
solcap_snp_c2_42451	83.24
solcap_snp_c2_42542	83.24
PotVar0123127	83.24
PotVar0128071	83.24
solcap_snp_c2_8302	83.24
PotVar0034986	83.24
solcap_snp_c2_8510	83.24
PotVar0034903	83.24
PotVar0034892	83.24
PotVar0128222	83.24
solcap_snp_c2_8256	83.24
PotVar0081880	83.24
PotVar0081936	83.24
PotVar0034964	83.24
PotVar0082094	83.67
PotVar0081674	84.11
PotVar0082112	84.11
PotVar0081632	84.11
PotVar0123144	84.21
PotVar0123062	84.21
PotVar0081696	84.53
PotVar0081566	84.81
PotVar0081536	85.03
PotVar0128198	85.62
PotVar0123145	86.27
PotVar0123206	87.38
PotVar0082093	88.01
PotVar0082108	88.01
PotVar0082107	88.01
PotVar0082096	88.11
PotVar0128203	88.47
PotVar0128174	88.47
PotVar0128205	88.47
PotVar0128091	88.47
PotVar0127929	88.9
PotVar0128038	88.9
PotVar0123022	89.85
PotVar0123092	89.85
solcap_snp_c2_42481	90.28

PotVar0034970	90.61
PotVar0128021	90.71
PotVar0034886	91.55
PotVar0123117	91.63
PotVar0123083	91.63
solcap_snp_c2_42452	91.63
solcap_snp_c2_8210	91.8
PotVar0035035	91.8
solcap_snp_c2_55239	92.05
solcap_snp_c2_8295	94.72
PotVar0128234	94.72
PotVar0128144	94.72
solcap_snp_c2_8428	94.72
PotVar0034966	94.72
solcap_snp_c1_1219	94.72

solcap_snp_c1_1125	94.72
PotVar0034812	94.72
solcap_snp_c1_2865	95.13
PotVar0034971	95.13
PotVar0034941	95.13
PotVar0034768	95.13
PotVar0034599	95.13
solcap_snp_c2_3449	95.13
PotVar0034566	95.13
PotVar0034978	95.57
PotVar0034973	95.57
PotVar0035034	95.57
PotVar0034467	96.72
PotVar0034404	96.72
PotVar0034649	96.72

PotVar0034950	96.83
PotVar0034862	96.83
PotVar0034580	97.64
solcap_snp_c1_1123	97.64
PotVar0034466	97.92
PotVar0034730	97.94
solcap_snp_c2_3512	98
solcap_snp_c2_3452	99.3
PotVar0034578	99.3
PotVar0034688	99.3
PotVar0034395	100.47
PotVar0034408	100.53
solcap_snp_c1_1163	101.75

Chromosome 6	
Name	cM
PotVar0083563	0
PotVar0083583	0
PotVar0083604	0
PotVar0083550	0
solcap_snp_c2_30595	0.09
PotVar0083339	0.86
PotVar0083062	0.86
solcap_snp_c2_36400	1.29
PotVar0083053	1.55
solcap_snp_c1_9224	3.5
PotVar0083246	3.5
solcap_snp_c2_30495	3.5
PotVar0082855	3.5
PotVar0027035	5.74
PotVar0026839	6.16
PotVar0027076	12.58
PotVar0026902	12.58
PotVar0027050	12.58
solcap_snp_c2_55553	12.71
solcap_snp_c1_16128	12.71
PotVar0026688	13.44
PotVar0026864	15.36
PotVar0083630	15.69
PotVar0027032	17.31
solcap_snp_c2_27620	17.31
PotVar0026970	17.31

solcap_snp_c2_36709	18.41
solcap_snp_c1_10939	18.83
solcap_snp_c1_10938	18.83
solcap_snp_c1_15811	19.68
solcap_snp_c2_49638	22.29
solcap_snp_c1_13871	22.72
solcap_snp_c2_50183	24.4
PotVar0131893	24.4
PotVar0131873	24.62
PotVar0004038	25.23
PotVar0004060	25.23
PotVar0069488	25.23
PotVar0069491	25.23
PotVar0069492	25.23
PotVar0004013	25.23
PotVar0027083	26.12
PotVar0026695	26.34
PotVar0090366	27.82
PotVar0090406	27.82
PotVar0090338	27.82
PotVar0131889	27.85
solcap_snp_c2_36590	27.85
PotVar0131863	27.85
solcap_snp_c2_36595	27.85
PotVar0131880	27.85
solcap_snp_c1_16656	29.75
solcap_snp_c2_17378	29.75
PotVar0003983	29.75

solcap_snp_c2_4590	29.75
PotVar0036573	29.75
PotVar0090345	29.75
PotVar0093229	29.75
PotVar0131933	29.75
solcap_snp_c2_27867	29.75
PotVar0131882	29.75
PotVar0096888	29.75
PotVar0093232	29.75
PotVar0090320	30.47
solcap_snp_c2_24297	30.9
PotVar0093261	30.9
solcap_snp_c2_42354	31.33
PotVar0093114	31.76
PotVar0104638	31.78
PotVar0104705	31.78
PotVar0133873	31.84
solcap_snp_c2_32893	32.61
solcap_snp_c1_10560	32.61
solcap_snp_c2_24050	32.61
PotVar0090309	32.61
solcap_snp_c2_42351	32.61
solcap_snp_c2_40266	32.61
PotVar0104660	32.61
PotVar0131877	32.61
solcap_snp_c2_51762	32.61
solcap_snp_c2_51768	32.61
solcap_snp_c2_51766	32.61

solcap_snp_c1_15233	32.61
solcap_snp_c2_33302	32.61
solcap_snp_c2_33365	32.61
solcap_snp_c2_56058	32.61
PotVar0133869	32.61
PotVar0104694	32.71
solcap_snp_c2_37603	33.04
solcap_snp_c2_32952	33.04
solcap_snp_c2_43068	33.74
PotVar0104703	34.17
solcap_snp_c2_51760	34.17
solcap_snp_c2_51771	34.17
PotVar0133895	34.6
solcap_snp_c2_33314	34.6
solcap_snp_c2_54220	34.6
solcap_snp_c2_57016	34.6
solcap_snp_c2_57019	34.6
solcap_snp_c2_43123	34.6
PotVar0127129	34.6
PotVar0127210	34.6
solcap_snp_c1_11275	34.6
solcap_snp_c2_37766	34.6
solcap_snp_c2_32918	34.6
solcap_snp_c1_10157	34.6
PotVar0093231	34.6
PotVar0104776	34.99
PotVar0133948	35.54
solcap_snp_c2_33346	36.25
PotVar0054869	36.25
PotVar0054938	37.03
PotVar0087364	37.55
PotVar0134018	38.32
solcap_snp_c2_31648	38.74
solcap_snp_c2_40242	38.99
PotVar0133549	38.99
solcap_snp_c2_37756	39.7
solcap_snp_c2_40236	39.94
PotVar0127164	40.18
PotVar0127225	40.18
PotVar0127196	40.18
PotVar0127331	40.18
PotVar0127104	40.18
PotVar0127224	40.61
PotVar0054901	41.4
PotVar0119434	41.92
PotVar0119420	41.92
solcap_snp_c2_56132	46.31
solcap_snp_c2_49052	46.77
solcap_snp_c2_49053	47.19
PotVar0087403	47.19
PotVar0127240	48.05
PotVar0133545	48.15
solcap_snp_c2_37762	48.15
PotVar0119498	48.15
solcap_snp_c2_49885	48.15
PotVar0070225	51.31
PotVar0070228	51.31
PotVar0070189	51.31
PotVar0070203	51.31
PotVar0070124	52.21
PotVar0070014	53.5
solcap_snp_c2_25929	54.31
PotVar0070093	54.39
solcap_snp_c2_16777	54.39
PotVar0069973	54.39
PotVar0090695	54.74
PotVar0090703	54.74
PotVar0070227	55.61
solcap_snp_c2_31893	55.61
PotVar0070150	55.61
PotVar0085941	55.7
PotVar0090673	55.7
PotVar0090556	55.7
solcap_snp_c2_54195	56.48
PotVar0086011	56.91
PotVar0090783	58.56
solcap_snp_c2_5858	59.66
PotVar0090705	60.41
PotVar0090785	60.41
PotVar0090474	60.41
PotVar0090465	60.41
PotVar0090460	60.41
PotVar0090449	60.41
PotVar0090458	60.41
PotVar0085050	60.55
PotVar0090868	60.62
solcap_snp_c1_10646	60.83
PotVar0084850	60.83
solcap_snp_c2_31180	61.26
solcap_snp_c2_41412	61.4
solcap_snp_c2_31144	61.49
PotVar0084854	61.49
solcap_snp_c2_41405	61.83
PotVar0073982	62.26
PotVar0074004	62.26
PotVar0073911	62.26
PotVar0073971	62.26
PotVar0073985	62.26
PotVar0074079	62.26
solcap_snp_c2_41406	62.26
solcap_snp_c2_56145	62.26
PotVar0073953	62.26
solcap_snp_c1_13135	62.69
PotVar0074175	63.12
solcap_snp_c1_2960	63.12
PotVar0074119	63.12
solcap_snp_c1_2953	63.12
solcap_snp_c1_3003	63.12
solcap_snp_c2_8867	63.12
PotVar0074198	63.12
solcap_snp_c2_8790	63.55
PotVar0085064	64.11
PotVar0085088	64.11
solcap_snp_c2_5772	64.11
solcap_snp_c1_2065	64.11
solcap_snp_c1_2116	64.11
solcap_snp_c1_2117	64.11
solcap_snp_c2_5771	64.11
solcap_snp_c2_5835	64.11
solcap_snp_c2_5868	64.11
solcap_snp_c2_8793	64.33
solcap_snp_c1_2979	64.33
solcap_snp_c2_33777	65.15
solcap_snp_c2_33891	65.58
solcap_snp_c2_33830	65.58
PotVar0085035	65.58
PotVar0040610	66.09
PotVar0040630	66.09
PotVar0040651	66.09
PotVar0040658	66.09
solcap_snp_c2_9010	66.19
solcap_snp_c1_10109	67.6

solcap_snp_c2_9009	70.64
solcap_snp_c1_2944	71.29
solcap_snp_c2_8663	71.29
solcap_snp_c2_8966	73.21
PotVar0040682	73.21
solcap_snp_c2_9001	73.21
solcap_snp_c2_9005	73.21
solcap_snp_c2_8652	73.21
solcap_snp_c2_8786	73.63
solcap_snp_c2_9002	73.67
solcap_snp_c2_8904	74.53
solcap_snp_c2_8999	74.86
PotVar0040680	74.86
PotVar0040538	75.38
solcap_snp_c2_22289	75.81
solcap_snp_c1_7005	76.24
PotVar0040499	76.24
PotVar0040249	76.24
solcap_snp_c1_6994	76.24
PotVar0040507	76.24
solcap_snp_c2_22336	76.24
PotVar0040397	76.24
solcap_snp_c2_9011	76.24
solcap_snp_c1_6997	76.24
PotVar0040162	77.94
PotVar0040532	78.93
PotVar0040491	80.87
PotVar0056976	81.71
PotVar0040236	81.77
PotVar0040125	81.79
PotVar0040426	82.21
PotVar0040161	82.21
PotVar0040122	82.21
PotVar0039905	82.21
PotVar0039962	82.21
PotVar0040351	82.21
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PotVar0040287	82.21
PotVar0040388	82.21
PotVar0040366	82.21
PotVar0039988	82.21
PotVar0040135	82.21
PotVar0039982	82.21
PotVar0039725	82.21
PotVar0039963	82.21

PotVar0039835	82.21
PotVar0041181	82.21
solcap_snp_c2_56590	82.21
solcap_snp_c2_37358	82.21
PotVar0127622	82.21
solcap_snp_c2_37329	82.21
PotVar0040257	83.94
PotVar0127585	83.94
solcap_snp_c1_3074	84.07
solcap_snp_c2_9039	84.69
PotVar0040137	84.89
PotVar0040182	84.89
solcap_snp_c2_24066	84.89
PotVar0041150	84.89
PotVar0039950	84.89
PotVar0039686	84.89
solcap_snp_c2_24229	84.89
PotVar0039692	84.89
PotVar0039687	84.89
PotVar0039697	84.89
solcap_snp_c2_9308	84.89
PotVar0041167	84.89
PotVar0041190	84.89
PotVar0041021	84.89
PotVar0041040	84.89
PotVar0041041	84.89
PotVar0127625	84.89
PotVar0041048	84.89
PotVar0041079	84.89
PotVar0040999	84.89
PotVar0056982	84.89
PotVar0057082	84.89
PotVar0057065	84.89
PotVar0057368	84.89
solcap_snp_c1_7029	84.89
solcap_snp_c1_7040	84.89
solcap_snp_c1_7688	84.89
PotVar0039728	84.89
solcap_snp_c2_24245	84.89
PotVar0039939	84.89
PotVar0039998	84.89
solcap_snp_c1_7031	84.89
solcap_snp_c1_7041	84.89
solcap_snp_c2_22404	84.89
PotVar0040289	84.89

PotVar0041199	84.89
PotVar0040540	84.89
PotVar0056998	84.99
solcap_snp_c2_9137	85.81
PotVar0057119	86.28
PotVar0057170	86.71
PotVar0057370	87.02
PotVar0132843	87.24
solcap_snp_c2_9043	87.45
PotVar0132862	88.43
PotVar0132845	88.74
PotVar0057041	89.36
PotVar0057120	89.78
solcap_snp_c2_37339	90.8
PotVar0040975	90.8
PotVar0066091	91.83
PotVar0057091	92.49
PotVar0056996	96.33
solcap_snp_c1_8679	96.94
PotVar0132863	96.94
PotVar0132754	96.94
solcap_snp_c2_50798	96.94
solcap_snp_c2_50802	97.21
solcap_snp_c1_16127	97.37
PotVar0057192	99.42
PotVar0057365	100.29
PotVar0065888	101.6
solcap_snp_c2_29187	104.15
PotVar0065920	104.96
solcap_snp_c2_1950	105.46
solcap_snp_c1_7679	107.89
PotVar0057109	107.89
solcap_snp_c2_9193	107.89
PotVar0132784	107.89
PotVar0057090	107.89
PotVar0132831	107.89
PotVar0066099	107.89
PotVar0065875	107.89
PotVar0065921	107.89
solcap_snp_c2_9247	109.73
solcap_snp_c1_3130	109.73
solcap_snp_c2_9202	110.23
PotVar0065852	111.49
solcap_snp_c1_15061	116.25
PotVar0065992	116.25

PotVar0065896	116.25

PotVar0065903	116.25

solcap_snp_c1_14614	121.2

Chromosome 7	
Name	cM
solcap_snp_c1_13663	0
solcap_snp_c2_46102	0
PotVar0023044	0
PotVar0022689	0.43
PotVar0022751	0.43
PotVar0022656	1.31
PotVar0022397	2.1
PotVar0022472	2.74
PotVar0022817	3.25
solcap_snp_c2_38828	3.25
PotVar0022437	4.16
PotVar0022654	4.2
PotVar0022114	5.02
PotVar0022108	5.02
solcap_snp_c1_15462	5.17
PotVar0023049	5.21
PotVar0022595	5.21
PotVar0022249	5.33
solcap_snp_c2_36067	5.33
PotVar0022526	6.52
PotVar0022452	6.52
PotVar0022711	6.99
PotVar0022288	7.2
PotVar0022541	7.22
PotVar0022266	7.38
PotVar0022225	7.38
PotVar0022443	7.43
PotVar0095725	7.43
PotVar0023040	7.43
PotVar0022997	7.43
solcap_snp_c2_43960	7.43
PotVar0022712	7.43
solcap_snp_c2_52663	7.43
solcap_snp_c2_26239	7.43
PotVar0102524	7.43
solcap_snp_c2_45643	7.53
solcap_snp_c2_26154	7.95
PotVar0130023	7.95
PotVar0022083	8.25

PotVar0022139	8.25
solcap_snp_c2_26145	8.38
PotVar0022653	8.41
solcap_snp_c2_26197	9.99
PotVar0130025	9.99
PotVar0130054	9.99
PotVar0130051	9.99
PotVar0130068	9.99
PotVar0130024	9.99
solcap_snp_c2_26182	10.12
PotVar0022442	10.15
PotVar0130065	12.76
PotVar0022264	12.84
PotVar0022115	12.84
PotVar0022369	12.84
solcap_snp_c2_26162	13.19
PotVar0102528	13.96
PotVar0130091	14.11
PotVar0102374	14.39
PotVar0102533	14.93
PotVar0095701	15.76
solcap_snp_c1_16225	15.76
PotVar0095825	15.76
solcap_snp_c1_16222	15.76
solcap_snp_c2_46736	16.51
PotVar0102540	16.51
PotVar0095918	16.51
PotVar0132140	16.51
PotVar0132139	16.51
PotVar0095833	16.51
solcap_snp_c2_46752	16.51
PotVar0095580	16.51
PotVar0132011	16.51
PotVar0102342	17.05
PotVar0132707	17.37
PotVar0132489	17.37
solcap_snp_c2_55830	17.56
PotVar0095739	17.56
solcap_snp_c2_55832	17.56
solcap_snp_c2_55837	17.56
PotVar0095883	17.56

PotVar0097757	17.8
PotVar0097696	17.8
PotVar0095511	18.15
PotVar0102371	18.26
solcap_snp_c2_42640	18.67
PotVar0103609	18.67
PotVar0095632	19.19
solcap_snp_c2_43588	19.19
PotVar0095478	19.19
PotVar0095628	19.35
PotVar0127530	19.54
PotVar0127427	19.54
PotVar0097752	19.54
PotVar0097761	19.54
PotVar0127381	19.97
PotVar0095645	20.19
PotVar0028319	20.85
PotVar0028351	20.85
PotVar0028271	21.06
PotVar0028147	21.06
solcap_snp_c2_46379	21.3
PotVar0132155	21.3
solcap_snp_c2_48715	21.71
PotVar0132505	22.14
solcap_snp_c2_55986	22.14
solcap_snp_c2_6601	22.14
solcap_snp_c2_55985	22.14
PotVar0097692	22.14
solcap_snp_c2_52374	22.14
PotVar0027925	22.57
PotVar0028053	22.57
solcap_snp_c2_52376	22.98
solcap_snp_c2_52377	22.98
solcap_snp_c2_31373	23.91
solcap_snp_c2_2856	23.91
solcap_snp_c2_49853	23.91
solcap_snp_c1_15484	23.93
solcap_snp_c1_15485	23.93
PotVar0032760	24.35
PotVar0012599	24.35
PotVar0086506	24.35

solcap_snp_c2_7712	24.35
solcap_snp_c2_7735	24.35
solcap_snp_c1_512	24.35
solcap_snp_c2_7715	24.35
solcap_snp_c1_14735	24.75
PotVar0132627	24.75
PotVar0132568	24.85
PotVar0132538	24.85
PotVar0097715	24.85
PotVar0086423	25.2
PotVar0032700	25.2
PotVar0037615	25.2
PotVar0086488	25.2
PotVar0086524	25.2
PotVar0032779	25.2
PotVar0097697	25.57
solcap_snp_c2_13908	25.65
PotVar0127459	25.68
solcap_snp_c2_52104	25.68
PotVar0028432	25.99
PotVar0103477	25.99
PotVar0028391	25.99
PotVar0027924	26.86
solcap_snp_c2_6622	26.86
PotVar0027937	26.86
solcap_snp_c2_6600	26.86
solcap_snp_c2_6617	26.86
solcap_snp_c2_6619	26.86
solcap_snp_c2_6620	26.86
PotVar0027956	26.86
solcap_snp_c2_6609	26.89
PotVar0134230	27.56
PotVar0127439	28.11
PotVar0127372	28.54
PotVar0127400	28.54
solcap_snp_c2_4530	28.96
solcap_snp_c2_13889	29.06
PotVar0028383	29.42
PotVar0028350	29.42
PotVar0028392	29.42
PotVar0069893	29.78
PotVar0069612	29.78
PotVar0069680	29.78
solcap_snp_c1_3153	29.78
PotVar0069827	29.78
solcap_snp_c1_10855	31.23
solcap_snp_c2_49836	31.23
PotVar0069919	31.29
PotVar0134260	31.29
PotVar0134371	31.29
solcap_snp_c2_4475	31.29
PotVar0069647	31.51
solcap_snp_c2_23391	31.52
PotVar0092761	31.52
solcap_snp_c1_15700	31.52
PotVar0092409	31.52
solcap_snp_c2_23396	31.52
PotVar0128797	31.52
PotVar0069634	32.4
PotVar0115368	32.4
PotVar0115281	32.4
PotVar0092426	32.4
PotVar0092775	32.4
PotVar0128906	32.4
solcap_snp_c1_7399	32.4
PotVar0128887	32.4
PotVar0093018	32.4
PotVar0092990	32.4
PotVar0093016	32.4
solcap_snp_c1_2404	33.13
PotVar0128900	33.4
PotVar0092660	33.4
solcap_snp_c1_5112	33.4
solcap_snp_c1_5126	33.4
PotVar0128963	33.4
PotVar0028081	33.4
solcap_snp_c2_6616	33.4
PotVar0028036	33.4
PotVar0028024	33.4
PotVar0027940	33.4
solcap_snp_c1_2405	33.4
PotVar0028084	33.4
PotVar0086496	33.4
solcap_snp_c1_2672	33.4
PotVar0032614	33.4
PotVar0032617	33.4
PotVar0134361	33.4
PotVar0069668	33.4
solcap_snp_c2_9357	33.48
solcap_snp_c1_16194	33.94
PotVar0092903	33.94
PotVar0092913	33.94
PotVar0115139	33.94
solcap_snp_c2_44120	33.94
PotVar0069620	33.94
PotVar0069656	33.94
PotVar0069878	33.94
solcap_snp_c2_9354	33.94
solcap_snp_c2_9355	33.94
solcap_snp_c2_47671	33.94
PotVar0115319	34.16
PotVar0115246	34.16
PotVar0115416	34.39
PotVar0115101	34.39
solcap_snp_c1_16193	34.39
PotVar0092875	34.39
PotVar0115020	34.39
solcap_snp_c2_15929	34.39
solcap_snp_c1_12976	34.39
PotVar0115415	34.39
PotVar0115039	34.39
PotVar0115344	34.39
PotVar0093655	34.39
PotVar0093742	34.39
PotVar0086359	35.02
solcap_snp_c2_19696	35.02
solcap_snp_c2_19698	35.02
PotVar0012598	35.02
solcap_snp_c1_9478	35.02
solcap_snp_c2_8193	35.02
solcap_snp_c2_34558	35.02
solcap_snp_c2_1975	35.02
solcap_snp_c2_1980	35.02
solcap_snp_c2_9359	35.02
solcap_snp_c1_7521	35.02
PotVar0012608	35.02
PotVar0092421	35.02
PotVar0092448	35.02
PotVar0092628	35.02
PotVar0128886	35.02
solcap_snp_c2_23075	35.02
PotVar0092298	35.02
solcap_snp_c1_3141	35.02
PotVar0115014	35.02
solcap_snp_c1_5115	35.02

solcap_snp_c1_5113	35.02
PotVar0092872	35.02
PotVar0093790	35.49
solcap_snp_c2_33495	35.49
solcap_snp_c2_33492	35.49
solcap_snp_c2_44095	35.49
PotVar0092770	35.5
PotVar0092830	35.5
solcap_snp_c2_45461	35.83
PotVar0119733	35.83
PotVar0115046	35.91
PotVar0093632	36.42
solcap_snp_c2_33488	36.79
PotVar0093025	36.83
PotVar0093776	37
PotVar0133600	37.42
solcap_snp_c2_25250	38.04
solcap_snp_c1_7405	38.26
PotVar0093572	38.43
solcap_snp_c2_15908	39.24
solcap_snp_c2_15923	39.67
PotVar0093555	40.6
PotVar0093513	40.6
PotVar0093634	40.6
solcap_snp_c2_33493	41.03
solcap_snp_c2_45445	44.21
PotVar0119736	44.21
solcap_snp_c1_6228	44.67
PotVar0133616	44.72
PotVar0088454	45.76
PotVar0093777	46.1
solcap_snp_c2_33491	46.1
solcap_snp_c2_45176	46.21
PotVar0133592	46.21
PotVar0133588	46.21
PotVar0133614	46.21
PotVar0119757	46.98
solcap_snp_c2_33429	46.98
PotVar0119730	46.98
PotVar0119726	46.98
solcap_snp_c1_7973	48.13
PotVar0134970	49.25
solcap_snp_c2_45181	50.59
solcap_snp_c2_38787	50.65

PotVar0134084	51.55
solcap_snp_c2_46329	51.76
solcap_snp_c1_6244	51.76
solcap_snp_c2_19748	53.72
PotVar0134031	53.72
solcap_snp_c1_6238	54.16
PotVar0133636	56.38
solcap_snp_c2_25207	56.38
solcap_snp_c2_35078	56.38
PotVar0104502	57.18
solcap_snp_c2_35110	57.57
PotVar0134105	57.57
solcap_snp_c2_35055	58.02
solcap_snp_c2_35058	58.79
PotVar0134065	59.66
PotVar0134990	60.09
solcap_snp_c1_10461	60.96
solcap_snp_c2_35053	61.26
solcap_snp_c2_35051	62.13
solcap_snp_c2_26006	62.71
solcap_snp_c2_26014	62.71
PotVar0134030	62.78
PotVar0134999	62.78
solcap_snp_c2_26041	63.05
PotVar0047676	64.42
PotVar0047482	64.85
Gro14_a_Paal_LG07	64.85
PotVar0047713	66.5
solcap_snp_c2_26015	67.14
PotVar0047739	67.14
PotVar0047767	67.14
PotVar0047816	67.24
PotVar0047993	67.29
PotVar0047949	67.29
PotVar0047836	67.29
PotVar0134086	68.33
PotVar0048010	68.59
PotVar0048065	69.38
solcap_snp_c2_28212	69.38
PotVar0044409	70.24
PotVar0044179	70.87
PotVar0044126	72.51
PotVar0044653	72.59
solcap_snp_c2_26040	72.81

PotVar0047616	72.81
solcap_snp_c2_26003	73.47
solcap_snp_c2_26011	73.47
solcap_snp_c2_33038	73.47
solcap_snp_c2_50620	74.1
PotVar0047901	74.11
PotVar0047847	74.11
solcap_snp_c2_26007	74.11
solcap_snp_c2_26012	74.11
solcap_snp_c2_28174	74.11
PotVar0047551	74.11
PotVar0044685	74.11
solcap_snp_c2_12420	74.16
PotVar0043929	74.47
PotVar0102878	74.47
PotVar0047595	75.26
PotVar0047459	75.26
PotVar0047829	75.26
PotVar0047976	75.26
solcap_snp_c2_33019	75.26
solcap_snp_c1_9918	75.26
solcap_snp_c2_28310	75.26
solcap_snp_c2_28195	75.26
PotVar0048050	75.26
PotVar0048012	75.36
solcap_snp_c2_28309	75.36
solcap_snp_c1_8709	75.36
solcap_snp_c1_8713	75.36
solcap_snp_c2_28167	75.36
solcap_snp_c2_28176	75.36
solcap_snp_c2_28186	75.36
PotVar0043885	75.46
PotVar0102788	76.13
solcap_snp_c2_12596	76.13
PotVar0102837	76.13
PotVar0102773	76.51
PotVar0044133	77.04
PotVar0044416	77.04
PotVar0048011	77.04
solcap_snp_c2_28171	77.04
PotVar0044024	77.04
PotVar0043970	77.04
PotVar0047769	77.04
PotVar0047982	77.04

solcap_snp_c2_42756	77.47
PotVar0044651	77.47
PotVar0044551	77.93
solcap_snp_c2_42807	77.93
solcap_snp_c2_16846	78.18
solcap_snp_c2_30416	78.21
PotVar0128563	78.21
PotVar0102649	78.21
PotVar0044169	78.39
solcap_snp_c2_12405	78.82
PotVar0044131	78.82
PotVar0044090	78.87
PotVar0044591	80.07
solcap_snp_c2_51513	80.16
PotVar0102784	80.16
solcap_snp_c2_51536	80.59
PotVar0044156	81.03
PotVar0044278	81.13
solcap_snp_c1_12597	81.13
PotVar0044411	81.13

PotVar0128566	81.36
PotVar0044305	81.62
solcap_snp_c2_18573	82.34
PotVar0043954	82.78
solcap_snp_c2_12411	82.78
PotVar0102877	82.78
PotVar0044087	83.93
solcap_snp_c2_18685	85.1
solcap_snp_c2_18667	85.1
solcap_snp_c2_18684	85.1
PotVar0037125	85.53
PotVar0037122	85.53
solcap_snp_c2_30428	86.35
solcap_snp_c2_30460	86.35
solcap_snp_c2_18745	86.4
PotVar0037035	86.4
PotVar0036819	86.79
solcap_snp_c2_12526	87.01
PotVar0037236	87.66
PotVar0102724	88.05

PotVar0102815	90.1
PotVar0036750	92.01
PotVar0036643	92.01
PotVar0036821	92.01
PotVar0036731	92.01
PotVar0036644	92.01
solcap_snp_c1_8830	92.01
solcap_snp_c2_28850	92.45
PotVar0037157	92.45
PotVar0037090	92.45
PotVar0037039	92.45
PotVar0036843	92.47
solcap_snp_c2_33279	92.67
solcap_snp_c2_33278	92.67
solcap_snp_c2_28851	92.9
solcap_snp_c2_28848	92.9
solcap_snp_c2_28846	92.9
solcap_snp_c2_33276	92.9
solcap_snp_c2_33273	94.78

Chromosome 8	
Name	cM
PotVar0113745	0
PotVar0113742	0
PotVar0113635	0.21
solcap_snp_c2_27452	0.36
PotVar0113623	0.43
solcap_snp_c2_51957	1.3
PotVar0088789	3.19
PotVar0088709	3.19
PotVar0088803	4.1
PotVar0118200	5.15
PotVar0118202	5.15
PotVar0108990	5.46
solcap_snp_c2_57750	5.46
PotVar0110053	5.46
PotVar0110028	5.93
solcap_snp_c2_29025	6.02
solcap_snp_c2_29020	6.02
PotVar0088684	7.54
PotVar0088692	7.96
solcap_snp_c1_14884	7.96
PotVar0088757	7.96

PotVar0088714	7.96
PotVar0088710	7.96
PotVar0088766	7.96
PotVar0110149	7.96
PotVar0110157	7.96
PotVar0088806	7.96
solcap_snp_c2_53516	7.96
PotVar0088738	7.96
PotVar0088760	7.96
PotVar0088739	8.02
PotVar0108992	8.71
PotVar0088783	8.78
PotVar0110066	8.89
solcap_snp_c2_24404	8.89
PotVar0110096	8.89
PotVar0110161	9.21
PotVar0063780	9.44
solcap_snp_c2_24410	9.83
solcap_snp_c1_7739	10.04
PotVar0110060	10.04
PotVar0108807	10.27
PotVar0108825	10.27
PotVar0109013	10.27

PotVar0108833	10.27
PotVar0108899	10.27
PotVar0108902	10.5
PotVar0110136	10.96
solcap_snp_c2_44855	11.87
PotVar0063749	12.06
solcap_snp_c2_34142	12.82
PotVar0108896	12.82
PotVar0108913	12.82
PotVar0063725	12.89
PotVar0063904	13.04
PotVar0063940	13.04
solcap_snp_c2_48951	13.53
PotVar0063845	13.53
solcap_snp_c2_34124	13.91
solcap_snp_c2_30037	13.91
PotVar0063938	13.91
PotVar0063693	13.96
PotVar0063692	13.96
PotVar0063624	13.96
solcap_snp_c2_34121	14.34
solcap_snp_c2_26893	14.77
PotVar0063591	14.83

PotVar0063939	15.86
solcap_snp_c2_19533	15.86
solcap_snp_c2_19534	15.86
solcap_snp_c2_34179	15.86
solcap_snp_c2_30104	15.86
PotVar0063844	15.86
solcap_snp_c2_48953	15.86
PotVar0063766	15.86
PotVar0063756	15.86
PotVar0063704	15.86
solcap_snp_c1_8380	15.86
PotVar0063755	15.86
solcap_snp_c2_26938	15.86
solcap_snp_c2_19638	15.86
solcap_snp_c2_47904	15.86
solcap_snp_c2_47905	15.86
solcap_snp_c2_19437	15.95
solcap_snp_c2_37599	15.95
solcap_snp_c2_47920	15.95
solcap_snp_c2_47923	15.95
solcap_snp_c2_57588	15.95
solcap_snp_c2_57589	15.95
solcap_snp_c2_37600	15.95
solcap_snp_c2_57591	15.95
solcap_snp_c2_54581	15.95
PotVar0081045	15.95
solcap_snp_c2_57849	15.95
solcap_snp_c2_2103	15.95
solcap_snp_c2_2102	15.95
solcap_snp_c2_19951	15.95
solcap_snp_c2_19940	15.95
PotVar0076488	15.95
solcap_snp_c2_2844	15.95
solcap_snp_c2_2843	15.95
solcap_snp_c2_2842	15.95
solcap_snp_c2_2837	15.95
solcap_snp_c1_846	15.95
solcap_snp_c2_8167	15.95
solcap_snp_c2_5909	15.95
solcap_snp_c2_29284	15.95
solcap_snp_c2_29283	15.95
solcap_snp_c2_19426	15.95
solcap_snp_c1_6130	15.95
solcap_snp_c1_6131	15.95
solcap_snp_c1_6138	15.95
solcap_snp_c2_30255	15.95
solcap_snp_c1_11442	15.95
solcap_snp_c2_30904	15.95
solcap_snp_c2_30907	15.95
solcap_snp_c1_2686	15.95
solcap_snp_c1_2687	15.95
PotVar0088658	15.95
solcap_snp_c1_15689	15.95
solcap_snp_c2_34078	15.95
solcap_snp_c2_34565	15.95
solcap_snp_c2_34564	15.95
solcap_snp_c2_42290	15.95
solcap_snp_c2_2178	15.95
PotVar0076384	15.95
solcap_snp_c2_19942	15.95
solcap_snp_c2_2840	15.95
solcap_snp_c2_2826	15.95
solcap_snp_c2_8169	15.95
solcap_snp_c2_8172	15.95
solcap_snp_c2_5915	15.95
solcap_snp_c2_29494	15.95
solcap_snp_c2_29498	15.95
solcap_snp_c2_29286	15.95
solcap_snp_c2_29280	15.95
solcap_snp_c2_19433	15.95
solcap_snp_c1_6136	15.95
solcap_snp_c1_6140	15.95
solcap_snp_c1_6142	15.95
solcap_snp_c1_9169	15.95
solcap_snp_c2_30293	15.95
solcap_snp_c2_19432	15.95
solcap_snp_c2_31354	16.42
solcap_snp_c2_12746	16.42
solcap_snp_c2_17305	16.42
solcap_snp_c2_47900	16.42
solcap_snp_c2_17317	16.48
solcap_snp_c2_17304	16.48
solcap_snp_c2_52253	19.12
solcap_snp_c2_52857	19.12
solcap_snp_c1_15451	19.12
solcap_snp_c2_42293	22.89
PotVar0124889	23.12
PotVar0076451	23.76
PotVar0076467	23.76
PotVar0076367	24.19
PotVar0060621	24.61
PotVar0076370	25.63
solcap_snp_c1_6262	25.63
PotVar0029800	25.63
PotVar0040861	25.63
solcap_snp_c2_49249	25.89
solcap_snp_c2_49243	25.89
solcap_snp_c2_33774	26.05
solcap_snp_c2_19631	27.25
solcap_snp_c2_17318	27.25
solcap_snp_c1_6252	27.35
solcap_snp_c2_19639	27.35
solcap_snp_c2_19949	27.35
solcap_snp_c2_53177	27.35
solcap_snp_c2_33771	27.45
solcap_snp_c2_48358	27.45
solcap_snp_c2_53880	27.45
solcap_snp_c2_19429	27.45
solcap_snp_c2_30256	27.45
solcap_snp_c1_9167	27.45
solcap_snp_c2_34082	27.45
solcap_snp_c2_56757	28.94
solcap_snp_c2_2746	29.27
solcap_snp_c1_822	29.82
solcap_snp_c2_2743	29.82
solcap_snp_c2_56491	30.33
solcap_snp_c2_41463	30.65
solcap_snp_c2_41470	30.65
solcap_snp_c2_32317	30.7
solcap_snp_c1_14542	31.57
solcap_snp_c2_2757	31.88
solcap_snp_c2_2744	31.88
solcap_snp_c1_12163	31.88
solcap_snp_c2_45763	32.46
PotVar0133433	33.31
solcap_snp_c1_14108	33.74
solcap_snp_c2_32302	35.41
solcap_snp_c2_32280	36.56
solcap_snp_c2_32300	36.56
PotVar0077284	36.7
PotVar0077225	36.7
solcap_snp_c2_15803	36.7

solcap_snp_c2_51328	36.99
solcap_snp_c2_40320	38.55
PotVar0103294	38.98
PotVar0103406	38.98
PotVar0103368	38.98
PotVar0134854	39.27
solcap_snp_c2_45759	39.4
solcap_snp_c1_15044	39.5
solcap_snp_c2_44334	39.5
solcap_snp_c1_16676	39.5
PotVar0133394	39.5
PotVar0103329	39.59
PotVar0134757	40.16
PotVar0134733	40.16
solcap_snp_c2_44307	40.25
solcap_snp_c2_32309	40.25
solcap_snp_c2_32310	40.25
solcap_snp_c2_32282	40.25
solcap_snp_c2_44331	41.09
solcap_snp_c1_13586	41.09
solcap_snp_c2_51320	41.09
PotVar0133361	41.09
solcap_snp_c1_15046	43.01
solcap_snp_c2_51369	43.01
solcap_snp_c2_51367	43.01
solcap_snp_c2_51329	43.01
solcap_snp_c2_44305	43.01
solcap_snp_c2_44304	43.01
PotVar0133399	43.01
solcap_snp_c2_18892	43.01
solcap_snp_c2_47459	43.01
PotVar0086641	43.01
solcap_snp_c2_33381	43.01
PotVar0086640	43.01
PotVar0086805	43.01
PotVar0086812	43.01
PotVar0123452	43.01
solcap_snp_c2_18943	43.01
PotVar0086745	43.01
solcap_snp_c2_47444	43.01
PotVar0134851	43.43
solcap_snp_c2_41044	43.43
solcap_snp_c1_12166	44.31
PotVar0134835	44.32
PotVar0134764	45.19

solcap_snp_c1_14271	45.19
solcap_snp_c2_33386	45.19
PotVar0134793	45.19
PotVar0134751	45.19
PotVar0134734	45.19
solcap_snp_c2_48182	45.19
PotVar0123397	45.19
PotVar0123415	45.19
solcap_snp_c1_11562	45.19
PotVar0134798	45.19
PotVar0086588	45.34
PotVar0123481	45.46
PotVar0123525	45.64
solcap_snp_c2_18894	46.28
solcap_snp_c2_18895	46.28
PotVar0086703	46.28
PotVar0086598	46.49
PotVar0086773	46.49
solcap_snp_c2_18922	47.13
PotVar0086822	47.13
PotVar0086646	47.13
PotVar0086766	47.13
PotVar0086744	47.13
PotVar0134786	47.58
solcap_snp_c2_48184	47.58
PotVar0077030	48.12
PotVar0077094	48.12
PotVar0077179	48.33
PotVar0077330	48.99
PotVar0077537	48.99
PotVar0077331	48.99
PotVar0077015	49.71
PotVar0125618	50.11
PotVar0125359	50.11
PotVar0125664	50.11
PotVar0125338	50.11
PotVar0077235	50.65
PotVar0077582	50.88
solcap_snp_c2_50150	50.88
solcap_snp_c2_50153	50.88
PotVar0076939	50.98
PotVar0077095	51.4
PotVar0077528	52.15
PotVar0077483	52.15
PotVar0077540	52.15

PotVar0125518	52.26
PotVar0077092	52.73
PotVar0077227	52.73
PotVar0077151	52.73
PotVar0125369	53.19
PotVar0077471	53.19
PotVar0125390	53.19
PotVar0077614	53.19
PotVar0125381	53.19
PotVar0125546	53.19
PotVar0125152	53.19
PotVar0077622	53.67
solcap_snp_c2_49377	54.26
solcap_snp_c2_50151	54.48
PotVar0103342	55.51
PotVar0103095	56.9
PotVar0103097	56.9
PotVar0103351	57.77
solcap_snp_c2_28555	57.9
PotVar0122021	58.2
PotVar0103305	58.67
PotVar0103303	58.67
PotVar0122082	58.67
solcap_snp_c2_28580	59.11
solcap_snp_c2_28637	60.37
PotVar0063401	60.86
PotVar0063512	60.86
PotVar0063421	61.29
solcap_snp_c2_28633	61.29
solcap_snp_c2_28634	61.29
PotVar0063331	61.29
PotVar0063339	61.29
PotVar0063157	61.29
PotVar0063427	63.83
solcap_snp_c2_28632	64.48
PotVar0063471	65.15
PotVar0063328	65.77
solcap_snp_c2_28548	65.99
PotVar0069362	66.42
PotVar0121994	67.38
PotVar0103331	67.38
PotVar0096167	68.57
PotVar0063060	68.57
PotVar0096182	68.77
solcap_snp_c1_13116	69.3

solcap_snp_c2_28635	69.3
PotVar0063169	69.3
PotVar0063333	69.3
PotVar0063486	69.3
PotVar0096216	69.41
PotVar0096433	69.41
PotVar0063115	70.12
PotVar0063501	70.3
solcap_snp_c2_34758	70.3
solcap_snp_c2_5332	70.3
PotVar0096178	70.55
PotVar0096223	70.55
PotVar0096222	70.97
PotVar0096218	70.97
PotVar0063283	70.98
solcap_snp_c2_52700	70.98
solcap_snp_c2_34709	70.98
solcap_snp_c2_34698	70.98
solcap_snp_c2_34717	70.98
PotVar0096416	70.98
PotVar0063073	70.98
solcap_snp_c2_34710	70.98
solcap_snp_c2_16998	70.98
solcap_snp_c2_16999	70.98
PotVar0096436	70.98
PotVar0096290	70.98
solcap_snp_c2_36731	71.6
PotVar0100204	72.06
PotVar0096463	72.16
PotVar0100067	72.27
solcap_snp_c2_36745	72.27
solcap_snp_c2_36777	73.36
PotVar0100304	73.36
PotVar0100459	74.32
PotVar0100389	75.11
PotVar0100350	75.11
PotVar0100471	75.11
PotVar0081240	75.11
solcap_snp_c2_19085	75.11
PotVar0100388	75.27
PotVar0081131	75.64
solcap_snp_c2_56726	75.69
PotVar0100045	75.69
PotVar0100194	75.69
PotVar0100132	75.69
PotVar0100303	75.69
PotVar0100427	75.69
solcap_snp_c2_19080	76.79
PotVar0081279	77.27
PotVar0119156	79.95
PotVar0119174	79.95
solcap_snp_c1_10384	80.67
PotVar0024022	80.72
PotVar0119088	80.82
PotVar0119169	80.88
PotVar0097448	81.12
PotVar0097455	81.12
PotVar0097439	81.12
solcap_snp_c1_5546	81.22
PotVar0119132	81.25
solcap_snp_c2_34634	81.76
PotVar0119101	81.76
solcap_snp_c1_8291	81.76
solcap_snp_c1_8235	81.76
PotVar0097495	82.55
PotVar0097491	82.55
PotVar0024073	83.01
solcap_snp_c1_8293	83.01
PotVar0024020	83.01
PotVar0024071	83.01
PotVar0097536	83.01
PotVar0024064	83.01
PotVar0097423	83.05
solcap_snp_c1_8297	83.05
PotVar0023748	83.06
PotVar0023717	83.46
PotVar0023875	83.46
PotVar0023806	83.46
solcap_snp_c1_5483	83.51
PotVar0097375	83.73
solcap_snp_c1_16495	85.2
PotVar0024101	85.42
PotVar0023678	85.64
PotVar0023850	85.64
solcap_snp_c1_5499	85.85
PotVar0023957	86.03
PotVar0024092	86.67
solcap_snp_c2_16994	86.93
solcap_snp_c1_8282	91.93
solcap_snp_c1_5560	92.91
PotVar0097615	93.18
PotVar0023867	93.18
PotVar0023990	93.18
PotVar0023981	93.18
PotVar0097603	93.18
PotVar0023743	93.61
PotVar0023689	93.61
PotVar0023429	94.87
PotVar0023313	94.87
solcap_snp_c1_8763	94.87
solcap_snp_c1_8760	95.09
PotVar0023506	95.67
PotVar0023324	95.67
solcap_snp_c1_8754	95.82
PotVar0023391	95.93
PotVar0023563	95.93
PotVar0023288	95.93
PotVar0023184	96.17
PotVar0023583	96.29
PotVar0023582	96.29
PotVar0023576	96.36
PotVar0023409	96.36
solcap_snp_c1_5179	96.43
PotVar0023140	96.8
solcap_snp_c2_28433	99.95
PotVar0023579	102.85

Chromosome 9	
Name	cM
PotVar0011657	0
solcap_snp_c1_1053	0
PotVar0130628	4.28
solcap_snp_c2_48673	6.91

solcap_snp_c1_975	6.91
solcap_snp_c2_48597	8.65
solcap_snp_c2_39029	9.52
PotVar0114517	9.67
PotVar0114492	10.33
solcap_snp_c2_39035	10.4
solcap_snp_c1_988	11.19
PotVar0114434	11.41
solcap_snp_c1_1000	11.41
solcap_snp_c1_14370	11.41
PotVar0011302	11.41
PotVar0011714	11.75
PotVar0011497	12.18
solcap_snp_c2_10966	13.01
PotVar0011522	13.44
solcap_snp_c2_39091	15.76
PotVar0011929	18.21
solcap_snp_c2_39084	20.88
solcap_snp_c2_39085	20.88
PotVar0011885	20.92
solcap_snp_c2_39086	21.58
solcap_snp_c1_3612	25.64
solcap_snp_c2_39082	28.03
solcap_snp_c2_39083	28.03
solcap_snp_c1_3608	29.02
PotVar0011225	29.02
PotVar0011713	29.02
PotVar0011849	29.02
solcap_snp_c2_10958	29.02
solcap_snp_c2_10956	29.02
PotVar0011481	29.02
PotVar0012073	30.24
PotVar0012446	31.79
PotVar0012077	32.42
PotVar0011708	32.6
solcap_snp_c2_10906	32.6
solcap_snp_c1_3597	32.6
PotVar0011839	33.28
PotVar0012007	33.28
solcap_snp_c2_4165	34.49
PotVar0012337	35.37
solcap_snp_c2_3962	35.6
PotVar0012114	36.07
PotVar0012230	36.17
PotVar0012274	36.17
PotVar0012284	36.44
solcap_snp_c2_3949	36.6
solcap_snp_c2_3943	36.82
solcap_snp_c2_4192	36.82
solcap_snp_c2_10961	37.9
PotVar0011361	37.9
PotVar0011392	37.9
PotVar0011927	37.9
solcap_snp_c2_4045	37.9
PotVar0011879	37.9
PotVar0012050	37.9
PotVar0012165	37.9
PotVar0012325	37.9
PotVar0012533	38.21
PotVar0132444	38.26
solcap_snp_c2_4415	38.78
solcap_snp_c1_13786	38.78
solcap_snp_c2_3934	39.26
solcap_snp_c2_4048	39.5
PotVar0012492	39.5
PotVar0073230	40.34
PotVar0073342	40.34
solcap_snp_c2_52240	40.34
solcap_snp_c2_13194	41.62
solcap_snp_c1_1420	42.36
solcap_snp_c2_3952	42.36
solcap_snp_c1_4243	42.36
solcap_snp_c2_13188	42.36
solcap_snp_c1_4238	42.36
PotVar0133733	42.36
solcap_snp_c2_13177	42.36
PotVar0133858	42.36
solcap_snp_c2_13180	42.36
PotVar0073321	42.36
solcap_snp_c2_35422	42.36
solcap_snp_c1_10528	42.36
PotVar0133799	42.36
PotVar0133086	42.36
solcap_snp_c2_3947	42.36
solcap_snp_c1_1426	42.36
solcap_snp_c2_3953	42.36
solcap_snp_c2_3969	42.36
PotVar0073418	42.36
PotVar0133769	42.36
solcap_snp_c2_52241	42.43
solcap_snp_c2_13322	42.43
solcap_snp_c2_13317	42.43
solcap_snp_c2_35411	42.43
solcap_snp_c2_13133	43.69
PotVar0133829	45.14
solcap_snp_c2_55129	45.39
solcap_snp_c1_4228	46.51
solcap_snp_c2_13139	46.61
solcap_snp_c2_52522	47.46
solcap_snp_c2_52519	47.46
PotVar0034276	48.8
PotVar0034334	48.8
PotVar0132961	48.8
PotVar0117779	49.66
solcap_snp_c2_49770	50.49
PotVar0107349	50.76
PotVar0012782	50.93
PotVar0054648	50.93
PotVar0111212	50.93
solcap_snp_c2_1484	50.93
solcap_snp_c2_21318	50.93
solcap_snp_c2_44951	50.93
PotVar0054663	50.93
PotVar0132977	50.93
solcap_snp_c2_50247	50.93
solcap_snp_c2_52518	50.93
solcap_snp_c2_52521	50.93
solcap_snp_c2_52515	50.93
solcap_snp_c1_14669	50.93
solcap_snp_c2_31988	51.42
PotVar0107326	51.63
PotVar0007597	51.63
solcap_snp_c2_56179	51.63
PotVar0131045	51.63
PotVar0131220	51.63
solcap_snp_c2_21320	51.63
PotVar0131152	51.63
solcap_snp_c2_53375	51.63
PotVar0107313	51.63
solcap_snp_c2_58236	51.63
solcap_snp_c2_52898	51.63
solcap_snp_c2_4381	51.63
solcap_snp_c2_4396	51.63
solcap_snp_c2_58373	51.63
solcap_snp_c2_26515	51.63

PotVar0054651	51.63
solcap_snp_c2_3205	51.63
PotVar0111163	51.63
PotVar0111157	51.63
solcap_snp_c2_689	51.63
PotVar0050913	51.63
solcap_snp_c1_14668	51.63
solcap_snp_c2_49764	51.63
PotVar0051729	51.63
PotVar0107348	51.63
PotVar0111200	51.63
PotVar0131000	51.63
PotVar0131102	51.63
PotVar0131026	51.63
PotVar0007492	51.86
solcap_snp_c1_16394	51.86
PotVar0007448	51.86
PotVar0007613	51.86
solcap_snp_c2_23431	54.91
solcap_snp_c1_6476	55.05
solcap_snp_c2_23439	57.46
solcap_snp_c1_7530	57.46
solcap_snp_c2_4404	57.46
PotVar0054644	57.46
PotVar0111226	57.46
PotVar0131150	57.46
PotVar0131182	57.85
solcap_snp_c2_21314	57.85
solcap_snp_c2_21331	57.85
solcap_snp_c1_8212	57.85
solcap_snp_c2_55124	57.85
solcap_snp_c2_1514	57.85
solcap_snp_c1_364	57.85
PotVar0027117	57.85
solcap_snp_c2_681	57.85
solcap_snp_c1_2319	57.85
solcap_snp_c2_6333	57.85
solcap_snp_c1_449	57.85
solcap_snp_c2_1908	57.85
solcap_snp_c2_1511	57.85
solcap_snp_c2_680	57.85
PotVar0027377	57.85
solcap_snp_c1_16738	58.39
solcap_snp_c2_4567	59.29
solcap_snp_c2_53558	59.38
solcap_snp_c2_22758	59.38
solcap_snp_c2_53559	59.38
solcap_snp_c2_16276	59.85
solcap_snp_c2_20469	59.95
PotVar0007465	60.19
PotVar0051493	60.79
PotVar0051475	60.79
PotVar0051101	61.08
solcap_snp_c2_20479	61.14
PotVar0051195	61.29
solcap_snp_c1_12802	61.5
solcap_snp_c2_27648	61.57
solcap_snp_c2_27644	61.57
solcap_snp_c2_27650	61.57
PotVar0058507	62.29
PotVar0058493	63.59
PotVar0058473	63.59
PotVar0094024	65.81
solcap_snp_c1_11777	67.32
solcap_snp_c2_12780	67.47
solcap_snp_c2_12761	67.47
solcap_snp_c2_44819	68.33
solcap_snp_c2_4196	69.92
solcap_snp_c1_4091	69.99
solcap_snp_c1_4084	69.99
solcap_snp_c2_12781	70.43
PotVar0051102	70.43
PotVar0051363	70.43
PotVar0051027	70.43
PotVar0051119	70.43
PotVar0051243	70.43
PotVar0051276	70.43
PotVar0051366	70.43
solcap_snp_c1_6192	70.43
PotVar0051418	70.43
solcap_snp_c1_6176	70.43
PotVar0051520	70.43
PotVar0051583	70.43
PotVar0051499	70.43
PotVar0051651	70.43
PotVar0051521	70.43
solcap_snp_c2_44815	70.43
PotVar0082816	70.43
solcap_snp_c2_12788	70.43
solcap_snp_c2_12778	71.18
solcap_snp_c1_4077	71.18
solcap_snp_c2_12779	71.18
solcap_snp_c2_12789	71.18
solcap_snp_c1_4090	71.18
solcap_snp_c2_12760	71.18
PotVar0051698	71.69
PotVar0051696	71.69
PotVar0129337	72.55
solcap_snp_c1_13996	74
solcap_snp_c2_43032	75.18
PotVar0101941	75.18
PotVar0058508	75.68
solcap_snp_c2_40867	77.52
PotVar0129355	77.75
PotVar0103851	77.83
PotVar0094050	79.66
PotVar0093817	79.66
solcap_snp_c2_43049	80.31
PotVar0094025	80.46
PotVar0129259	80.46
solcap_snp_c1_16414	80.46
PotVar0129270	80.46
PotVar0129386	80.46
solcap_snp_c1_1425	80.46
PotVar0129336	81.33
PotVar0118577	81.58
PotVar0093997	82.9
PotVar0093848	82.9
solcap_snp_c1_15041	83.32
solcap_snp_c2_26979	83.44
solcap_snp_c2_40848	83.75
solcap_snp_c2_43031	83.75
solcap_snp_c2_26945	84.73
PotVar0101691	85.92
solcap_snp_c2_42964	85.92
PotVar0101814	85.92
PotVar0103895	86.03
solcap_snp_c2_27054	87.66
PotVar0103704	87.66
PotVar0103737	87.66
PotVar0103788	87.66
PotVar0103876	90.5

PotVar0107543	90.61
PotVar0107780	92.28
solcap_snp_c1_12178	92.49
PotVar0103918	92.79
PotVar0118718	94.15
solcap_snp_c2_46784	94.58
solcap_snp_c1_13886	95.44
PotVar0107708	95.45
solcap_snp_c2_22003	97.43
PotVar0107676	97.43
solcap_snp_c1_6936	97.43
PotVar0061844	98.1
PotVar0061749	98.1
PotVar0107475	98.31
PotVar0072548	99.06
solcap_snp_c2_22040	99.4
solcap_snp_c2_22069	99.62
PotVar0118727	99.85
PotVar0072689	100.35
PotVar0072691	100.35
PotVar0072578	100.35
PotVar0072727	101.2
PotVar0072913	101.2
PotVar0072996	102.05
solcap_snp_c1_12179	104.16
solcap_snp_c2_54325	104.16
solcap_snp_c2_21992	104.97
PotVar0107548	104.97
solcap_snp_c2_22076	104.97
PotVar0118734	104.97
PotVar0061794	104.97
PotVar0073127	104.97
PotVar0073119	104.97

PotVar0072968	104.97
PotVar0072670	104.97
PotVar0011079	104.97
PotVar0010985	104.97
PotVar0072482	104.97
solcap_snp_c1_11853	104.97
solcap_snp_c2_40084	104.97
PotVar0105198	104.97
PotVar0072477	104.97
solcap_snp_c2_29945	104.97
PotVar0105291	104.97
PotVar0072536	104.97
PotVar0072729	104.97
PotVar0072917	104.97
PotVar0073121	104.97
solcap_snp_c1_6585	104.97
solcap_snp_c2_20640	104.97
PotVar0011160	104.97
PotVar0011130	104.97
solcap_snp_c1_11866	104.97
solcap_snp_c2_40075	104.97
PotVar0011129	104.97
PotVar0105281	104.97
PotVar0105280	104.97
PotVar0061732	104.97
PotVar0107781	104.97
PotVar0107751	104.97
solcap_snp_c2_43241	105.29
PotVar0011188	106.24
PotVar0011164	106.24
PotVar0105194	106.77
PotVar0108690	108.67
solcap_snp_c2_48042	108.67

PotVar0108699	108.67
solcap_snp_c2_48041	109.63
solcap_snp_c2_3079	109.78
PotVar0108622	110.07
PotVar0108613	110.07
PotVar0108629	110.07
solcap_snp_c1_914	110.65
PotVar0105349	110.65
PotVar0105170	110.65
PotVar0105228	110.65
PotVar0105056	110.65
PotVar0108681	111.5
PotVar0108689	111.5
solcap_snp_c2_47952	112.81
PotVar0097335	113.13
PotVar0097174	113.13
PotVar0097065	113.13
PotVar0097245	113.13
PotVar0096975	113.13
PotVar0108630	113.25
solcap_snp_c1_8566	113.57
PotVar0122158	113.57
solcap_snp_c2_27715	113.57
solcap_snp_c2_27765	113.57
solcap_snp_c1_8549	113.57
solcap_snp_c2_27692	113.57
PotVar0097077	114.13
PotVar0097004	114.13
solcap_snp_c2_27762	114.49
solcap_snp_c2_3063	115.25
solcap_snp_c2_27719	118.19
solcap_snp_c1_8574	119.06

Chromosome 10	
Name	cM
solcap_snp_c2_950	0
solcap_snp_c1_307	0
PotVar0065809	0
PotVar0065664	0
PotVar0116620	1.41
PotVar0108387	11.87
solcap_snp_c2_24746	12.3
PotVar0107947	12.3

PotVar0107956	12.3
PotVar0116711	16.37
PotVar0116629	16.37
PotVar0116626	17.35
PotVar0065754	17.39
solcap_snp_c1_329	19.14
solcap_snp_c2_1305	19.14
solcap_snp_c2_1101	19.33
solcap_snp_c1_289	19.33
solcap_snp_c2_1093	19.33

PotVar0104004	19.76
PotVar0104010	19.76
PotVar0116820	20.43
PotVar0116672	20.43
solcap_snp_c1_16114	20.86
PotVar0120166	21.06
PotVar0104285	21.09
solcap_snp_c1_9799	21.97
solcap_snp_c2_32768	22.48
solcap_snp_c1_14048	22.48

solcap_snp_c1_14053	23.49
solcap_snp_c1_16651	23.49
solcap_snp_c2_826	23.63
solcap_snp_c1_6068	25.72
solcap_snp_c2_33008	26.58
solcap_snp_c2_33005	26.58
solcap_snp_c1_14531	27.02
solcap_snp_c2_24711	28.79
PotVar0108182	29.1
solcap_snp_c2_24747	29.1
PotVar0108271	29.1
solcap_snp_c2_24745	29.65
solcap_snp_c1_13025	30
solcap_snp_c1_13006	31.21
PotVar0108442	31.53
solcap_snp_c1_12594	31.78
solcap_snp_c2_42739	31.78
solcap_snp_c2_32790	31.97
PotVar0107984	32.73
PotVar0108276	32.73
PotVar0104021	34.02
PotVar0108273	34.03
PotVar0108060	34.03
solcap_snp_c2_19222	34.04
solcap_snp_c2_19223	34.04
solcap_snp_c2_19225	34.48
PotVar0108199	35.06
PotVar0107954	35.06
solcap_snp_c2_1263	35.06
PotVar0120148	35.22
PotVar0120165	35.22
PotVar0108099	35.34
solcap_snp_c2_57296	36.66
PotVar0029603	38.4
solcap_snp_c2_55085	39.11
PotVar0131630	39.72
PotVar0131645	40.4
PotVar0131644	40.4
solcap_snp_c2_32740	40.62
solcap_snp_c1_11801	40.62
PotVar0112028	40.62
PotVar0112050	40.62
PotVar0112053	40.62
solcap_snp_c2_40522	40.62

PotVar0007417	40.62
PotVar0099300	40.62
PotVar0004372	40.62
solcap_snp_c2_18265	40.62
PotVar0119513	40.62
PotVar0119518	40.62
PotVar0099304	40.62
PotVar0004373	40.62
PotVar0085827	40.62
PotVar0080928	40.62
PotVar0123577	40.62
solcap_snp_c1_11806	40.62
solcap_snp_c2_48927	41.26
solcap_snp_c2_40822	41.9
PotVar0096861	44.33
PotVar0051881	47.78
solcap_snp_c2_48929	47.78
solcap_snp_c2_48928	47.78
solcap_snp_c1_12027	47.78
PotVar0051833	47.78
PotVar0051902	47.78
PotVar0106287	47.78
solcap_snp_c2_38274	49.47
PotVar0051879	49.57
PotVar0051918	49.9
solcap_snp_c2_41395	51.76
solcap_snp_c2_41396	51.76
solcap_snp_c2_54951	51.76
solcap_snp_c2_41393	51.99
solcap_snp_c2_56514	52.89
solcap_snp_c1_11535	54.29
PotVar0119199	54.29
solcap_snp_c2_48926	54.79
solcap_snp_c1_12024	54.79
solcap_snp_c1_11991	54.79
solcap_snp_c2_57635	54.79
solcap_TUBER_SHAPE_c2_25527	54.79
solcap_TUBER_SHAPE_c2_25528	54.79
solcap_TUBER_SHAPE_c2_25529	54.79
solcap_snp_c2_45611	54.79
solcap_snp_c1_8021	54.79

solcap_snp_c2_25469	54.79
solcap_snp_c2_40762	55.48
solcap_snp_c2_40765	55.48
solcap_snp_c2_40763	55.48
solcap_snp_c1_16001	56.29
PotVar0132240	56.63
solcap_snp_c2_27806	56.68
solcap_snp_c2_56344	56.92
solcap_snp_c1_13524	56.92
solcap_TUBER_SHAPE_c2_25532	57.56
solcap_snp_c1_8020	57.88
solcap_snp_c1_16351	57.88
solcap_TUBER_SHAPE_c2_25530	57.88
solcap_TUBER_SHAPE_c2_25523	58.56
solcap_snp_c2_45603	59.35
solcap_snp_c2_56515	60.38
solcap_snp_c2_45612	61.03
PotVar0111683	62.35
PotVar0134570	62.52
solcap_snp_c1_15698	62.52
solcap_snp_c2_25549	63.21
solcap_snp_c1_8018	63.21
solcap_snp_c2_51215	64.22
solcap_snp_c2_51202	65.31
PotVar0004484	67.32
solcap_snp_c1_15218	72.56
solcap_snp_c2_27827	72.56
PotVar0004666	73.41
PotVar0004674	73.41
PotVar0004562	73.41
PotVar0004795	75.9
PotVar0004719	76.53
PotVar0004792	76.96
PotVar0004789	76.96
solcap_snp_c1_4989	76.96
solcap_snp_c1_14236	76.96
PotVar0005549	77.11
PotVar0005644	77.56
PotVar0005662	77.56
PotVar0004885	78.71
solcap_snp_c2_48127	78.92

solcap_snp_c1_9059	80.23
solcap_snp_c1_7187	80.66
PotVar0005589	81.1
PotVar0005681	81.31
solcap_snp_c1_7148	81.31
solcap_snp_c1_7165	81.31
PotVar0058133	81.31
PotVar0058175	81.31
PotVar0057954	81.31
PotVar0058146	81.52
PotVar0057984	82.39
PotVar0058094	82.39
PotVar0057840	83.59
PotVar0005590	83.71
PotVar0005666	83.71
PotVar0057888	83.91
PotVar0057846	83.91
PotVar0057905	84.23
solcap_snp_c1_9058	84.56
solcap_snp_c2_45239	84.87
PotVar0057605	84.87
PotVar0122838	84.87

PotVar0122771	84.87
PotVar0005256	85.24
PotVar0005016	85.5
PotVar0057431	85.64
PotVar0122647	86.09
PotVar0122661	86.09
PotVar0122870	86.09
PotVar0122826	86.09
PotVar0122866	89.6
PotVar0122679	90.03
PotVar0122649	90.03
PotVar0122859	90.03
PotVar0122765	90.03
PotVar0057719	90.88
PotVar0057860	91.11
PotVar0057721	92.07
PotVar0057500	92.31
PotVar0057635	92.31
solcap_snp_c2_28789	92.74
PotVar0057421	93.4
PotVar0122775	94.95
solcap_snp_c1_13243	95.38

PotVar0122789	95.38
PotVar0122668	96.09
PotVar0122690	96.09
solcap_snp_c1_12236	96.09
solcap_snp_c1_12234	96.53
solcap_snp_c1_12229	96.53
solcap_snp_c1_12224	96.75
PotVar0057515	99.74
PotVar0057514	100.65
PotVar0057644	100.65
solcap_snp_c2_28740	107.45
solcap_snp_c2_28697	108.75
PotVar0122769	109.83
PotVar0122635	109.83
solcap_snp_c2_45023	109.83

Chromosome 11	
Name	cM
PotVar0064140	0
PotVar0064625	0
PotVar0063963	8.02
solcap_snp_c2_13350	8.02
PotVar0063984	8.02
PotVar0063965	9.18
solcap_snp_c1_4296	9.6
PotVar0064617	10.04
PotVar0064549	10.04
PotVar0064694	10.04
PotVar0064699	10.04
PotVar0064474	10.04
solcap_snp_c1_4322	10.47
solcap_snp_c1_4319	10.47
PotVar0064182	11.16
solcap_snp_c1_4336	11.34
solcap_snp_c2_37194	12.2
PotVar0064663	12.46
PotVar0122617	12.63

PotVar0066165	12.63
solcap_snp_c1_4347	15.44
solcap_snp_c2_33657	19.36
PotVar0066338	19.36
PotVar0066186	20.67
PotVar0066210	20.67
PotVar0066142	20.67
PotVar0064787	20.81
PotVar0066219	22.35
PotVar0064963	23.53
PotVar0067013	23.53
PotVar0066299	23.85
PotVar0064473	24.96
PotVar0066476	28.21
PotVar0066709	28.21
PotVar0067177	28.21
PotVar0067029	28.21
PotVar0067330	29.08
PotVar0067381	29.08
PotVar0067565	29.52
PotVar0067682	29.52

solcap_snp_c2_6173	29.94
PotVar0067403	30.37
PotVar0110497	30.37
PotVar0067477	30.44
PotVar0067345	30.44
PotVar0067018	30.85
PotVar0067025	30.85
PotVar0067303	30.85
PotVar0067187	30.85
PotVar0067347	31.55
PotVar0067438	31.55
PotVar0110434	32.17
PotVar0105739	35.25
PotVar0105649	35.25
solcap_snp_c1_2314	35.3
PotVar0105481	37.1
PotVar0105750	37.1
PotVar0106272	37.1
PotVar0067664	37.1
PotVar0105904	37.1
PotVar0106051	39.1

PotVar0106025	39.1
solcap_snp_c1_14083	39.1
solcap_snp_c1_16496	39.53
solcap_snp_c1_11246	40.41
solcap_snp_c2_20947	40.41
solcap_snp_c2_20941	40.41
PotVar0106087	42.51
solcap_snp_c2_37638	42.51
solcap_snp_c2_57917	42.73
solcap_snp_c1_16301	43.37
PotVar0106089	43.37
PotVar0106072	43.37
solcap_snp_c2_21053	46.1
PotVar0058600	46.1
solcap_snp_c1_7658	46.44
PotVar0105987	47.17
PotVar0058653	48.62
solcap_snp_c2_23921	48.82
PotVar0105735	49.7
PotVar0066337	49.7
PotVar0105694	50.97
solcap_snp_c2_20946	52.27
solcap_snp_c1_6644	52.27
PotVar0059041	52.47
PotVar0060167	52.47
solcap_snp_c2_20953	52.79
PotVar0059223	53.71
PotVar0059116	53.81
solcap_snp_c2_24318	53.89
PotVar0059988	53.89
PotVar0060007	53.89
PotVar0059286	54.56
PotVar0059315	54.56
PotVar0058597	54.93
PotVar0059581	55.85
PotVar0059692	55.85
PotVar0059736	55.85
PotVar0059554	55.85
PotVar0059121	55.89
solcap_snp_c2_49311	56.05
PotVar0059889	56.28
PotVar0059714	56.92
PotVar0059682	56.92
PotVar0059394	57.01

PotVar0058763	57.16
solcap_snp_c2_2896	57.16
solcap_snp_c2_12297	57.78
PotVar0058578	58.6
PotVar0058729	58.7
PotVar0059284	61.49
PotVar0059055	61.85
PotVar0059608	61.92
PotVar0059886	61.92
PotVar0059811	61.92
PotVar0059222	62.12
PotVar0059351	62.12
solcap_snp_c2_12276	62.83
PotVar0059951	62.83
PotVar0059796	64.77
PotVar0059350	65.56
PotVar0059593	65.56
PotVar0059779	65.56
PotVar0060119	65.56
PotVar0060181	65.56
solcap_snp_c2_32997	65.56
solcap_snp_c2_32994	65.56
PotVar0060232	65.56
PotVar0059280	65.56
PotVar0059677	66.07
PotVar0059598	66.07
PotVar0059401	66.62
PotVar0060133	67.48
solcap_snp_c2_53682	67.48
solcap_snp_c2_56630	67.64
solcap_snp_c2_49294	67.91
PotVar0060023	67.91
solcap_snp_c2_53678	67.91
PotVar0059066	68.5
PotVar0059128	68.93
PotVar0059696	70.23
PotVar0060154	71.09
solcap_snp_c1_15655	71.09
PotVar0060183	71.09
solcap_snp_c2_56623	73.91
PotVar0060312	73.91
solcap_snp_c2_33911	73.91
solcap_snp_c2_32337	73.91
solcap_snp_c2_29089	73.91

solcap_snp_c2_29096	73.91
solcap_snp_c1_3992	75.01
PotVar0060365	75.18
solcap_snp_c2_12263	75.32
PotVar0060051	75.32
PotVar0059973	75.32
PotVar0060091	75.32
solcap_snp_c2_32999	75.32
PotVar0060082	75.32
solcap_snp_c2_33917	76.55
PotVar0130698	77.15
PotVar0054040	77.46
PotVar0060496	77.52
solcap_snp_c2_56629	77.57
solcap_snp_c2_56627	77.57
solcap_snp_c2_57107	77.57
PotVar0059933	77.57
solcap_snp_c2_12259	77.57
PotVar0054058	77.97
PotVar0054079	77.97
PotVar0021602	78.98
PotVar0101542	78.98
PotVar0101550	78.98
PotVar0113358	78.98
PotVar0061519	79.42
solcap_snp_c2_50977	79.42
PotVar0060273	79.85
solcap_snp_c2_33916	79.85
PotVar0060548	79.85
solcap_snp_c2_29088	79.85
solcap_snp_c2_29113	79.85
PotVar0054261	80.59
solcap_snp_c2_37586	80.84
PotVar0054060	80.99
solcap_snp_c2_50332	81.02
solcap_snp_c2_29434	81.02
PotVar0054073	81.27
solcap_snp_c2_11364	81.28
solcap_snp_c2_11366	81.28
PotVar0061347	82.02
PotVar0053942	82.12
solcap_snp_c2_57617	82.12
solcap_snp_c2_50980	82.12
PotVar0113312	82.12

solcap_snp_c2_31444	82.29
PotVar0005842	82.44
PotVar0005888	82.44
solcap_snp_c2_41084	82.78
PotVar0054330	82.78
PotVar0054089	82.78
PotVar0005899	82.78
solcap_snp_c2_31472	83.16
solcap_snp_c1_9499	83.16
PotVar0021746	83.36
PotVar0021631	83.36
PotVar0130677	83.48
solcap_snp_c1_16325	83.48
PotVar0061719	83.78
PotVar0061379	83.78
solcap_snp_c2_4961	83.91
solcap_snp_c1_5940	83.91
solcap_snp_c1_16555	83.91
solcap_snp_c2_18245	83.91
solcap_snp_c2_18526	83.91
solcap_snp_c1_14951	83.91
PotVar0021694	83.91
solcap_snp_c1_1781	83.91
solcap_snp_c1_1779	83.91
solcap_snp_c1_1778	83.91
solcap_snp_c2_44637	83.91
solcap_snp_c2_44635	83.91
PotVar0022012	83.91
solcap_snp_c1_1784	84.07
solcap_snp_c1_5411	84.07
solcap_snp_c2_16709	84.07
solcap_snp_c2_17332	84.07
solcap_snp_c2_4989	84.07
solcap_snp_c1_1774	84.07
PotVar0021898	84.07
solcap_snp_c2_4957	84.07
solcap_snp_c1_5942	84.53
solcap_snp_c1_16586	84.53
solcap_snp_c2_4993	84.76
PotVar0021994	84.76
solcap_snp_c2_2957	84.76
solcap_snp_c1_16585	84.76
solcap_snp_c2_44633	84.86
solcap_snp_c1_5965	84.98
PotVar0061673	85.78

solcap_snp_c1_12160	85.78
solcap_snp_c1_5716	85.78
PotVar0005841	85.78
PotVar0061578	86.1
PotVar0061301	86.22
solcap_snp_c1_1468	86.22
solcap_snp_c1_1470	86.22
PotVar0061300	86.22
solcap_snp_c2_4276	86.44
solcap_snp_c2_53718	86.44
solcap_snp_c2_30368	86.44
solcap_snp_c2_30367	86.44
solcap_snp_c1_12078	87.16
solcap_snp_c2_36581	87.16
solcap_snp_c2_55963	87.16
PotVar0110595	87.16
PotVar0110592	87.16
solcap_snp_c1_4371	87.16
solcap_snp_c2_13636	87.16
solcap_snp_c2_44269	87.33
PotVar0071276	87.33
solcap_snp_c2_3841	89.18
PotVar0047274	89.18
solcap_snp_c1_4359	89.18
solcap_snp_c2_41083	89.32
solcap_snp_c2_13633	89.8
solcap_snp_c2_56243	89.8
solcap_snp_c2_13632	89.8
solcap_snp_c2_51545	90.11
solcap_snp_c2_51544	90.11
solcap_snp_c2_49808	91.91
solcap_snp_c1_4822	92.23
solcap_snp_c2_3805	92.57
PotVar0112755	92.57
solcap_snp_c2_3679	92.67
solcap_snp_c2_54589	92.68
PotVar0112934	93.13
solcap_snp_c2_13593	93.89
solcap_snp_c2_13594	94.11
solcap_snp_c2_31433	94.11
solcap_snp_c2_31484	94.11
solcap_snp_c2_31443	94.11
solcap_snp_c2_14952	94.11
solcap_snp_c1_15081	94.11
solcap_snp_c2_14946	94.11

solcap_snp_c1_4376	94.98
solcap_snp_c2_13613	96.27
PotVar0110626	96.87
solcap_snp_c2_49812	97.79
PotVar0047211	98.44
PotVar0008666	98.64
PotVar0008668	98.64
PotVar0008826	99.07
PotVar0124397	99.5
PotVar0047409	100.14
PotVar0118030	100.37
PotVar0047229	100.93
PotVar0113183	101.45
solcap_snp_c2_3691	102.27
solcap_snp_c2_3823	102.27
PotVar0113080	102.27
PotVar0112873	102.27
PotVar0112981	102.27
PotVar0112613	102.27
PotVar0112532	102.27
PotVar0112664	102.27
PotVar0112736	102.27
PotVar0112743	102.27
PotVar0112967	102.27
PotVar0112987	102.27
PotVar0113261	102.27
PotVar0113195	102.27
Plocus_F35H_a2_LG11	102.37
Plocus_F35H_c2_LG11	102.37
Plocus_F35H_a1_LG11	102.37
PotVar0112167	102.7
PotVar0008128	102.7
PotVar0112185	102.7
PotVar0008113	102.7
PotVar0112275	103.14
PotVar0047372	103.18
PotVar0112668	103.24
PotVar0112779	103.24
PotVar0113131	103.24
PotVar0113193	103.24
PotVar0112357	103.24
PotVar0112455	103.24
PotVar0113005	103.24
PotVar0112971	103.24
PotVar0112957	103.99

solcap_snp_c1_1323	104.06
PotVar0113059	106.37
PotVar0112205	106.43
PotVar0112286	106.8
PotVar0112207	106.88
PotVar0008146	106.88
PotVar0008149	106.88
solcap_snp_c2_15388	106.88
PotVar0008184	107.71
PotVar0008553	107.85
solcap_snp_c1_4947	108.14
PotVar0008220	108.14
PotVar0008239	108.14
solcap_snp_c1_1271	108.21
PotVar0112968	108.21
solcap_snp_c2_56752	108.21
PotVar0008243	109.68
PotVar0112739	110.43
PotVar0112531	110.43
solcap_snp_c2_15268	111.66
PotVar0008207	111.9
solcap_snp_c2_22187	112.2
solcap_snp_c1_6964	112.2

solcap_snp_c2_15340	113.22
PotVar0008494	113.66
solcap_snp_c2_30298	113.66
PotVar0008262	113.66
PotVar0008237	114.96
PotVar0008194	115.28
solcap_snp_c2_15341	115.39
PotVar0008636	115.47
PotVar0008569	115.9
PotVar0008903	116.75
PotVar0008904	117.18
PotVar0008281	117.91
PotVar0008279	117.91
PotVar0008293	117.91
PotVar0130354	118.05
PotVar0130423	118.48
PotVar0124367	118.91
solcap_snp_c2_34229	119.77
PotVar0117920	120.63
PotVar0117899	120.63
solcap_snp_c2_34194	120.63
solcap_snp_c2_31579	120.94
PotVar0118016	121.09

solcap_snp_c2_34193	121.09
solcap_snp_c2_34191	121.09
solcap_snp_c2_34204	121.09
PotVar0118308	121.54
PotVar0118401	121.97
PotVar0008554	122.79
PotVar0117889	123.7
solcap_snp_c2_30297	125.82
PotVar0008637	126.3
PotVar0008380	127.58
PotVar0008447	128.44
PotVar0008511	128.87
PotVar0124374	130.26
PotVar0008887	132
PotVar0130497	132.44
PotVar0130503	132.44
PotVar0130324	132.44
PotVar0008860	133.72
solcap_snp_c2_43880	135.08
PotVar0130323	135.42
PotVar0118026	135.75
PotVar0118303	136.1

Chromosome 12	
Name	cM
PotVar0098059	0
solcap_snp_c2_24595	0.63
solcap_snp_c2_24536	4.31
PotVar0098080	4.31
PotVar0098277	4.31
PotVar0097963	4.31
PotVar0098047	4.31
PotVar0098087	4.31
PotVar0097922	5.28
PotVar0097926	5.28
PotVar0098023	5.28
PotVar0098373	6.59
PotVar0098367	7.03
PotVar0098245	7.88
PotVar0098172	10.75
PotVar0098280	10.75
PotVar0098129	10.75

PotVar0098260	14.27
PotVar0097929	14.27
PotVar0098257	14.27
PotVar0098049	14.27
PotVar0098071	14.37
PotVar0098029	14.37
PotVar0053656	14.47
PotVar0053573	15.59
PotVar0022107	16.5
PotVar0053636	16.96
solcap_snp_c2_16182	17.41
PotVar0053705	18.16
PotVar0053701	18.34
PotVar0068409	18.44
solcap_snp_c2_31338	19.76
solcap_snp_c1_8646	19.76
solcap_snp_c2_31337	19.76
PotVar0053907	19.92
PotVar0053841	19.92

PotVar0031150	20.16
PotVar0031559	20.16
PotVar0031644	20.16
PotVar0031118	20.16
PotVar0031194	20.16
PotVar0069242	20.16
PotVar0031212	20.16
PotVar0053629	20.62
PotVar0053659	20.62
solcap_snp_c2_39765	20.62
PotVar0053855	20.62
PotVar0068881	20.62
PotVar0068893	20.62
PotVar0068793	20.62
PotVar0031174	20.81
solcap_snp_c2_16204	21.24
PotVar0053640	21.24
PotVar0031093	21.25
PotVar0031195	21.25

PotVar0031564	21.25
PotVar0125939	21.68
PotVar0053859	21.68
PotVar0053790	21.68
PotVar0053791	21.68
PotVar0069011	21.68
PotVar0068642	21.68
PotVar0031023	21.68
PotVar0031664	21.68
PotVar0030968	21.68
PotVar0031039	21.68
PotVar0031117	21.68
PotVar0031277	21.68
PotVar0031560	21.68
PotVar0068972	21.68
PotVar0031645	21.68
PotVar0031514	21.68
PotVar0031207	21.68
PotVar0030960	21.68
PotVar0031147	21.68
PotVar0031136	21.68
PotVar0068822	21.68
PotVar0068849	21.68
PotVar0068584	21.68
PotVar0069135	21.68
PotVar0053739	21.68
PotVar0031211	21.68
PotVar0068890	21.68
PotVar0069075	21.68
PotVar0069136	21.68
PotVar0030982	21.68
PotVar0068587	21.68
PotVar0031599	22.54
PotVar0053857	23.68
PotVar0053914	23.68
PotVar0069155	23.84
PotVar0069259	23.84
PotVar0068428	23.84
PotVar0068889	23.84
solcap_snp_c1_8641	24.12
PotVar0031486	24.58
PotVar0031530	24.58
PotVar0031589	24.58
PotVar0068194	25.21
PotVar0068187	25.41

solcap_snp_c2_28012	25.6
PotVar0132363	27.24
PotVar0068383	27.24
PotVar0069139	27.24
PotVar0068447	27.24
PotVar0068253	27.24
PotVar0068388	27.77
solcap_snp_c2_24645	28.91
solcap_snp_c2_46296	29.14
solcap_snp_c2_46289	30.32
solcap_snp_c1_13767	30.32
solcap_snp_c2_46285	31.3
PotVar0068182	32.38
PotVar0061979	33.41
solcap_snp_c2_46299	33.49
solcap_snp_c2_40699	33.6
solcap_snp_c2_24650	34.09
PotVar0061959	34.46
PotVar0118812	34.96
solcap_snp_c2_34789	35.52
PotVar0061956	35.52
PotVar0118838	36.4
PotVar0118853	36.4
solcap_snp_c2_34762	36.4
PotVar0061934	36.4
solcap_snp_c2_34780	36.65
solcap_snp_c2_34806	37.94
PotVar0027783	38.1
PotVar0027729	38.1
PotVar0061899	38.5
PotVar0061906	38.6
solcap_snp_c2_27379	38.6
PotVar0027810	38.6
PotVar0027811	38.74
PotVar0027707	38.81
PotVar0027746	38.81
solcap_snp_c2_48900	38.81
PotVar0027678	39.24
PotVar0066128	40.1
solcap_snp_c2_44932	40.1
solcap_snp_c2_16286	40.1
solcap_snp_c2_45743	40.1
solcap_snp_c2_48391	40.1
PotVar0082752	40.1
solcap_snp_c2_57161	40.1

solcap_snp_c2_4214	40.1
PotVar0012947	40.1
PotVar0013114	40.1
PotVar0036483	40.1
PotVar0036410	40.1
solcap_snp_c1_10054	40.1
PotVar0012951	40.82
solcap_snp_c1_8914	40.82
PotVar0066107	41
solcap_snp_c2_44928	41
solcap_snp_c2_44926	41
PotVar0044799	41.16
PotVar0118860	41.31
solcap_snp_c2_57453	41.38
solcap_snp_c2_48890	41.74
solcap_snp_c2_16299	41.75
PotVar0044792	41.75
solcap_snp_c2_10055	41.75
PotVar0014978	41.75
solcap_snp_c2_27773	41.75
PotVar0012912	41.75
PotVar0036461	41.75
solcap_snp_c2_27771	41.75
PotVar0027702	42.08
solcap_snp_c2_53383	42.08
solcap_snp_c1_403	42.08
PotVar0037501	42.1
PotVar0037523	42.1
solcap_snp_c2_54917	42.19
solcap_snp_c2_3185	42.19
PotVar0027759	42.19
PotVar0019164	42.32
PotVar0036430	42.32
PotVar0087430	42.32
PotVar0095247	42.32
solcap_snp_c2_49334	42.32
PotVar0019161	42.32
solcap_snp_c2_48013	42.42
solcap_snp_c1_14767	42.42
solcap_snp_c1_8913	42.42
solcap_snp_c1_13066	42.42
PotVar0036521	42.42
solcap_snp_c1_16695	42.42
PotVar0027781	42.42
PotVar0027766	42.42

solcap_snp_c1_10050	42.42
PotVar0031913	42.42
PotVar0031882	42.42
PotVar0036535	42.42
solcap_snp_c2_30296	42.42
PotVar0036451	42.42
PotVar0012999	42.52
PotVar0012983	42.52
PotVar0037640	43.44
PotVar0037409	43.66
PotVar0031836	44.28
solcap_snp_c2_43152	45.7
solcap_snp_c2_17613	46.55
solcap_snp_c2_18788	47.65
solcap_snp_c2_23308	48.74
solcap_snp_c2_18816	48.74
solcap_snp_c2_18836	49.33
PotVar0109205	49.33
solcap_snp_c2_18848	49.33
PotVar0109143	50.22
PotVar0109080	50.22
PotVar0110871	51.13
PotVar0110849	51.13
PotVar0110868	51.64
solcap_snp_c2_23284	53.6
PotVar0110859	53.6
PotVar0107187	53.6
PotVar0110843	54
solcap_snp_c1_11644	54.65
PotVar0107214	54.65
PotVar0107233	55.05
PotVar0107181	55.15
PotVar0107182	55.15

PotVar0107202	55.15
PotVar0104537	56.57
solcap_snp_c2_32466	57
solcap_snp_c2_48483	57.35
PotVar0104542	58.49
solcap_snp_c2_32467	58.49
solcap_snp_c2_32519	58.49
PotVar0107177	58.49
PotVar0104553	58.49
solcap_snp_c2_32082	60.02
PotVar0104561	61.38
solcap_snp_c2_6469	62.21
PotVar0124993	62.25
solcap_snp_c2_32482	62.25
PotVar0124931	62.25
solcap_snp_c1_2350	62.81
solcap_snp_c2_32077	63.58
solcap_snp_c2_6500	64.85
solcap_snp_c2_6466	64.85
PotVar0018635	66.17
solcap_snp_c1_2366	66.85
PotVar0018646	68.53
PotVar0018524	68.69
PotVar0018463	68.69
PotVar0018476	68.84
PotVar0018564	69.51
PotVar0018569	69.52
PotVar0018389	69.52
PotVar0018377	69.52
PotVar0018406	69.74
PotVar0018214	69.8
PotVar0018263	70.5
PotVar0018140	70.67

solcap_snp_c1_2689	71.4
PotVar0018060	72.74
solcap_snp_c2_7860	72.74
PotVar0053309	72.76
PotVar0018194	72.76
PotVar0053463	72.98
PotVar0053461	73.79
PotVar0053387	73.79
PotVar0052761	74.99
solcap_snp_c1_13697	76.32
PotVar0052987	76.32
PotVar0052458	76.32
PotVar0052776	76.32
PotVar0052873	76.32
solcap_snp_c2_5440	76.32
solcap_snp_c2_5443	76.32
PotVar0052756	77.2
PotVar0052632	77.61
PotVar0052628	77.61
solcap_snp_c1_1954	78.3
PotVar0052061	79.4
solcap_snp_c1_1985	79.84
PotVar0052399	80.15
PotVar0052662	80.15
solcap_snp_c2_5307	80.63
PotVar0052083	80.97
PotVar0052447	80.97
PotVar0052284	81.03
solcap_snp_c1_1944	81.31
PotVar0052766	82.7
PotVar0053344	83.13
PotVar0053291	83.13

Appendix 10: Updated physical positions in chromosome 3

In addition to the comparison the map positions with the physical positions, the physical positions themselves can be evaluated by such a comparison. In Programmes, Data and Assumptions, it was mentioned that during this thesis an updated version of the physical positions became available. In most cases this only involved an update of previously unknown physical positions, but one chromosome, chromosome 3, did undergo major revisions. In the region from 4mbp to 5mbp, the physical positions are inverted when the two versions are compared (Figure 32). This can be clearly seen in both parents while looking at the SxN markers. Although it appears that on three homologs the physical positions are in correspondence with the map positions, on one homolog this is not the case. It is therefore expected that the physical positions will likely change once again when a new update becomes available.

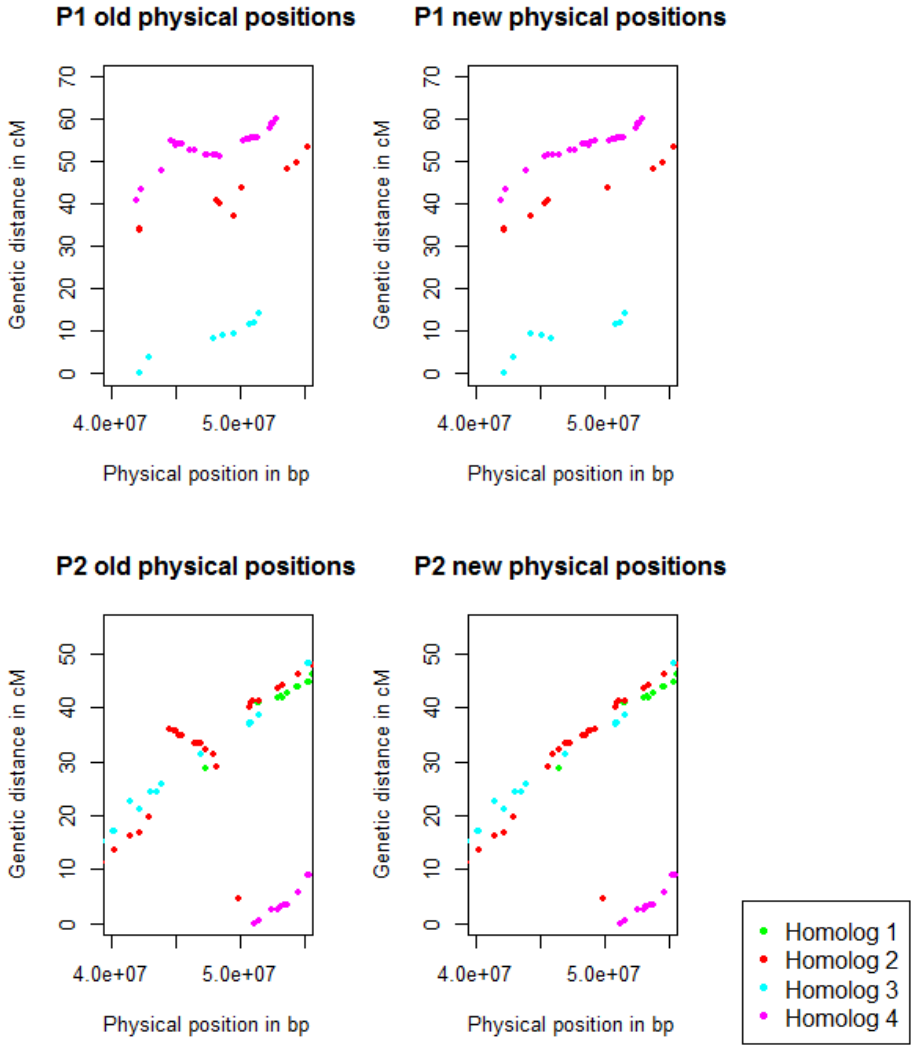
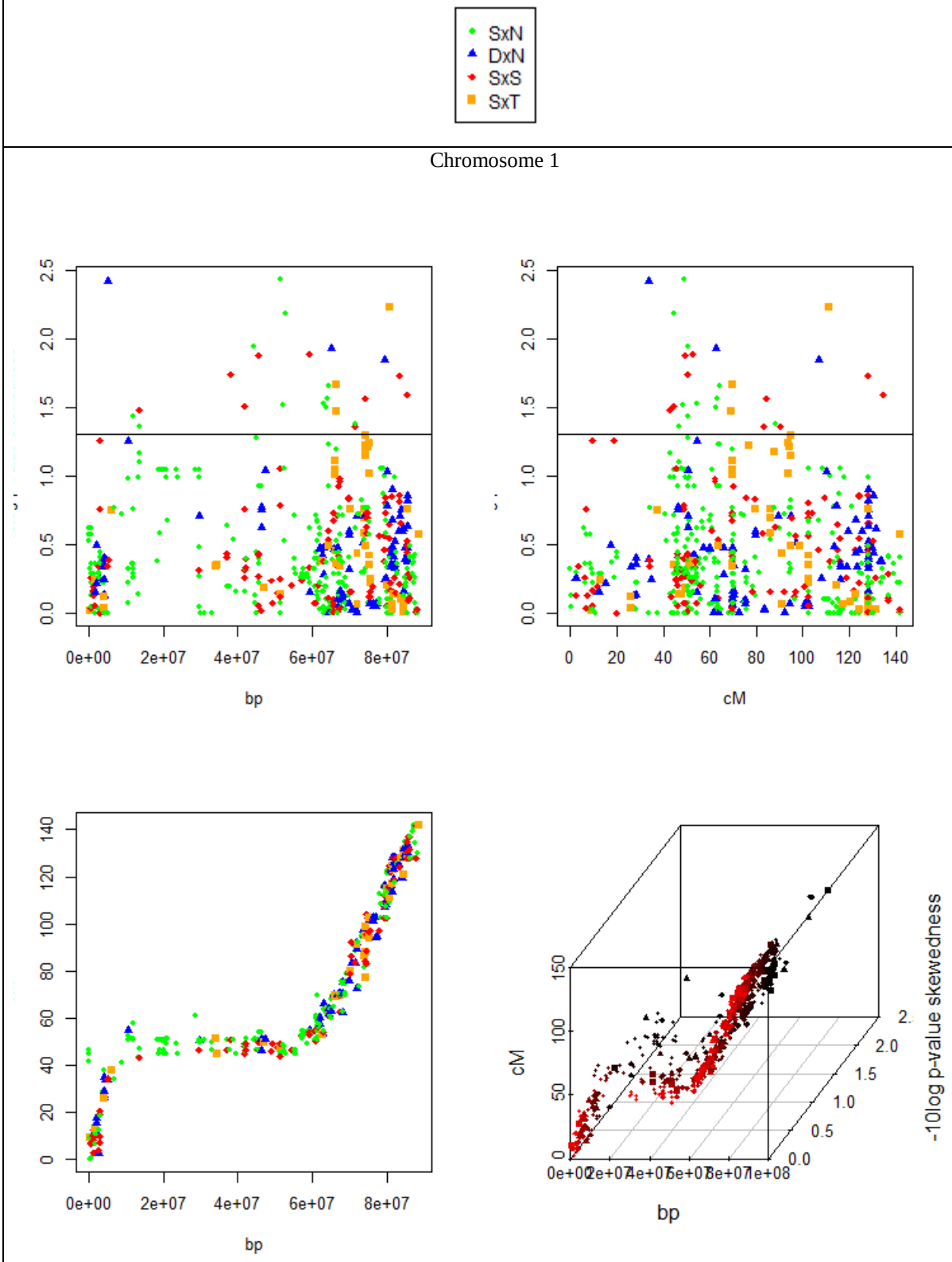


Figure 32. The comparison of the physical positions and SxN maps in the region of chromosome 3 where the physical positions were updated. In the region from 4mbp to 5mbp the physical positions were inverted.

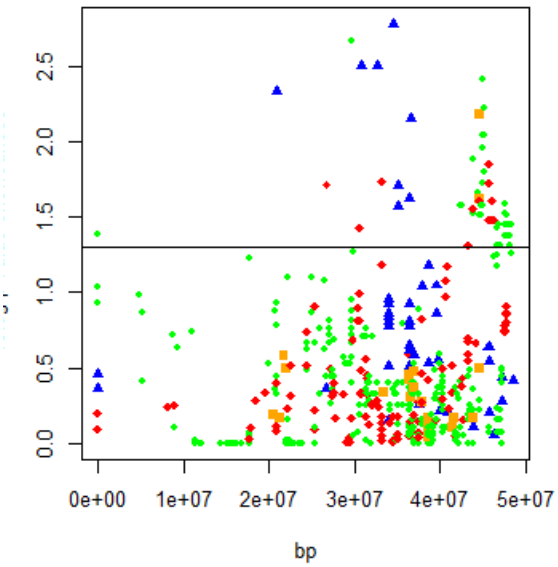
Appendix 11: Segregation distortion of markers on the integrated map

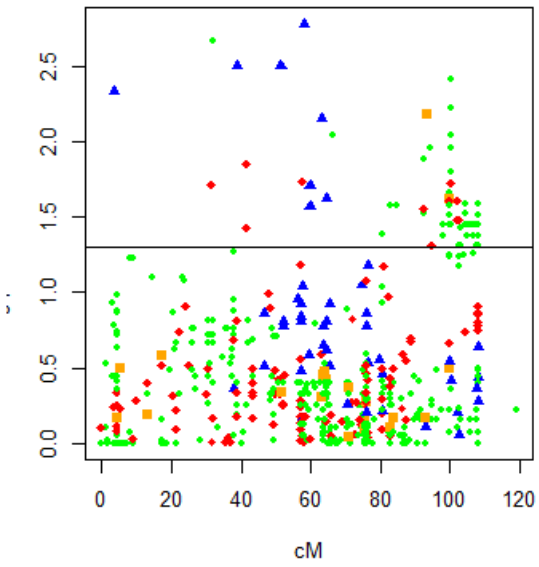
According to literature, the self- incompatibility locus of potato is located on chromosome 1 (Gebhardt *et al.*, 1991).The self- incompatibility caused skewed segregation in this region. To investigate if this is also true in this population, the skewedness of the markers on the integrated map were calculated. The SxN markers were tested for skewedness by using a Binomial test, while the other marker types were tested with a Chi-square test, with the null-hypothesis that markers followed the Mendelian segregation ratios (Table 1). From plotting the skewedness against the map positions and physical positions, the region of the self-incompatibility gene could not be found. It would be interesting to map the Segregation Distortion Loci (SDL) in a similar way as mapping a QTL (Vogl & Xu, 2000), however both QTL and SDL mapping was beyond the scope of this thesis.

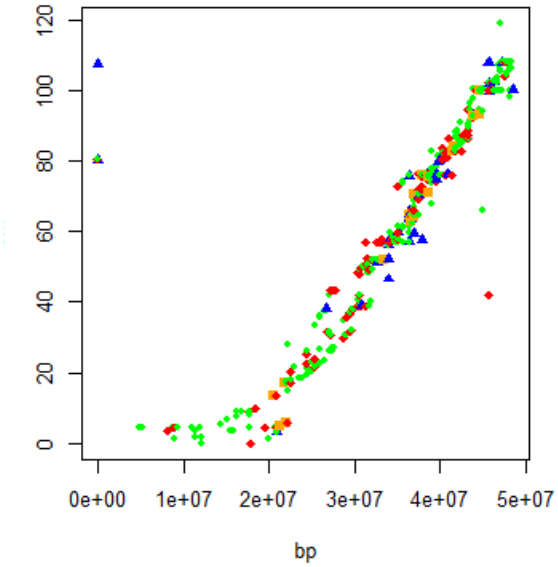
Figure 33, next page. Skewedness of the integrated chromosomes. The top left plot shows the 10log p-value for skewedness against the physical positions. The top right plot shows the 10log p-value for skewedness against the map positions. The bottom left plot shows the map positions against the physical positions. The bottom right shows a 3d plot of the three.

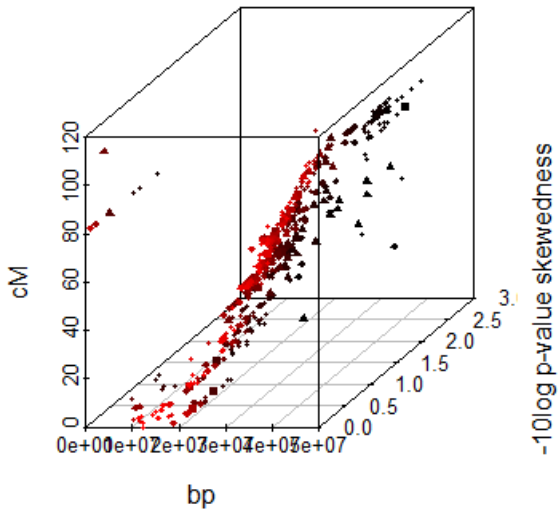

SxN
DxN
SxS
SxT
Chromosome 1
0.0
0.5
1.0
1.5
2.0
2.5
0e+00
2e+07
4e+07
6e+07
8e+07
bp
0
20
40
60
80
100
120
140
cM
0
50
100
150
-10log p-value skewedness

Chromosome 2

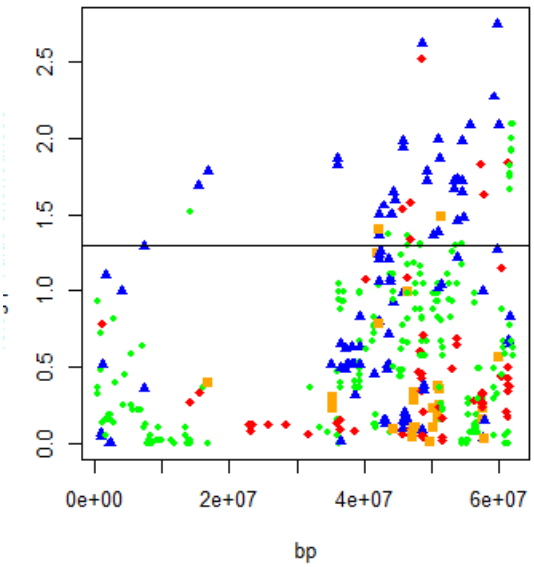


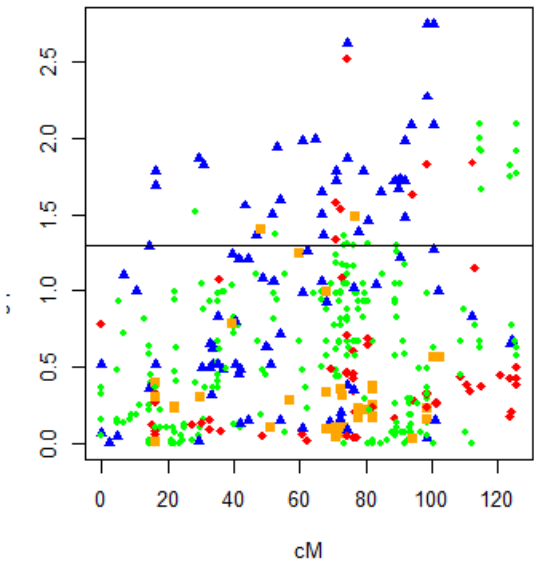


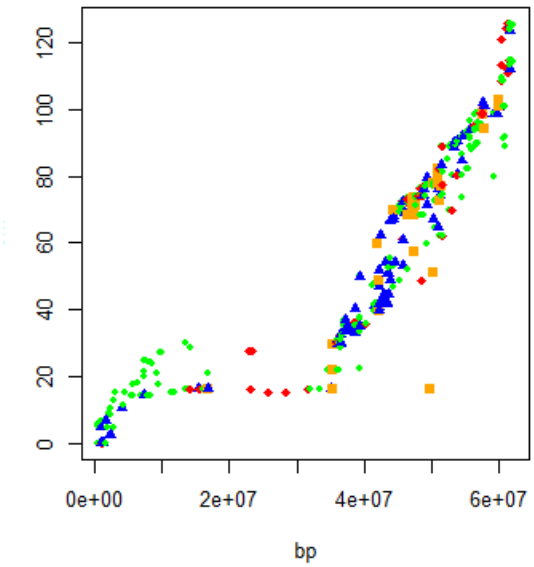


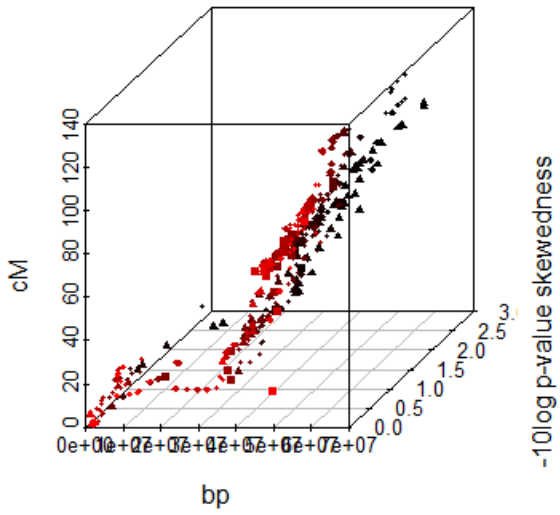


Chromosome 3

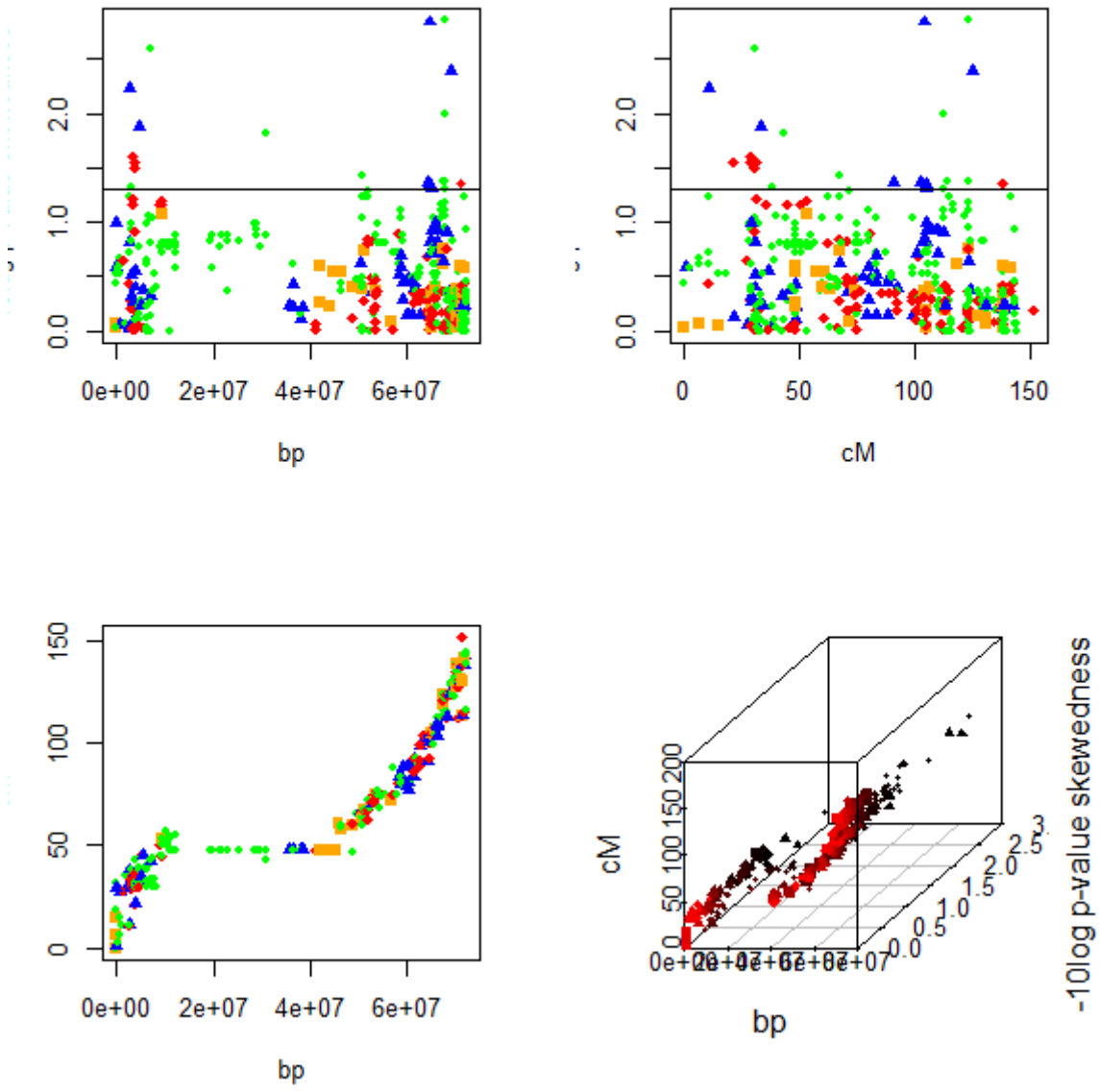




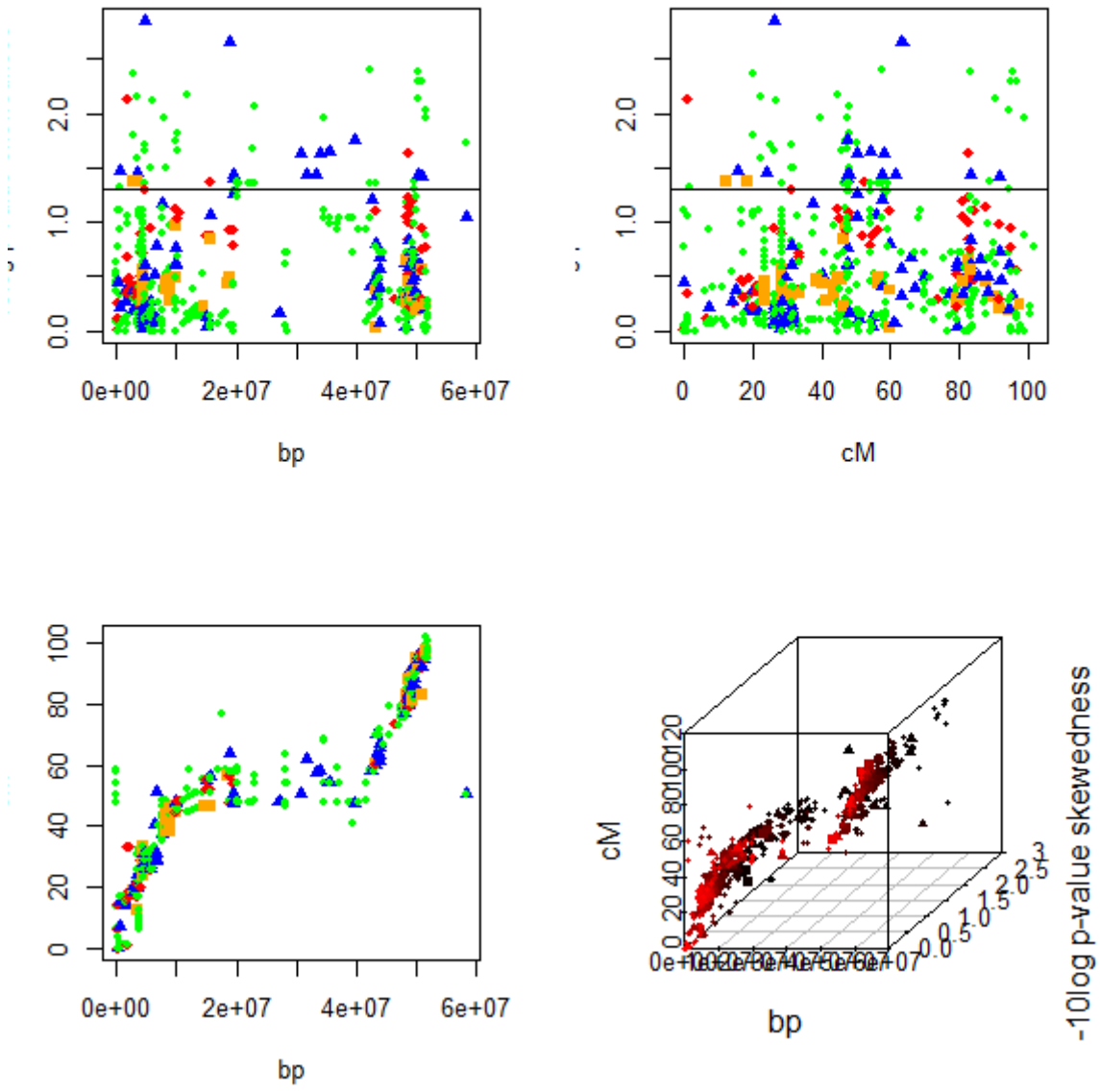




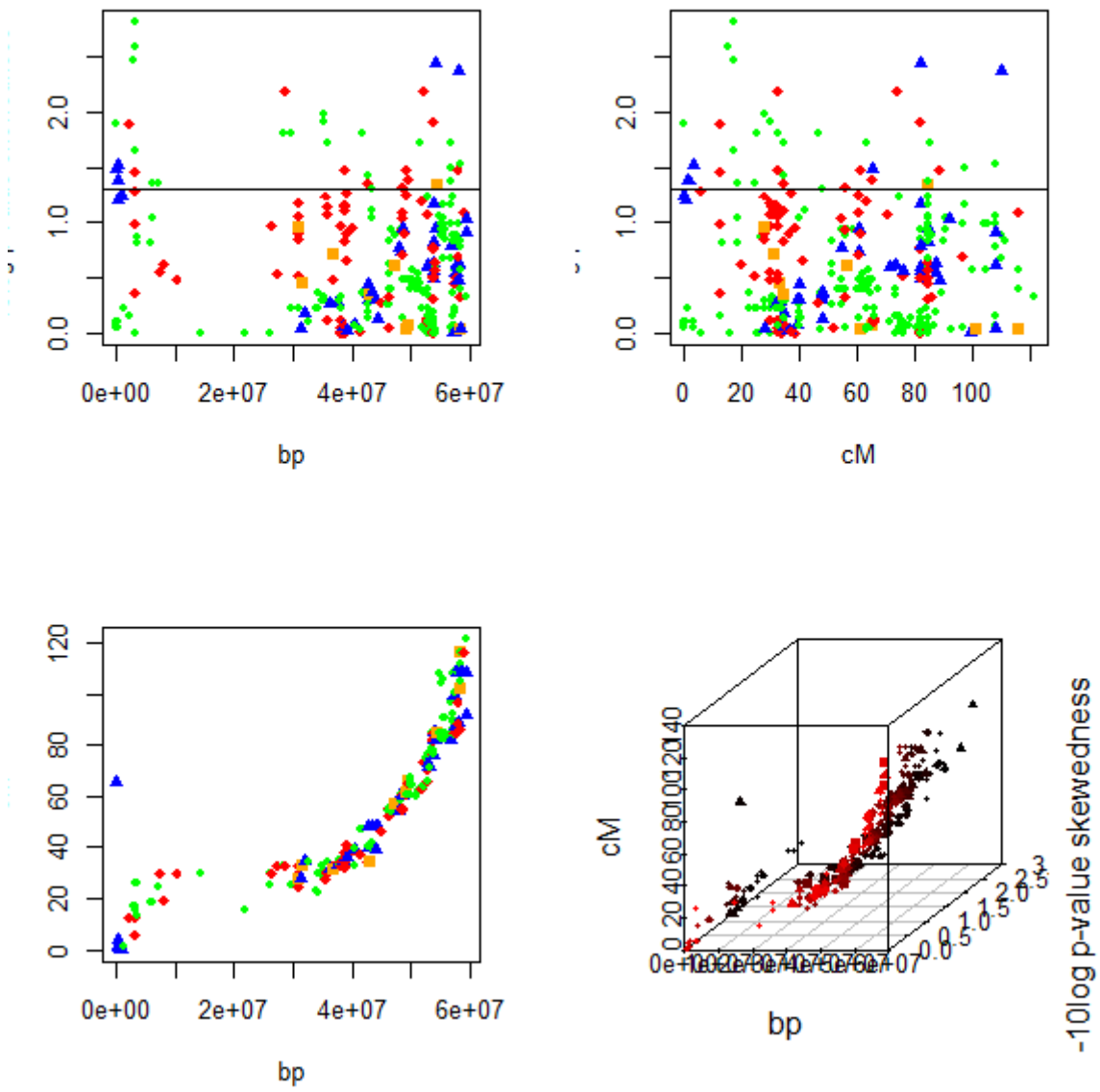
Chromosome 4



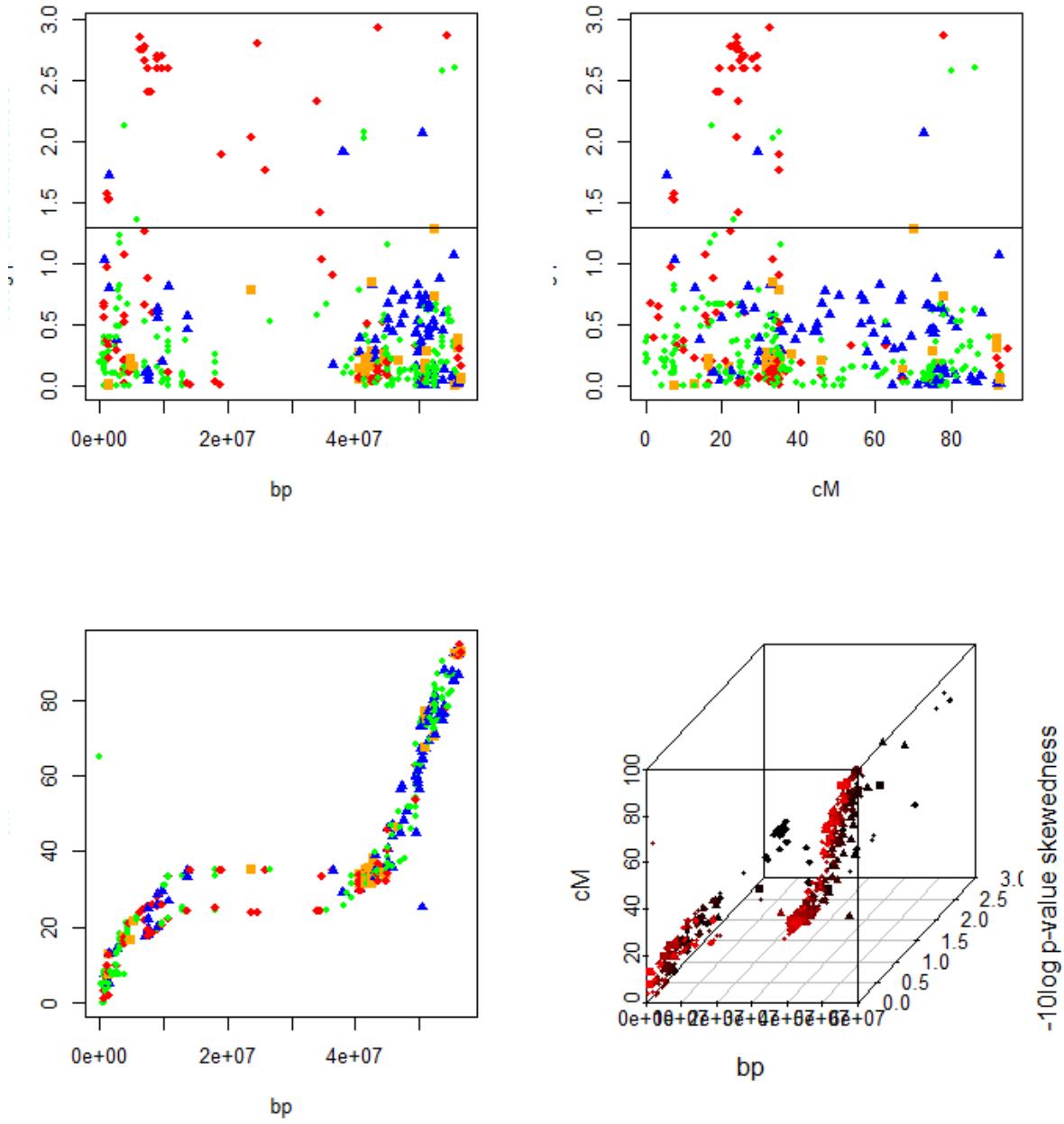
Chromosome 5



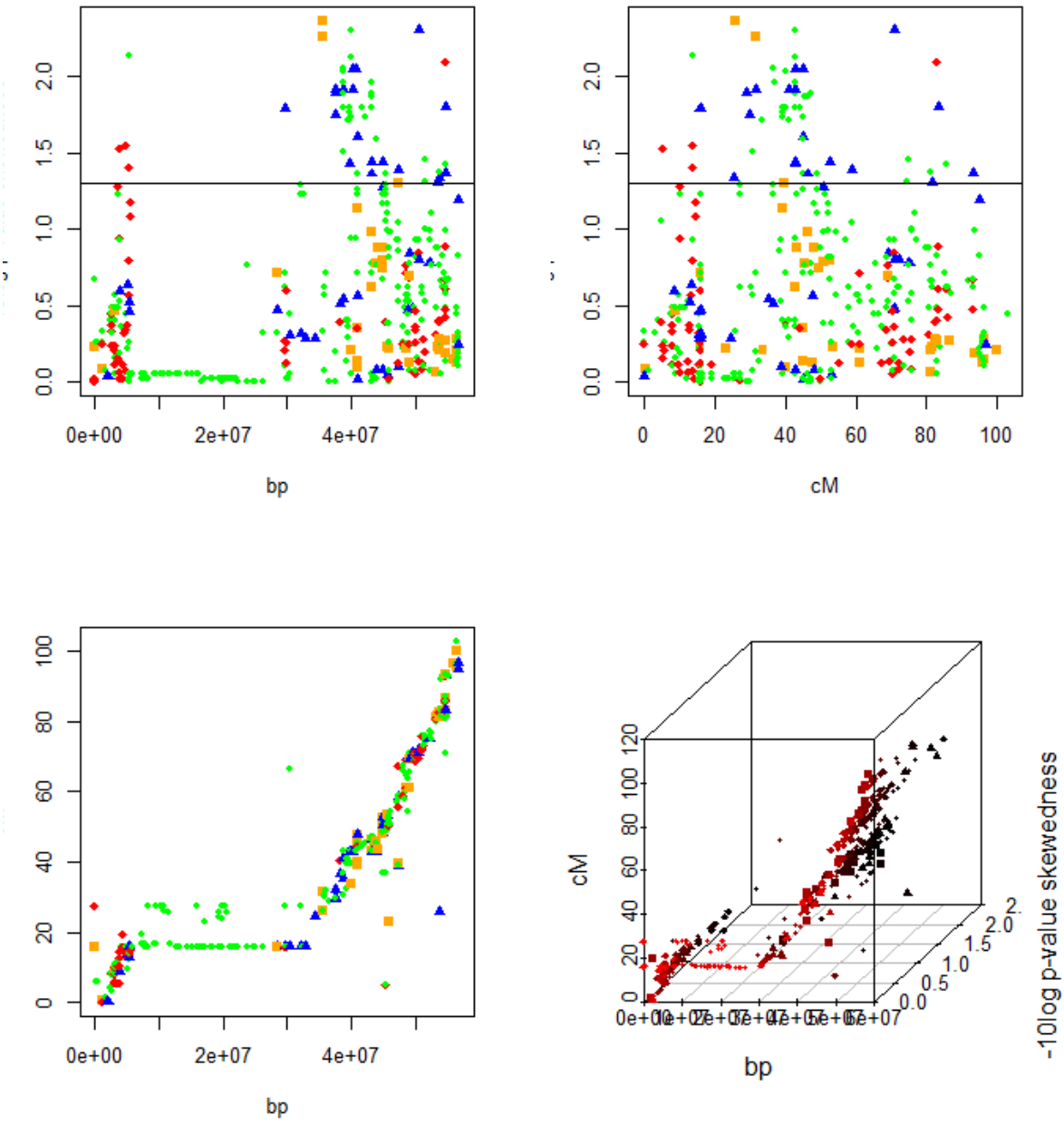
Chromosome 6



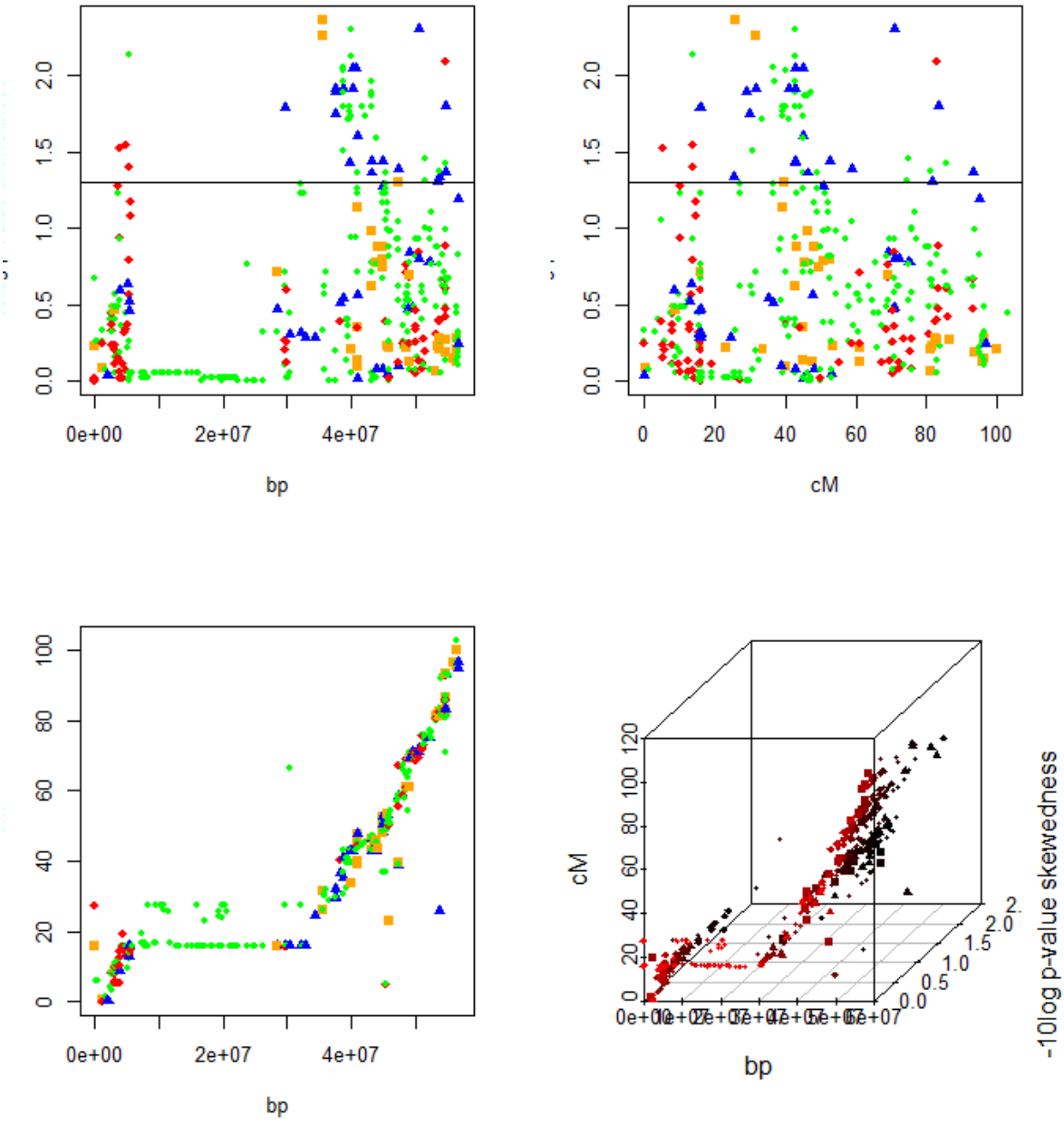
Chromosome 7



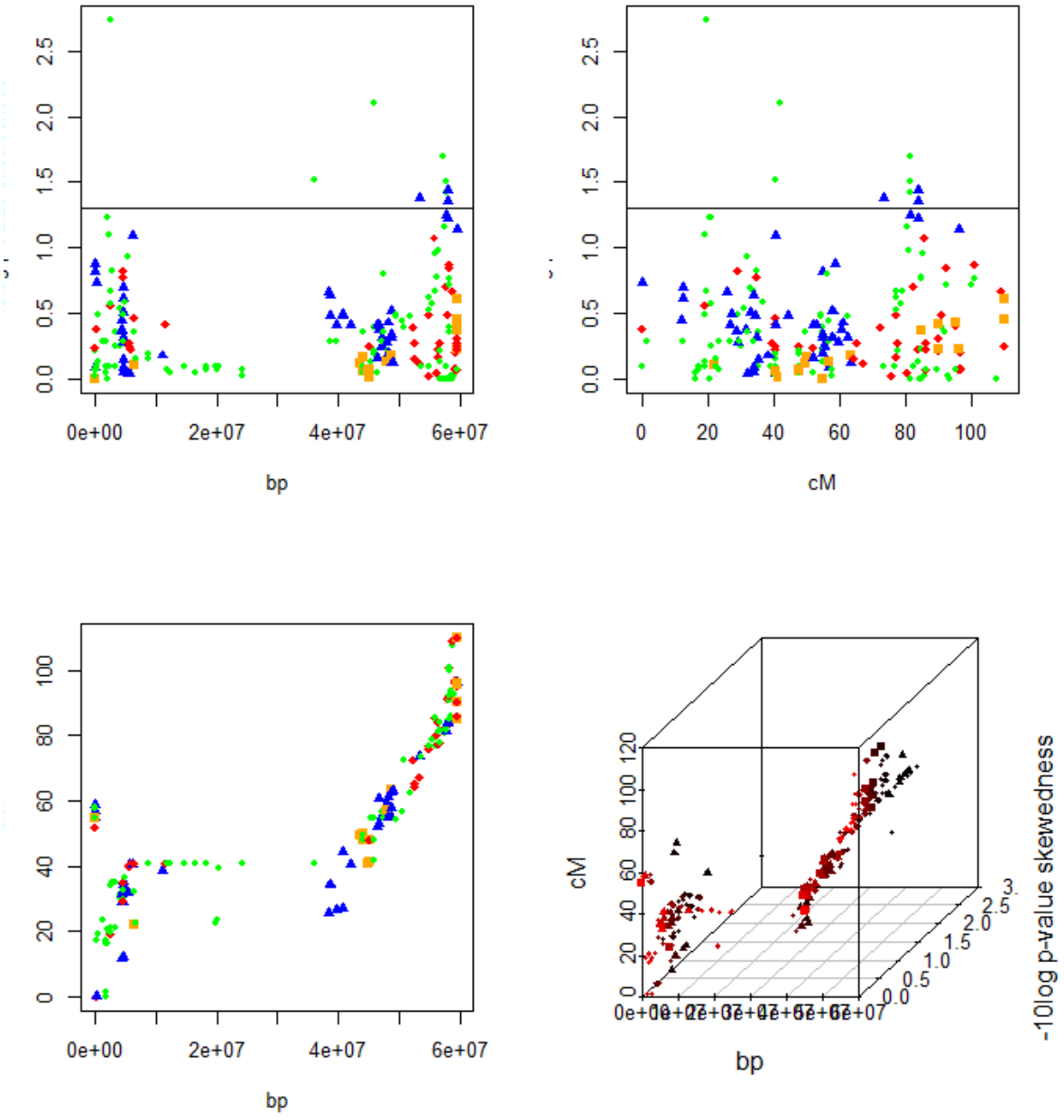
Chromosome 8



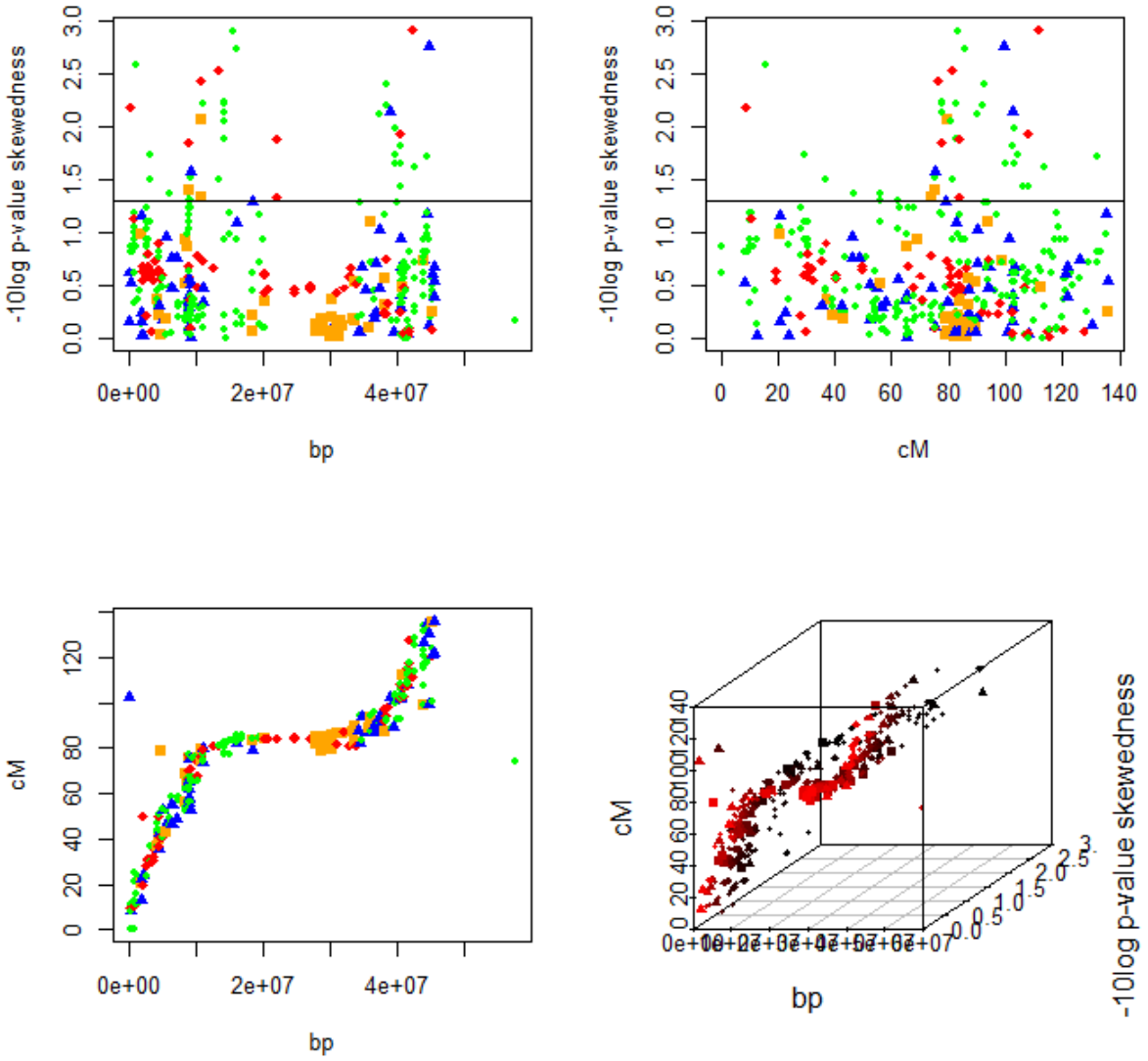
Chromosome 9



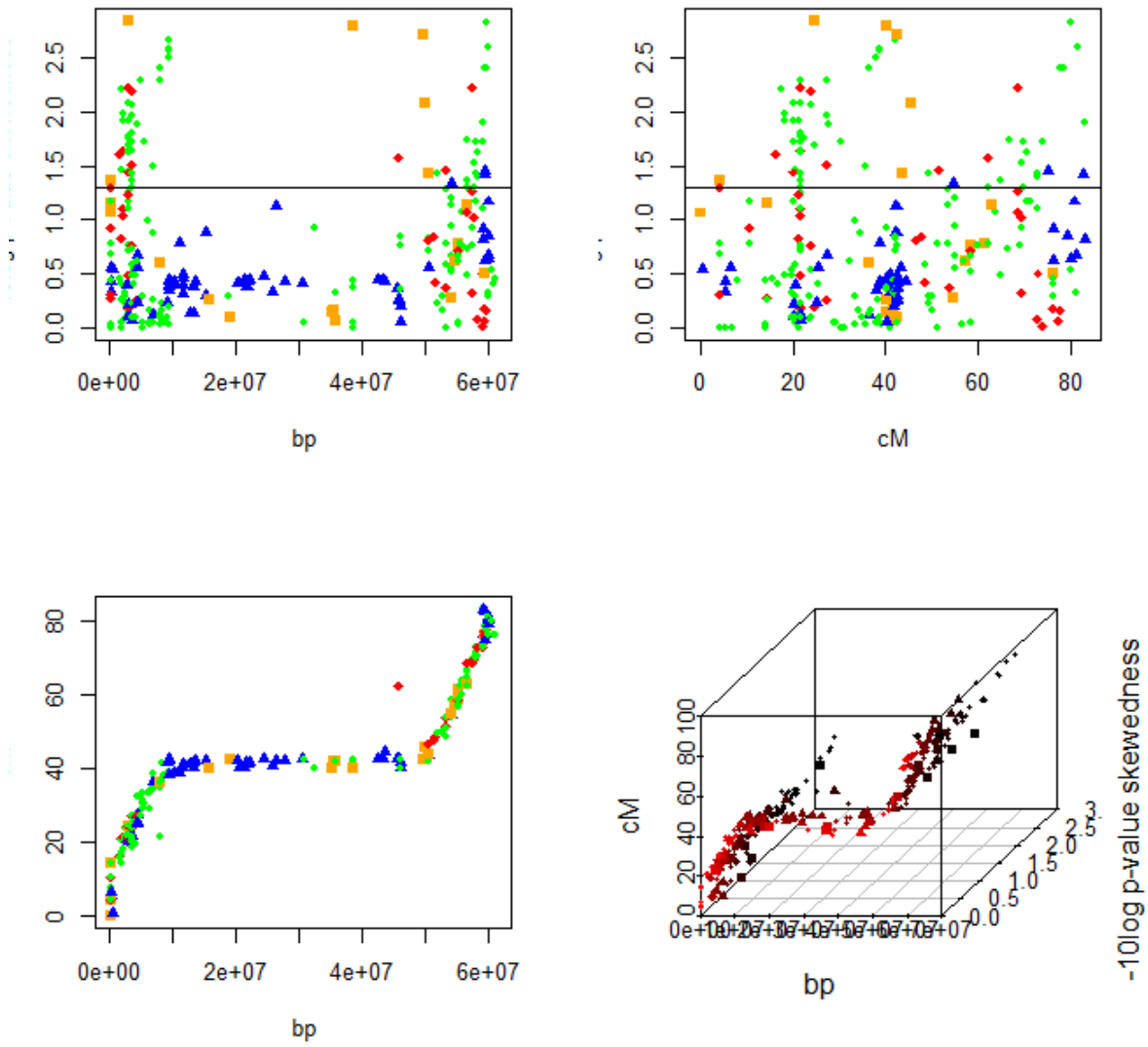
Chromosome 10



Chromosome 11



Chromosome 12



Appendix 12: Summary r and LOD-estimators

Maximum likelihood (ML) is a statistical method for estimating parameters. By obtaining the maximum likelihood value, the estimate of the parameter will be good. To find the maximum likelihood, the likelihood function is differentiated and equated to zero. Since the log-likelihood is much easier to differentiate than the likelihood itself, this is in general done.

Here the exact ML-estimators of the recombination frequency for different marker segregation type combinations are given when this could be estimated by the maximum likelihood method (Table 20). Although many scientists have calculated the recombination frequencies of marker types, no paper has shown yet how they came to the ML estimator for the recombination frequency for the different marker segregation type pairs for tetraploids. Furthermore, the LOD-score, which is based on the likelihood ratio, is also given for those recombination frequency estimates. How the ML estimator and the LOD-score is obtained is explained in Figure 34 based on Van Ooijen & Jansen (2013), after which the combinations of the marker segregation types follow.

Table 20. The maximum likelihood estimators or likelihood functions of the different marker type and phase combinations. The table is divided in two parts, following the exact analytical estimator and the iterative approach. The multinomial nominal coefficient and 1/2N do not depend on r and are therefore abbreviated to MC and left out in equations. x=dosage of marker A; y=dosage of maker B; log=log10.

Exact approach					
Marker segregation type	*Phase*	*Dosages*	*nxy*	*ML estimator of* $\hat{r}$	*LOD*
Simplex x Nulliplex Simplex Nulliplex	Coupling	Aaaa x aaaa Bbbb x bbbb	n10=1/2r n00=1/2(1-r) n01=1/2r n11=1/2(1-r)	(n01+n10)/ (n10+n01+n10+n11)	ntot*log(2/ntot)+(n00+n11)log(n00+n11)+(n10+n01)log(n10+n01)
	Repulsion	Aaaa x aaaa bBbb x bbbb	n10=1/6+1/6(1-r) n11=1/6+1/6r n01=1/6+1/6(1-r) n00=1/6+1/6r	(2(n00+n11)-(n10+n01))/ (n10+n01+n10+n11)	ntot*log(2/ntot)+(n00+n11)log(n00+n11)+(n10+n01)log(n10+n01)
	Repulsion under complete preferential pairing	Aaaa x aaaa bBbb x bbbb	n10=1/2(1-r) n00=1/2r n01=1/2(1-r) n11=1/2r	(n11+n00)/ (n10+n01+n10+n11)	ntot*log(2/ntot)+(n00+n11)log(n00+n11)+(n10+n01)log(n10+n01)
Duplex x Nulliplex Simplex Nulliplex	Coupling	AAaa x aaaa Bbbb x bbbb	n10=1/6+1/6(1-r) n11=1/6r+1/3 n21=1/6(1-r) n00=1/6(1-r) n20=1/3r n01=1/3r	(n20+n01)/ (n00+n21+n20+n01)	(n00+n21+n20+n01)*log(2)+(n00+n21)*log(1-r)+(n20+n01)*log(r)

	Repulsion	AAaa x aaaa bbBb x bbbb	n10=1/3 n11=1/3 n21=1/6r n00=1/6r n20=1/3 n01=1/6(1-r)	(n00+n21)/ (n20+n01+n00+n21)	(n00+n21+n20+n01)*log(2)+(n00+n21)*log(r)+(n20+n01)*log(1-r)
Simplex x Simplex Simplex Nulliplex	Coupling	Aaaa x Aaaa Bbbb x bbbb	n10=1/4 n00=1/4 (1-r) n01=1/4r n11=1/4 n21=1/4 (1-r) n20=1/4r	(n01+n20)/(n21+n00+n01+n20)	(n21+n00+n01+n20)*log(2/(n21+n00+n01+n20))+(n01+n20)*log(n01+n20)+ (n01+n20)*log(n21+n00)
	Repulsion	Aaaa x Aaaa bBbb x bbbb	n10=1/4 n00=1/12+1/12r n01=1/12+1/12(1-r) n11=1/4 n21=1/12+1/12r n20=1/12+1/12(1-r)	(2(n00+n21)-(n01+n20))/ (n01+n20+n00+n21)	(n01+n20+n00+n21)*log(2/(n01+n20+n00+n21))+(n01+n20)*log(n01+n20)+(n00+n21)*log(n00+n21)
Simplex x Triplex Simplex Nulliplex	Coupling	Aaaa x AAAa Bbbb x bbbb	n31=1/4-1/4r n20=1/4 n30=1/4r n11=1/4r n21=1/4 n10=1/4-1/4r	n30+n11/(n30+n11+n31+n10)	log((1/4*(n20+n11+n21+n10+n31+n30)*(1-r)*(n11+n30)*r*(n10+n31))/(1/4*(n20+n11+n21+n10+n31+n30)*(1-1/2)*(n11+n30)*1/2*(n10+n31)))
	Repulsion	Aaaa x AAAa bBbb bbbb	n31= 1/12+1/12r n20=1/4 n30=1/12+1/12r n21=1/4 n10=1/12+1/12r n11=1/6-1/12r	(2*(n10+n31)- (n11+n30))/ (n11+n30+n10+n31)	log((1/4*(n21+n20)*(1/12+1/12*r)*(n10+n31)*(1/6-1/12*r)*(n11+n30))/(1/4*(n21+n20)*(1/12+1/12*1/2)*(n10+n31)*(1/6-1/12*1/2)*(n11+n30))
Triplex x simplex Simplex x nulliplex	Coupling	AAAa x Aaaa Bbbb x bbbb	n21=1/4 n10=1/6-1/12r n20=1/4 n11=1/12r+1/12 n31=1/6-1/12r n30=1/12r+1/12	(2*(n10-n31)- (n30+n11))/ (n10+n11+n31+n30)	log((1/12*(n21+n10+n20+n11+n31+n30)*(2-r)*(n31+n10)*(1+r)*(n11+n30))/(1/12*(n21+n10+n20+n11+n31+n30)*(2-1/2)*(n31+n10)*(1+1/2)*(n11+n30)))
	Repulsion	AAAa x Aaaa bbbB x bbbb	n20=1/4 n11=1/4-1/4r n21=1/4 n10=1/4r n31=1/4r n30=1/4-1/4r	(n11+n30)/(n11+n30+n10+n31)	$Log((1/4^{(n20+n11+n21+n10+n31+n30)}*(1-r)^{(n11+n30)}*r^{(n10+n31)})/(1/4^{(n20+n11+n21+n10+n31+n30)}*(1-r)^{(n11+n30)}*r^{(n10+n31)})$

Iterative approach				
Marker segregation type	*Phase*	*Dosages*	*nxy*	*Likelihood L(r)*
Simplex x Simplex Simplex Simplex	Coupling	Aaaa x Aaaa Bbbb x Bbbb	n11=1/2r2+1/2(1-r)^2 n00=1/4(1-r)^2 n01=1/2r(1-r) n10=1/2r(1-r) n21=1/2r(1-r) n20=1/4r^2 n22=1/4(1-r)^2 n12=1/2r(1-r) n02=1/4r^2	$1/2^{(n11+n01+n10+n21+n12)}*1/4^{n00+n20+n22+n02}*(r^2)^{n02+n20}*((1-r)^2)^{n00+n22}*(r*(1-r))^{n01+n10+n21+n12}*(r^2+(1-r)^2)^{n11}$
	Mixed	Aaaa x Aaaa bBbb x Bbbb	n11=1/6+1/3r-1/3r^2 n00=1/12(1-r^2) n01=1/6-1/6r+1/6r^2 n10=1/6-1/6r+1/6r^2 n21=1/6-1/6r+1/6r^2 n20=1/12(1-r^2) n12=1/6-1/6r+1/6r^2 n02=1/12r(2-r)	$1/12^{n00+n01+n02+n10+n12+n10+n22}*(1-r^2)^{n00+n22}*(2r^2-2*r+2)^{n01+n10+n21+n12}*(r*(2-r))^{(n01+n20)}*(4*r-4*r^2+2)^{n11}$
	Repulsion	Aaaa x Aaaa bBbb x bBbb	n11=5/18-1/6r+1/9r^2 n00=1/36+1/18r+1/36r^2 n01=1/9+1/18r-1/18r^2 n10=1/9+1/18r-1/18r^2 n211/9+1/18r-1/18r^2 n20=1/9-1/9r+1/36r^2 n22)=1/36+1/18r+1/36r^2 n12)=1/9+1/18r-1/18r^2 n02=1/9-1/9r+1/36r^2	$(5/18-1/6r+1/9r^2)^{n11}*(1/36+1/18r+1/36r^2)^{(n00+n22)}*(1/9+1/18r-1/18r^2)^{(n01+n10+n21+n12)}*(1/9-1/9r+1/36r^2)^{(n20+n02)}$
Duplex x Nulliplex Duplex Nulliplex	Coupling	AAaa x aaaa BBbb x bbbb	n11=1/3+1/3(1-r)^2+1/3r^2 n00=1/6(1-r)^2 n01 =1/3r(1-r) n10 =1/3r(1-r) n21 =1/3r(1-r) n20=1/6r^2 n22=1/6(1-r)^2 n12 =1/3r(1-r) n02=1/6r^2	$(1/3+1/3*(1-r)^2*1/3r^2)^{n11}*(1/6(1-r)^2)^{n22+n00}*(1/6r^2)^{n20+n02}*(1/3r(1-r))^{n01+n10+n21+n12}$
	Repulsion	AAaa x aaaa bbBB x bbbb	n11=1/3+1/3r2+1/3(1-r)^2 n00=1/6r^2 n01=1/3r(1-r) n10=1/3r(1-r) n21=1/3r(1-r) n20=1/6(1-r)^2 n22=1/6r^2 n12=1/3r(1-r) n02=1/6(1-r)^2	$(1/3+1/3*(1-r)^2*1/3r^2)^{n11}*(1/6(1-r)^2)^{n20+n20}*(1/6r^2)^{n00+n22}*1/3r(1-r))^{n01+n10+n21+n12}$
	Mixed	AAaa x aaaa BbBb x bbbb	n11=1/3+1/3(1-r)r n00=1/12r(1-r)	$(1/3+1/3(1-r)r)^{n11}*(1/12r(1-r))^{n20+n20+n00+n22}*(1/12+1/12(1-r)^2+1/12r^2)^{n01+n10+n21+n12}$

			$n01=1/12+1/12(1-r)^2+1/12r^2$ $n10=1/12+1/12(1-r)^2+1/12r^2$ $n21=1/12+1/12(1-r)^2+1/12r^2$ $n20=1/12r(1-r)$ $n22=1/12r(1-r)$ $n12=1/12+1/12(1-r)^2+1/12r^2$ $n02=1/12r(1-r)$	
Duplex x Nulliplex Simplex x Simplex	Coupling	AAaa x aaaa Bbbb x Bbbb	$n11=1/3$ $n00=1/12-1/12r$ $n01=1/12$ $n10=1/6$ $n21=1/12$ $n20=1/12r$ $n12=1/6$ $n02=1/12r$ $n22=1/12-1/12r$	$1/3^{n11}*1/12^{n00+n01+n10+n21+n20+n12+n02+n22}*2^{n10+n12}*(1-r)^{n00+n22}*r^{n20+n02}$
	Repulsion	AAaa x aaaa bbBb x Bbbb	$n11=1/3$ $n00=1/12r$ $n01=1/12$ $n10=1/6$ $n21=1/12$ $n20=1/12-1/12r$ $n12=1/6$ $n02=1/12-1/12r$ $n22=1/12r$	$MC*1/12^{(n00+n01+n10+n21+n20+n12+n02+n22}*1/3^{n11}*r^{(n00+n22)}*2^{(n10+n12)}*(1-r)^{(n20+n02)}$
Simplex x Triplex Duplex x Nulliplex	Coupling	Aaaa x AAAa BBbb x bbbb	$n31=1/6$ $n21=1/3$ $n11=1/6$ $n32=1/12-1/12r$ $n22=1/12$ $n12=1/12r$ $n20=1/12$ $n10=1/12-1/12r$ $n30=1/12r$	$(1/12*r)^{(n30+n12)}*(1/6)^{(n31+n22+n20+n11)}*(1/12-1/12*r)^{(n32+n10)}*(1/3)^{n21}$
	Repulsion	Aaaa x AAAa bBBb x bbbb	$n31=1/6$ $n21=1/3$ $n11=1/6$ $n32 =1/12r$ $n22=1/12$ $n12=1/12-1/12*r$ $n20=1/12$ $n10 =1/12*r$ $n30=1/12-1/12*r$	$(1/12-1/12*r)^{(n30+n12)}*1/6^{(n31+n22+n20+n11)}*(1/12*r)^{(n32+n10)}*1/3^{n21}$
Simplex x Triplex Simplex x Simplex	Coupling	Aaaa x AAAa Bbbb Bbbb	$n32=1/6-1/4r+1/12r^2$ $n22=1/12+1/6r-1/6r^2$	$(1/12*r+1/12*r^2)^{(n30+n12)}*(1/12+1/6*r-1/6*r^2)^{(n31+n22+n20+n11)}*(1/6-1/4*r+1/12*r^2)^{(n32+n10)}*(1/3-$

			n21=1/3-1/3r+1/3r^2 n20=1/12+1/6r-1/6r^2 n11=1/12+1/6r-1/6r^2 n10=1/6-1/4r+1/12r^2 n31=1/12+1/6r-1/6r^2 n30=1/12r+1/12r^2 n12=1/12r+1/12 r^2	1/3*r+1/3*r^2)^{n21}
	Repulsion	Aaaa x AAAa bBbb bbbB	n32=1/12r+1/12 r^2 n21=1/3-1/3r+1/3 r^2 n22=1/12+1/6r-1/6 r^2 n20=1/12+1/6r-1/6 r^2 n11=1/12+1/6r-1/6 r^2 n10=1/12r+1/12 r^2 n31=1/12+1/6r-1/6 r^2 n30=1/6-1/4r+1/12 r^2 n12=1/6-1/4r+1/12 r^2	(1/6-1/4*r+1/12*r^2)$^{(n30+n12)}$*(1/12+1/6*r-1/6*r^2)$^{(n31+n22+n20+n11)}$*(1/12*r+1/12*r^2)$^{(n32+n10)}$*(1/3-1/3*r+1/3*r^2)^{n21}
	Mixed 1	Aaaa x AAAa bBbb x Bbbb	n32=1/18+1/36r-1/36 r^2 n21=2/9+1/9r-1/9 r^2 n22=5/36-1/18r+1/18 r^2 n20=5/36-1/18r+1/18 r^2 n11=5/36-1/18r+1/18 r^2 n10=1/18+1/36r-1/36 r^2 n31=5/36-1/18r+1/18 r^2 n30=1/18+1/36r-1/36 r^2 n12=1/18+1/36r-1/36 r^2	(1/18+1/36*r-1/36* r^2)$^{(n30+n12)}$*(5/36-1/18*r+1/18*r^2)$^{(n31+n22+n20+n11)}$*(1/18+1/36*r-1/36*r^2)$^{(n32+n10)}$*(2/9+1/9*r-1/9* r^2)^{n21}
	Mixed 2	Aaaa x AAAa Bbbb x bbbB	n31=1/4-1/2r+1/2 r^2 n22=1/4-1/2r+1/2 r^2 n32=r- r^2 n20=1/4-1/2r+1/4 r^2 n11=1/4-1/2r+1/2 r^2 n10=1/4r-1/4 r^2 n30=1/4r-1/4 r^2 n02=1/4 r^2 n12=1/4r-1/4 r^2	(1/4*r-1/4* r^2)$^{(n30+n12)*}$(1/4-1/2*r+1/2*r^2)$^{(n31+n22+n20+n11)}$*(1/4*r-1/4*r^2)$^{(n32en10)*}$(r- r^2)^{n21}
Simplex x Triplex Simplex x Triplex	Coupling	Aaaa x AAAa Bbbb BBBb	n33=1/4-1/2r+1/4r^2 n22=1/2-r+r^2 n11=1/4-1/2r+1/4r^2 n32=1/2r-1/2r^2 n23=1/2r-1/2r^2 n21=1/2r-1/2r^2 n12=1/2r-1/2r^2 n13=1/4r^2 n31=1/4r^2	(1/4*r^2)$^{(n13+n31)}$*(1/2*r-1/2*r^2)$^{(n23+n32+n12+n21)}$*(1/4-1/2*r+1/4*r^2)$^{(n33+n11)}$*(1/2-r+r^2)^{n22}
	Repulsion	Aaaa x AAAa	n33=1/36+1/18r+1/36r^2	(1/9-1/9*r+1/36*r^2)$^{(n13+n31)}$*(1/9+1/18*r-

		bBbb x BBbB	$n22=5/18-1/9r+1/9r^2$ $n11=1/36+1/18r+1/36r^2$ $n31=1/9-1/9r+1/36r^2$ $n13=1/9-1/9r+1/36r^2$ $n32=1/9+1/18r-1/18r^2$ $n21=1/9+1/18r-1/18r^2$ $n23=1/9+1/18r-1/18r^2$ $n12=1/9+1/18r-1/18r^2$	$1/18*r^2)^{(n23+n32+n12+n21)}*(1/36+1/18*r+1/36*r^2)^{(n33+n11)}*(5/18-1/9*r+1/9*r^2)^{n22}$
	Mixed 1	Aaaa x AAAa bBbb x BBBb	$n33=1/12-1/12r^2$ $n22=1/6+1/3r-1/3r^2$ $n11=1/12-1/12r^2$ $n31=1/6r-1/12r^2$ $n13=1/6r-1/12r^2$ $n32=1/6-1/6r+1/6r^2$ $n21=1/6-1/6r+1/6r^2$ $n23=1/6-1/6r+1/6r^2$ $n12=1/6-1/6r+1/6r^2$	$(1/6*r-1/12*r^2)^{(n13+n31)}*(1/6-1/6*r+1/6*r^2)^{(n23+n32+n12+n21)}*(1/12-1/12*r^2)^{(n33+n11)}*(1/6+1/3*r-1/3*r^2)^{n22}$
	Mixed 2	Aaaa x AAAa Bbbb x BBbB	$n33=1/12-1/12r^2$ $n22=1/6+1/3r-1/3r^2$ $n11=1/12-1/12r^2$ $n31=1/6r-1/12r^2$ $n13=1/6r-1/12r^2$ $n32=1/6-1/6r+1/6r^2$ $n21=1/6-1/6r+1/6r^2$ $n23=1/6-1/6r+1/6r^2$ $n12=1/6-1/6r+1/6r^2$	$(1/6*r-1/12*r^2)^{(n13+n31)}*(1/6-1/6*r+1/6*r^2)^{(n23+n32+n12+n21)}*(1/12-1/12*r^2)^{(n33+n11)}*(1/6+1/3*r-1/3*r^2)^{n22}$

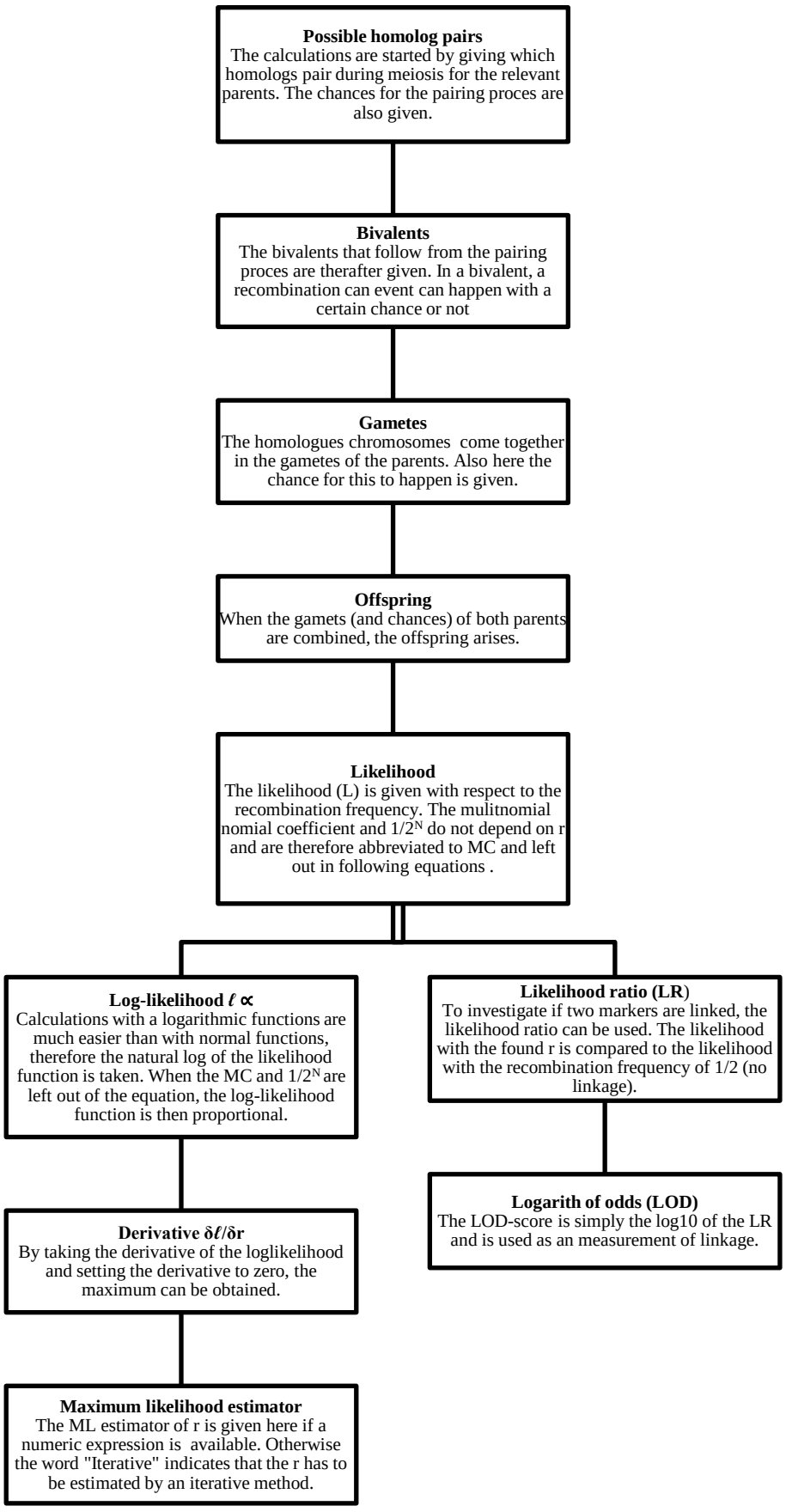


Figure 34. Procedure of calculating the recombination frequencies of the different marker type and phase combinations. This procedure is described in more detail in (Van Ooijen & Jansen, 2013).

Appendix 13: Map comparison with other populations and *Solanum* species

In Chapter 7 and the Discussion, the integrated map was compared with maps of other potato populations and *Solanum* species. The statistics of some of those maps and mapping population are shown here (Table 21).

Table 21. Map statistics of different potato and *Solanum* maps. The maps vary in the population size used. The map statistics include the number of markers, map length per chromosome, coverage, and number of markers with a specific marker type.

Potatoes								
Thesis								
Chromosome	**N markers**	**cM**	**Coverage N/cM**	**Coverage N/MB**	**SN**	**DN**	**SS**	**TS**
1	624	141.7	4.403669725	9.984	338	95	129	62
2	544	118.9	4.575273339	12.65116279	359	46	118	21
3	459	125.57	3.655331688	18	262	95	65	37
4	478	151.26	3.160121645	9.192307692	267	74	103	34
5	545	101.75	5.356265356	15.13888889	353	93	55	44
6	352	121.2	2.904290429	8.8	219	45	78	10
7	447	94.78	4.716184849	14.19047619	227	93	91	36
8	450	102.85	4.375303841	16.36363636	228	46	78	38
9	369	119.06	3.099277675	12.09836066	197	72	72	28
10	213	109.83	1.93936083	5.195121951	110	48	38	17
11	396	136.1	2.909625276	12.375	229	57	66	44
12	288	83.13	3.464453266	7.384615385	165	64	39	20
Total (sum or average)	*5165*	*1406.13*	*3.71326316*	*11.78113083*	*2954*	*828*	*932*	*391*
Tetraploid potato (Hackett *et al.*, 2013)								
Chromosome	**N markers**	**cM**	**Coverage N/cM**	**Coverage N/MB**	**SN**	**DN**	**SS**	**TS**
1	142	115.3	1.231569818	2.272	43			
2	120	91.9	1.305767138	2.790697674	27			
3	74	91.5	0.808743169	2.901960784	29			
4	152	95.8	1.586638831	2.923076923	46			
5	119	73.1	1.627906977	3.305555556	34			
6	122	90.8	1.343612335	3.05	32			
7	89	90	0.988888889	2.825396825	47			
8	85	62.3	1.364365971	3.090909091	22			
9	91	121.6	0.748355263	2.983606557	37			

10	104	71.9	1.446453408	2.536585366	26			
11	85	96.2	0.883575884	2.65625	35			
12	118	87.1	1.354764638	3.025641026	32			
Total	*1301*	*1087.5*	*1.224220193*	*2.863473317*	*410*			
Diploid potato (Prashar *et al.*, 2014)								
Chromosome	**N markers**	**cM**	**Coverage N/cM**	**Coverage N/MB**	**SN**	**DN**	**SS**	**TS**
1	170	85.4	1.990632319	2.72				
2	119	52.9	2.24952741	2.76744186				
3	120	66.9	1.793721973	4.705882353				
4	151	69.2	2.182080925	2.903846154				
5	77	58.4	1.318493151	2.138888889				
6	91	55.6	1.636690647	2.275				
7	157	64.3	2.441679627	4.984126984				
8	111	53.4	2.078651685	4.036363636				
9	115	67.5	1.703703704	3.770491803				
10	78	57	1.368421053	1.902439024				
11	106	59.8	1.772575251	3.3125				
12	60	63.4	0.94637224	1.538461538				
Total	*1355*	*753.8*	*1.790212499*	*3.08795352*				
Other* Solanum *species								
Tomato (EXPEN2000 population of a *S. lycopersicum x S. pennellii* cross) (Sim *et al.*, 2012)								
Chromosome	**N markers**	**cM**	**Coverage N/cM**	**Coverage N/MB**	**SN**	**DN**	**SS**	**TS**
1	252	201.8	1.24876115	2.795961389				
2	416	165.5	2.513595166	8.407437348				
3	286	121.7	2.350041085	4.420401855				
4	385	159.5	2.413793103	6.014685205				
5	363	154.3	2.352559948	5.59235865				
6	374	111.3	3.360287511	8.151700087				
7	224	108.2	2.070240296	3.447214528				
8	289	124.4	2.323151125	4.589487057				
9	218	144.2	1.511789182	3.220088626				
10	167	122.8	1.359934853	2.579548965				
11	466	114.4	4.073426573	8.746246246				
12	163	141.9	1.148696265	2.476450927				
Total	*3603*	*1670*	*2.227189688*	*5.036798407*				
Eggplant (Gramazio *et al.*, 2014)								
Chromosome	**N**	**cM**	**Coverage**	**Coverage**	**SN**	**DN**	**SS**	**TS**

	markers		**N/cM**	**N/MB**				
1	23	132.9	0.173062453					
2	18	78.7	0.228716645					
3	21	94.3	0.222693531					
4	16	76	0.210526316					
5	18	58.6	0.307167235					
6	27	111.9	0.241286863					
7	21	101.7	0.206489676					
8	20	78.3	0.255427842					
9	22	96.1	0.2289282					
10	19	96.7	0.196483971					
11	19	79.7	0.238393977					
12	19	80.1	0.237203496					
Total	*243*	*1085*	*0.228865017*					
***Solanum bulbocastanum* (Iorizzo *et al.*, 2014)**								
Chromosome	**N markers**	**cM**	**Coverage N/cM**	**Coverage N/MB**	**SN**	**DN**	**SS**	**TS**
1	49	49.1	0.99796334					
2	53	48.3	1.097308489					
3	49	36.5	1.342465753					
4	67	83.7	0.800477897					
5	20	40.7	0.491400491					
6	40	45.6	0.877192982					
7	30	58.4	0.51369863					
8	19	51.4	0.369649805					
9	25	60.4	0.413907285					
10	9	61.5	0.146341463					
11	22	40.2	0.547263682					
12	26	69.1	0.376266281					
Total	*409*	*644.9*	*0.664494675*					

Appendix 14: Map integration of two rose populations

A mapping population of rose was used to validate the integration procedure described in Chapter 7. Two maps (maternal and paternal) of one chromosome were used for integration. The maps were first put in right orientation based on the Pearson correlation of the common markers. Thereafter, the maps were integrated twice. The first time, the maternal map had a mapping error since one of the chromosome arms was inverted (Figure 35), while the second time, the maps had no structural errors (Figure 36). In the latter, the integration went well, while the integration with an inverted arm went not well.

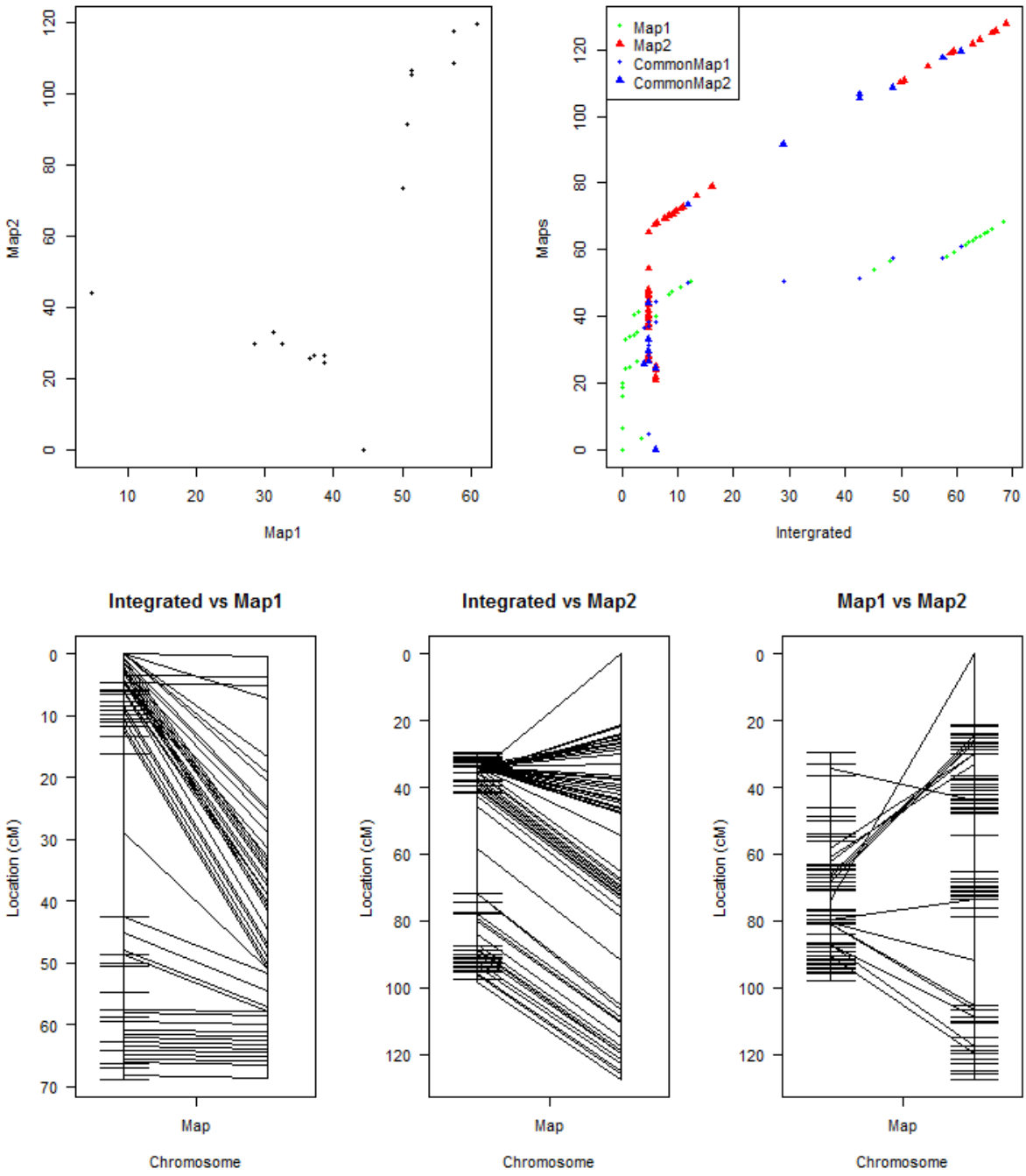


Figure 35. Integration of the maternal map (Map 2) with an inverted arm and the paternal map (Map 1). The top left plot shows the map positions of the common markers. The top left plot shows the integrated map distances based on the two underlying maps. The bottom right plot shows the comparison of map positions between the paternal map and the integrated map. The bottom middle plot shows the comparison of map positions between the maternal map and the integrated map. The bottom right plot shows the comparison of the map position of the common markers.

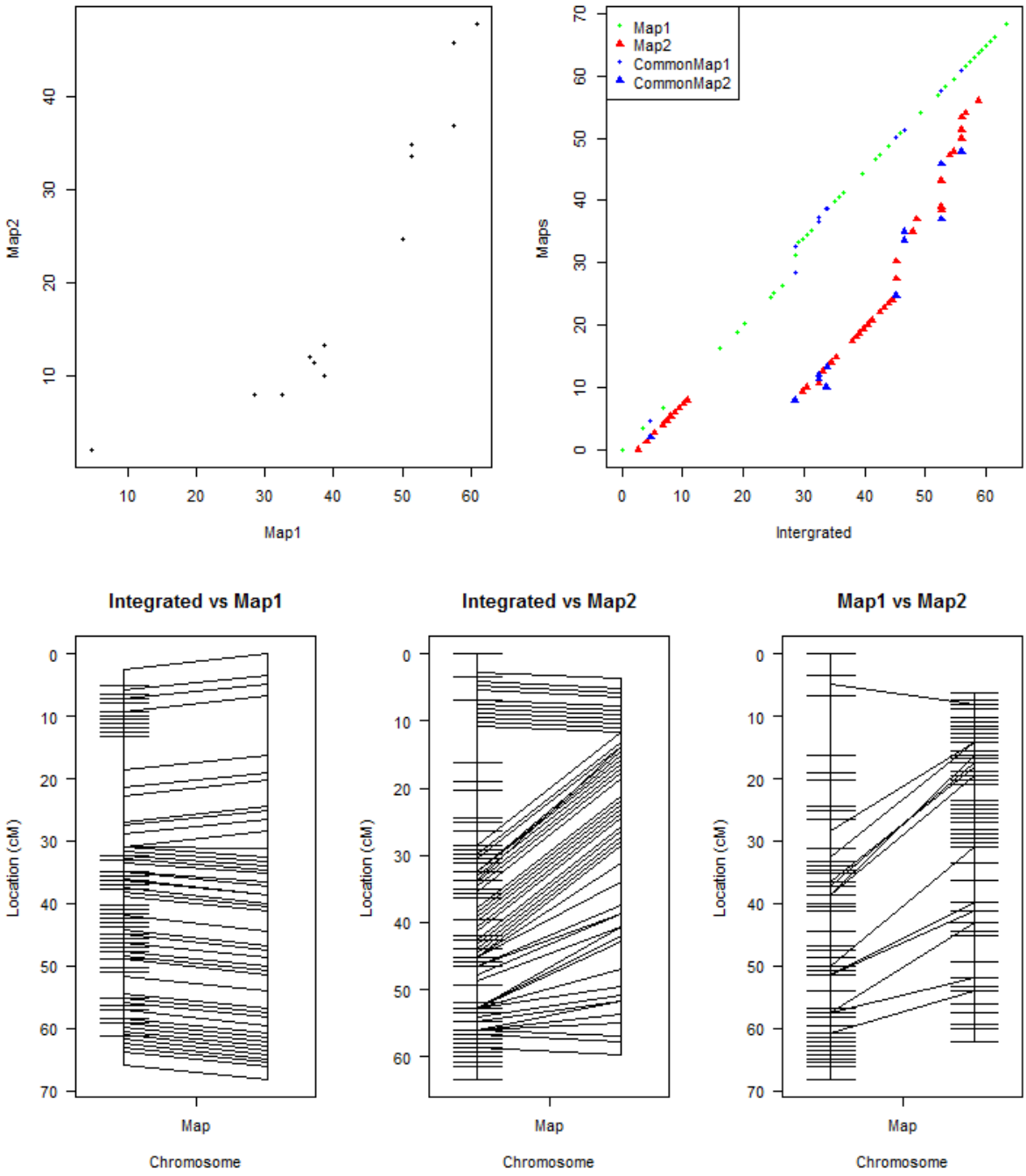


Figure 36. Integration of the maternal map (Map 2) with the correct ordering and the paternal map (Map 1). The top left plot shows the map positions of the common markers. The top left plot shows the integrated map distances based on the two underlying maps. The bottom right plot shows the comparison of map positions between the paternal map and the integrated map. The bottom middle plot shows the comparison of map positions between the maternal map and the integrated map. The bottom right plot shows the comparison of the map position of the common markers.

Appendix 15: *Alstroemeria*

During this thesis, the method for the determination of the mode of inheritance and calculation of recombination frequencies of SxN markers was used for an *Alstroemeria* population. First, the recombination frequencies were calculated under the assumption of tetrasomic inheritance (Figure 37). However, the coupling and repulsion phase were too much overlapping for linkage group assignment. Therefore, only SxN markers with less than 5% missing values were used (Figure 38). In addition, the recombination frequency calculation allowing for preferential pairing was also calculated (Figure 39). What the effect of preferential pairing is on the linkage group and homolog assignment is currently not known.

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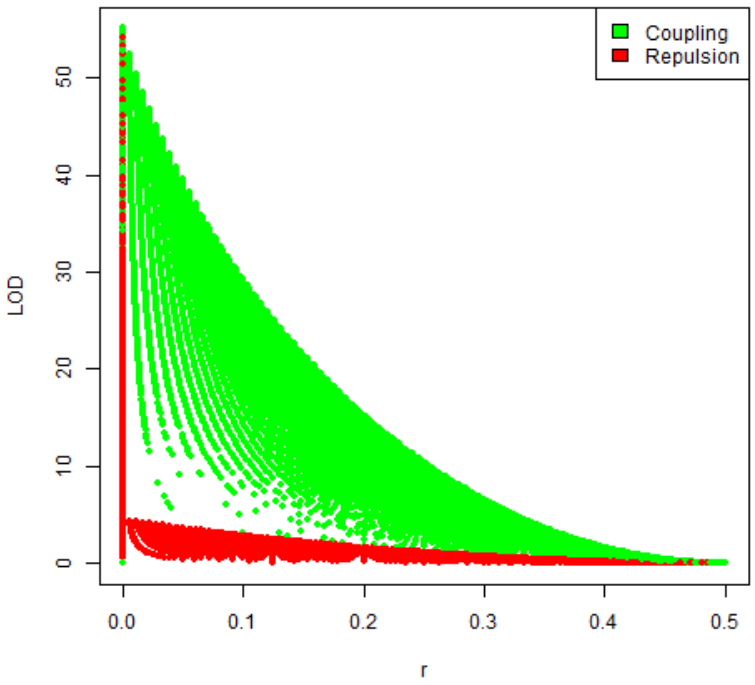


Figure 37. Recombination frequencies plotted against the LOD-score for SxN markers of *Alstroemeria*. All SxN markers were used**.**

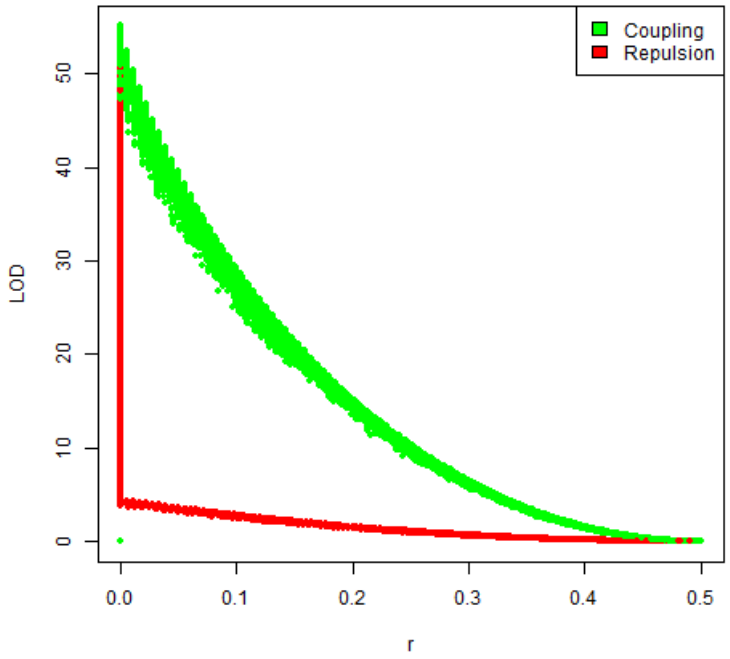


Figure 38. Recombination frequencies plotted against the LOD-score for SxN markers of *Alstroemeria*. Only SxN markers with less than 5% missing values were used. This already gave a clear distinction between Coupling and Repulsion phase.

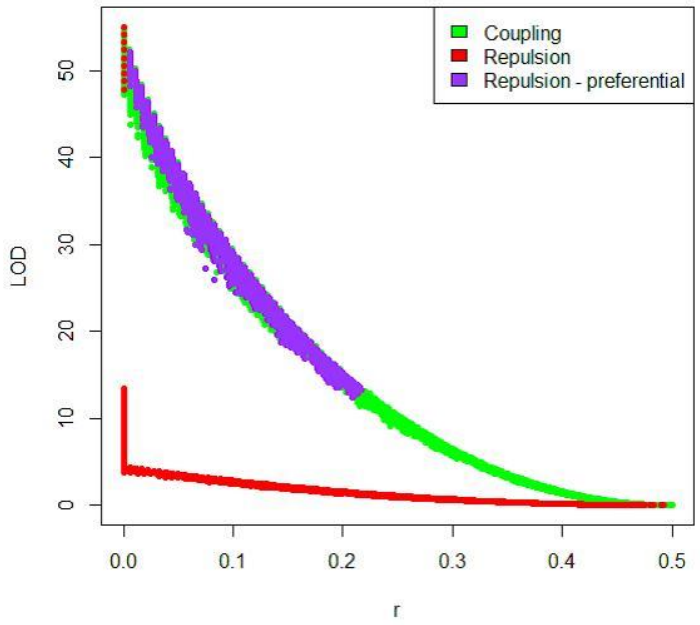


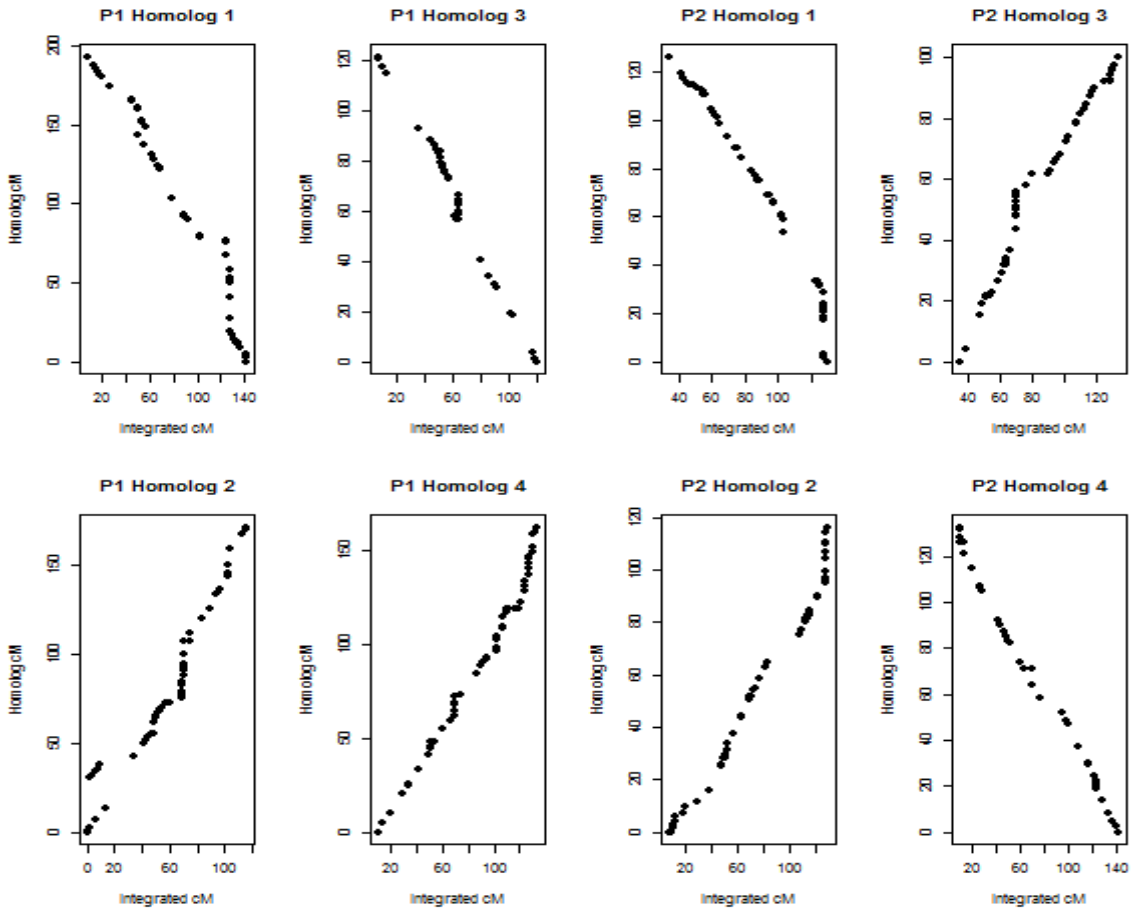
Figure 39. Recombination frequencies plotted against the LOD-score for SxN markers of *Alstroemeria*. Only SxN markers with less than 5% missing values were used. The recombination frequency calculation also allowed for repulsion phase under preferential pairing. There were SxN markers that tested positively for preferential pairing, which could indicate preferential pairing on one or more of the chromosomes.

Appendix 16: Integrated map against homolog maps

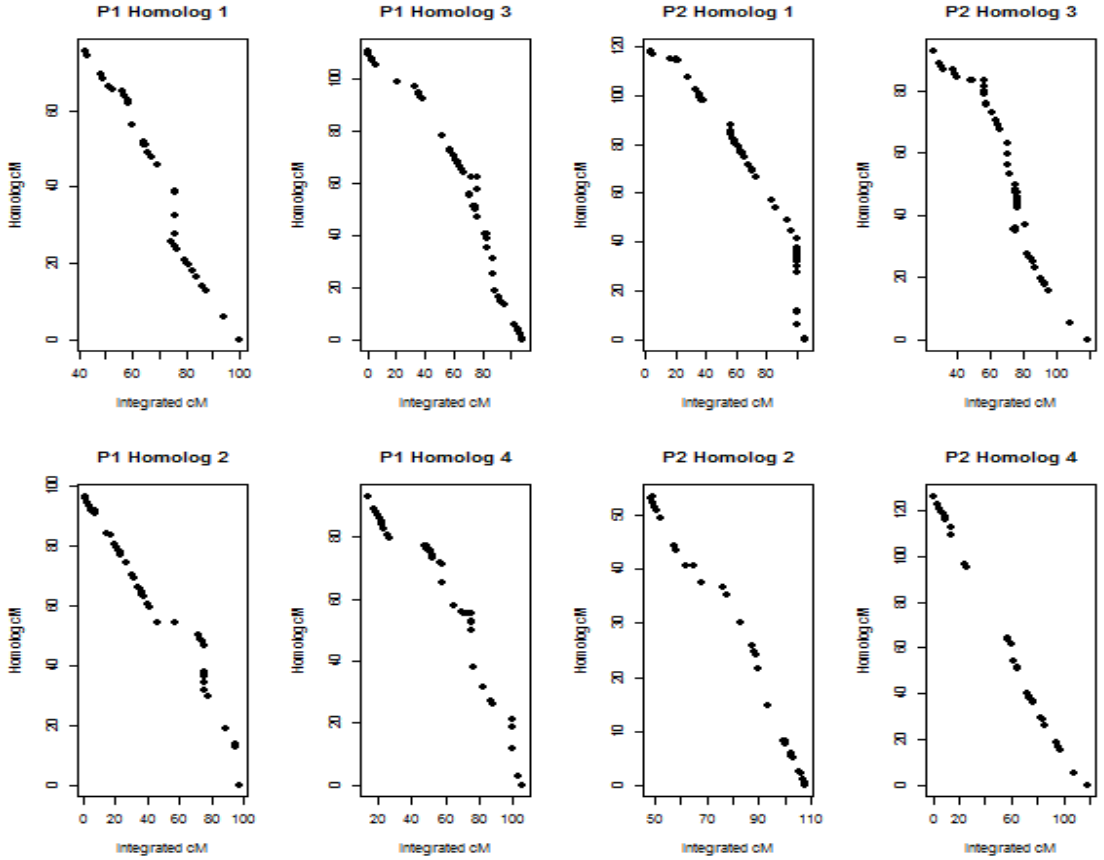
In Chapter 7, all the homologs were integrated into one consensus map per chromosome. In this chapter the map positions of the markers on the homolog maps of chromosome 11 were plotted against the map positions of markers on the integrated chromosome. In Figure 40 this was done for all chromosomes.

Figure 40. Comparison of the map positions of the markers on the homolog maps with the map positions on the integrated map for all the chromosomes. The homolog maps per parent are shown. The homolog maps are the maps used for the integration procedure.

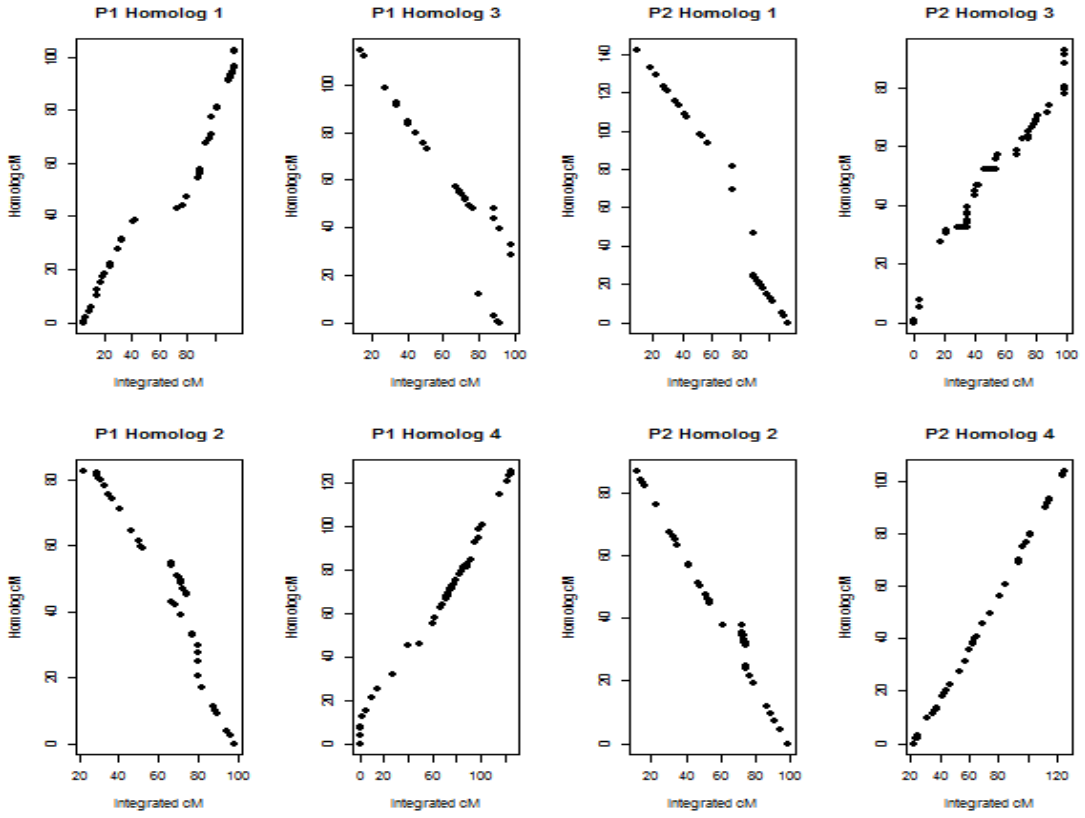
Chromosome 1



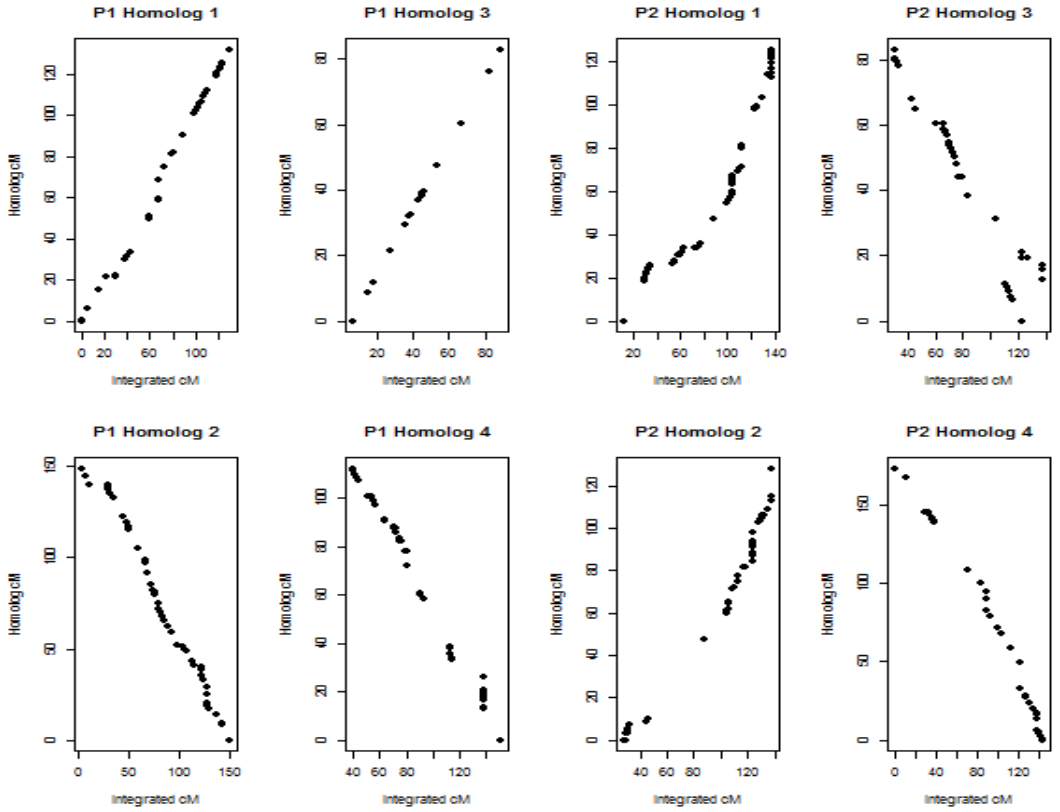
Chromosome 2



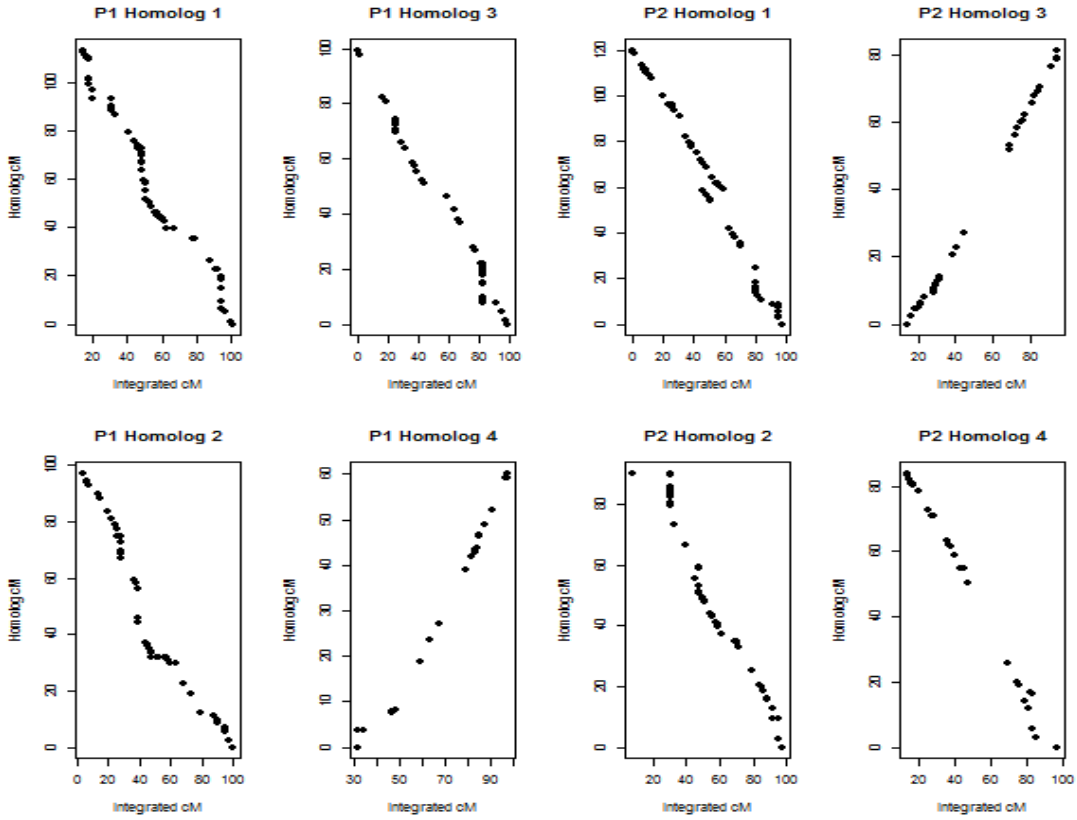
Chromosome 3



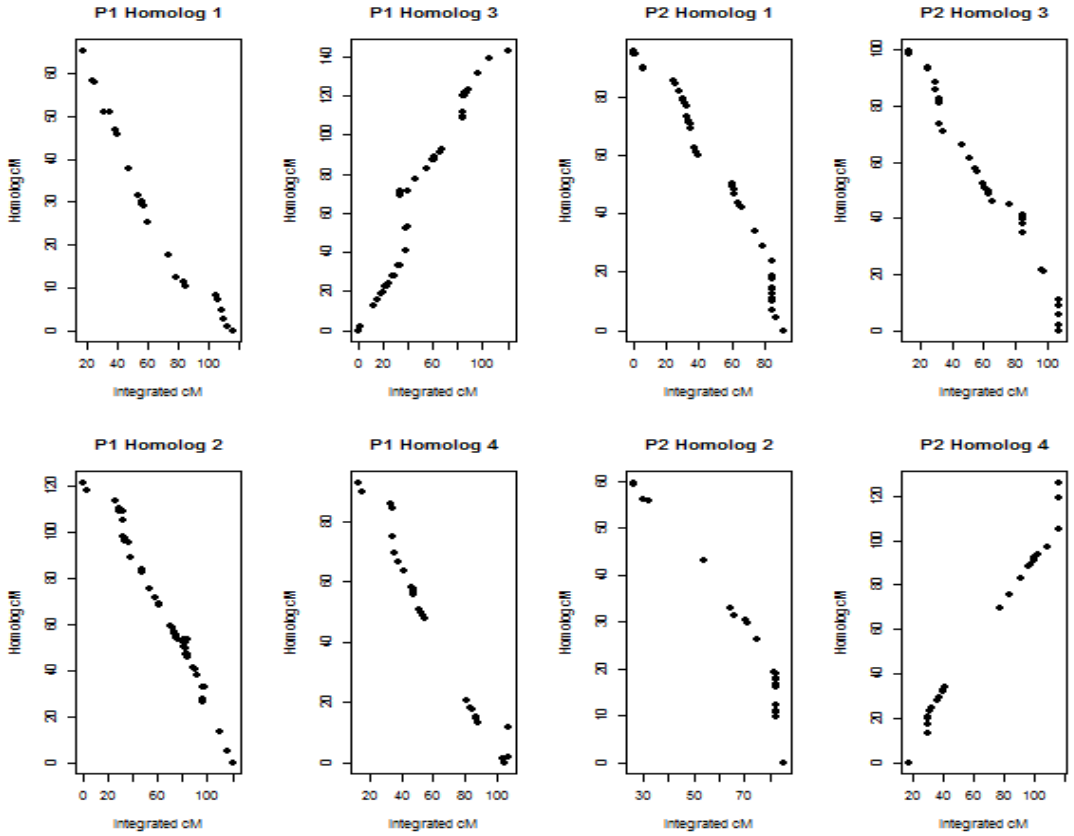
Chromosome 4



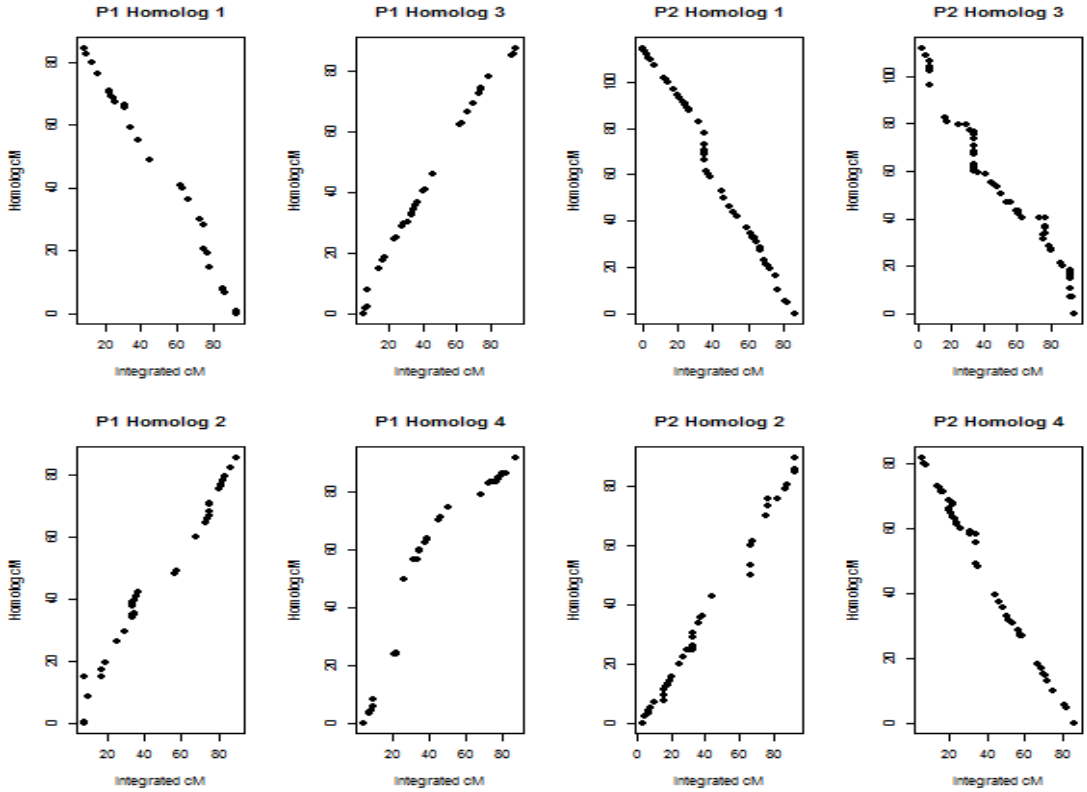
Chromosome 5



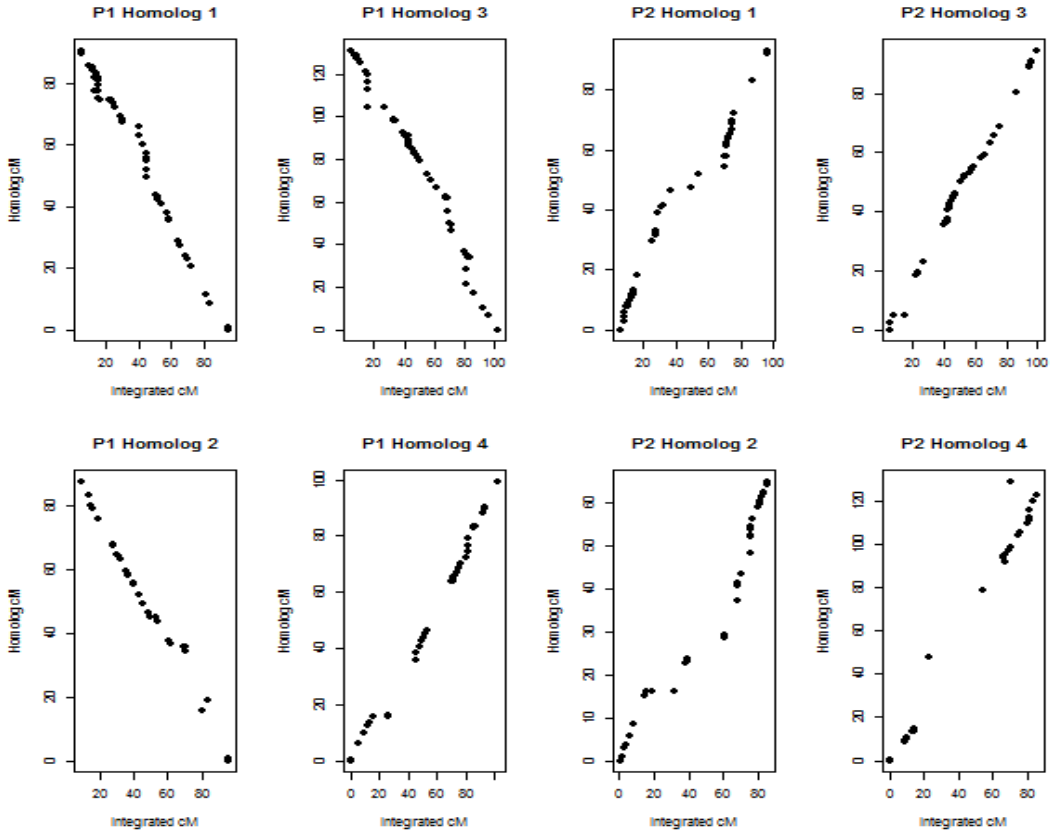
Chromosome 6



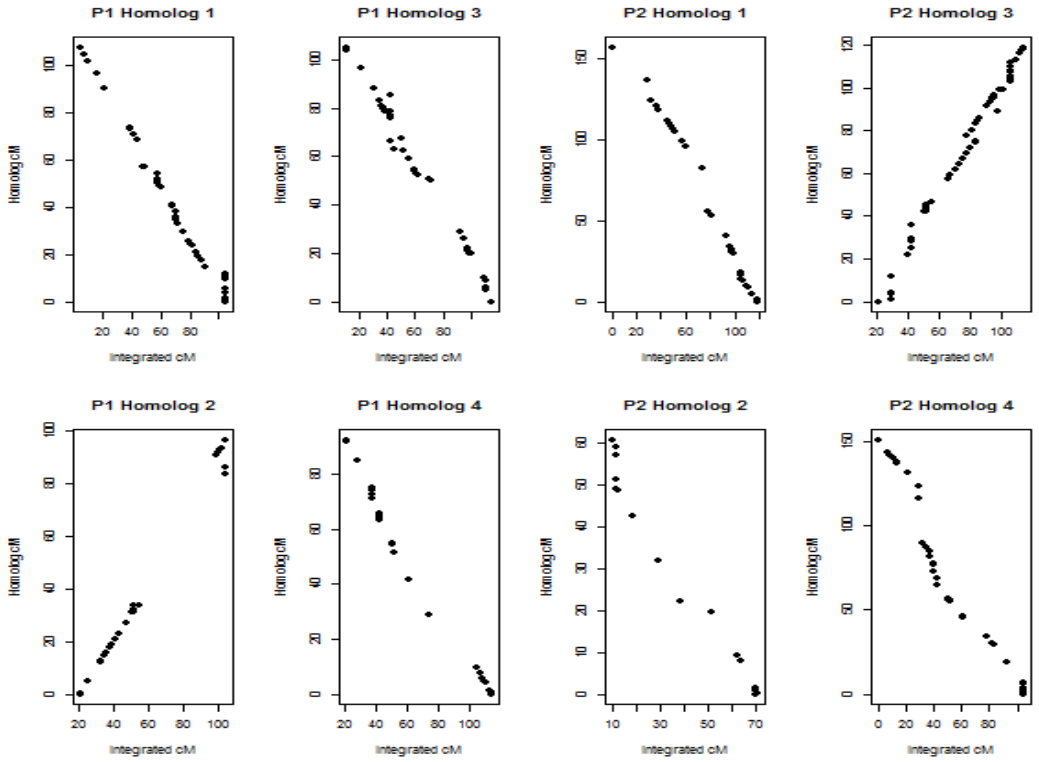
Chromosome 7



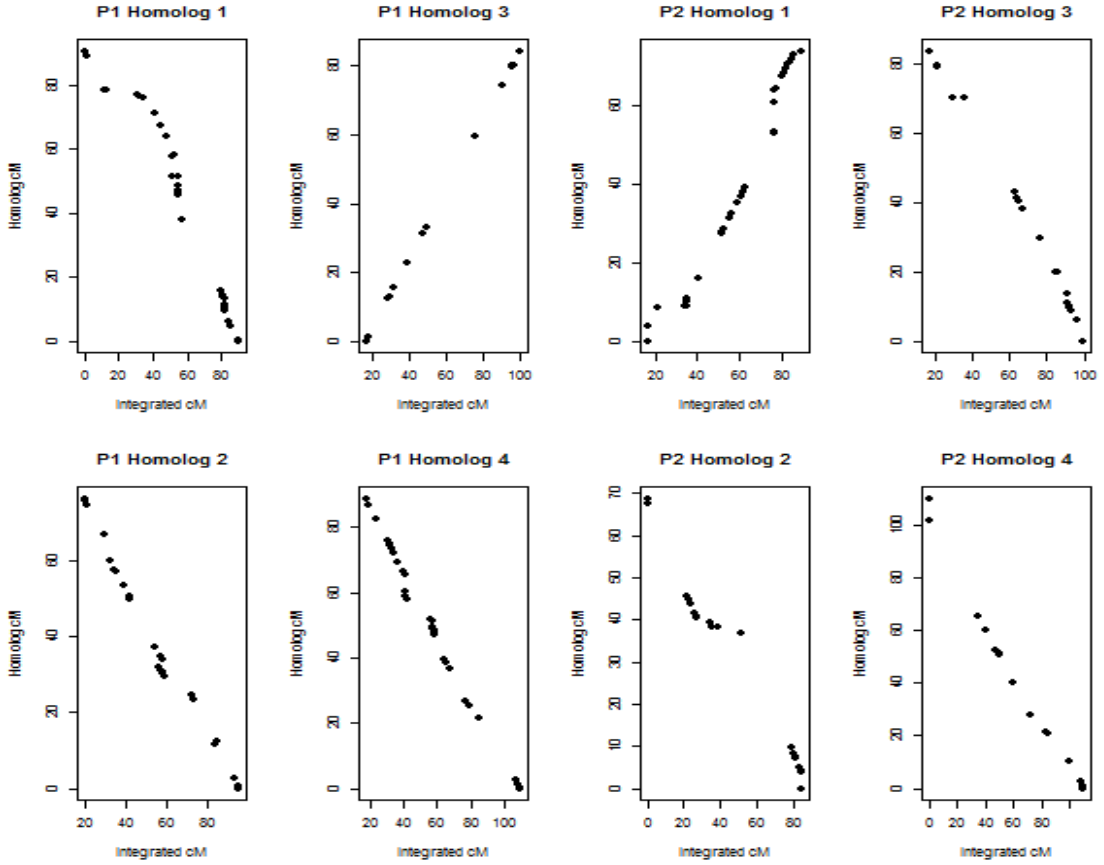
Chromosome 8



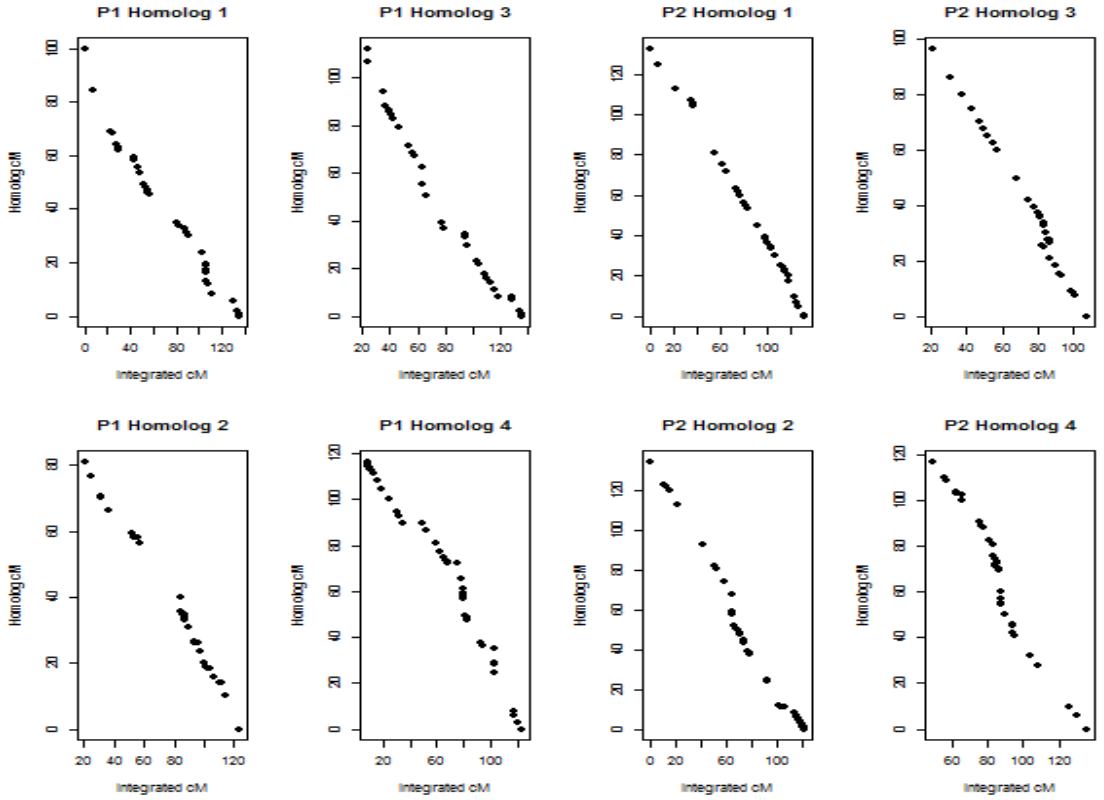
Chromosome 9



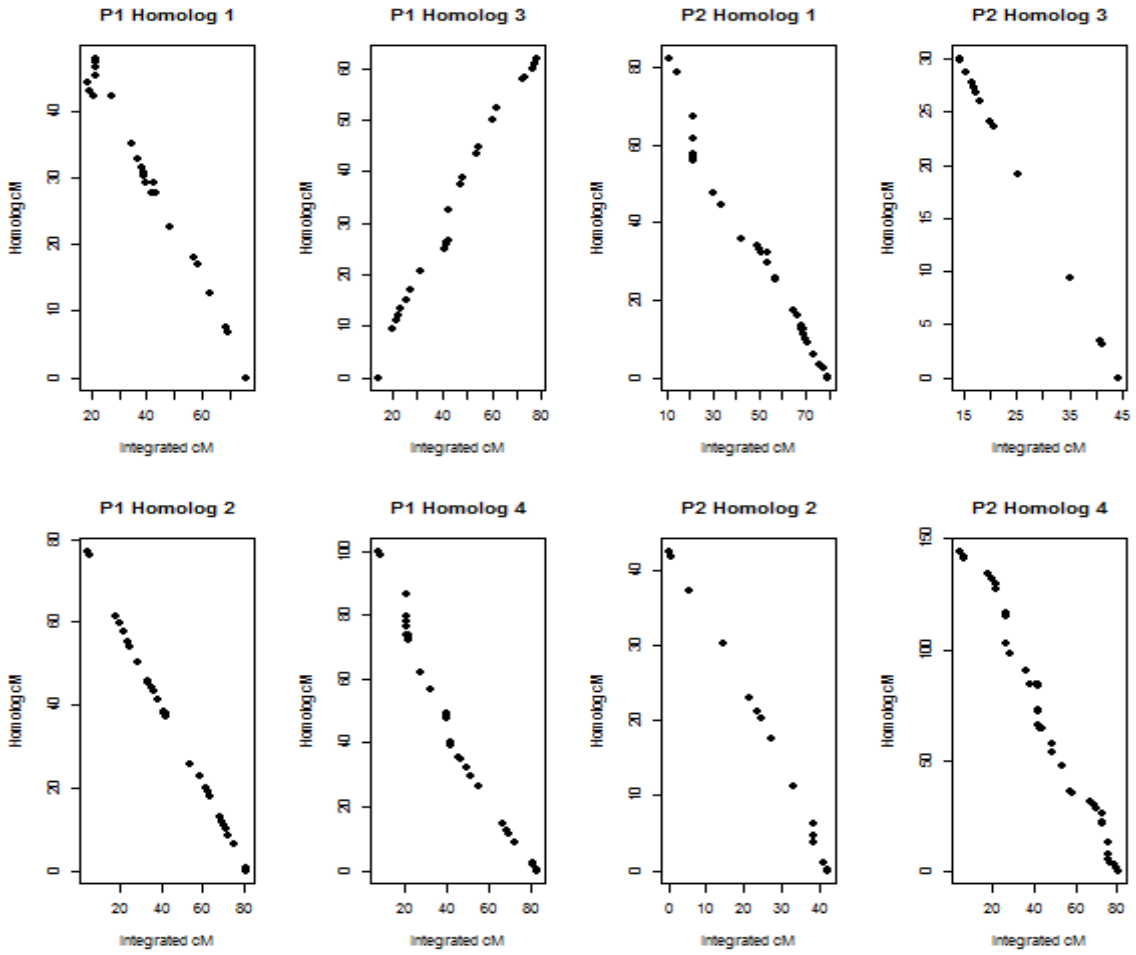
Chromosome 10



Chromosome 11



Chromosome 12



Appendix 17: Gaps

In Chapter 7, the homolog maps were integrated into one integrated map per chromosome. Table 11 showed the number of gaps on the integrated linkage maps. Here, some plots are presented to further investigate the distribution and the size of the gaps. Figure 41 shows that every chromosome contains gaps of different sizes. Gap sizes of a length of 1 cM are most abundant as is expected, while larger gaps are less often present. Figure 42 shows that the gaps are randomly distributed over the integrated linkage maps. This shows that all chromosomal regions are equally well represented by markers.

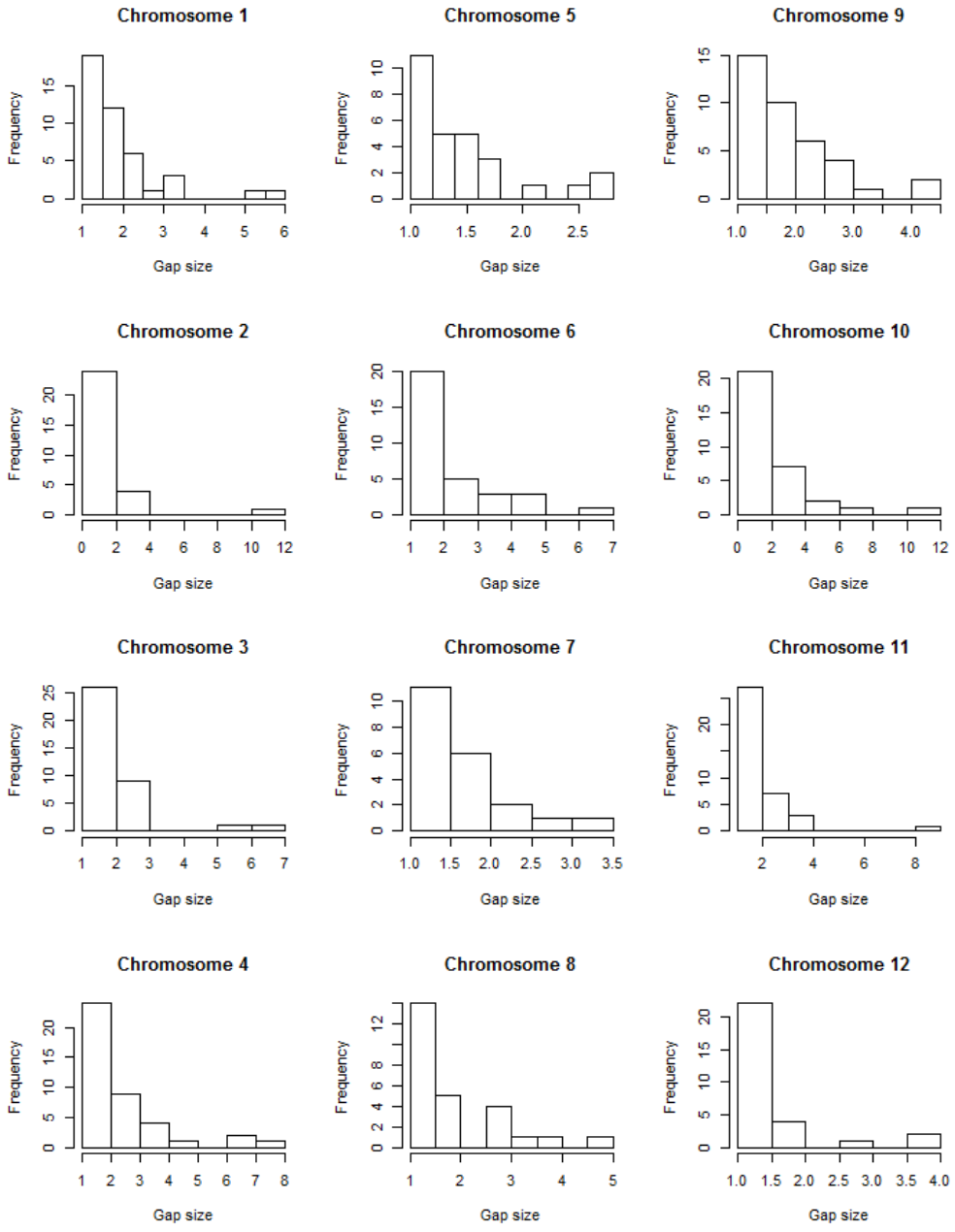


Figure 41. The frequency of gap size per integrated map. The 12 integrated maps all contain gaps of different sizes.

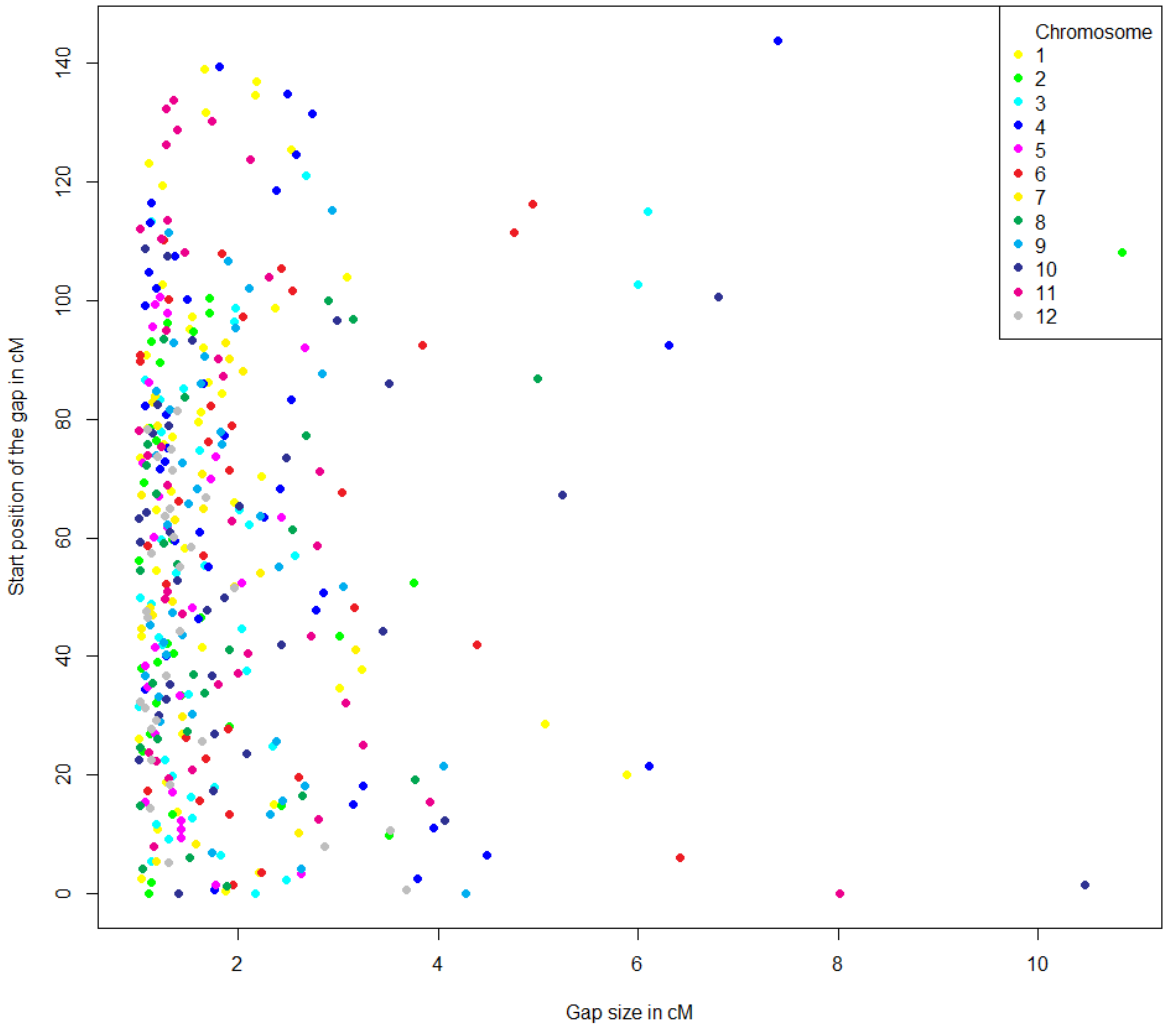


Figure 42. The distribution of gaps on the integrated linkage maps. The gap size in cM is plotted against the starting position of the gap in cM for all the 12 integrated chromosomes.